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The Influence of Bacteria

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I. BACTERIA IN PLANTS

A. Introduction

Bacteria exist on plants as part of complex microbial ecosystems (Upper et al., 1989). Established members of these ecosystems are called *residents*, whereas microbes that are introduced into these ecosystems and survive for various lengths of time but fail to become established are *casuals* (Leben, 1961). Microbes living on plant surfaces are also called *epiphytes* (Hirano and Upper, 1983; Leben, 1965). Certain bacteria have been found inside healthy vegetables (Samish et al., 1963), but whether these bacteria qualify as endophytes has not been established (Upper et al., 1989).

B. Bacteria on the Phylloplane

The composition of the microbial ecosystem on vegetables in the field, at harvest, and during marketing and eventual consumption of the crop is unknown (Upper et al., 1989). Epiphytes on the above-ground parts of plants or phylloplane are adapted to survive through desiccation, extreme heat, and solar radiation during the daytime and fluctuating or low temperatures at night (Leben, 1974). Epiphytes are most common where structures shelter their environment from physical extremes. Thus, the base of trichomes or leaf hairs, broken or dead trichomes, depressions in the leaf surface between adjacent epidermal cells, and closed or open flower buds contain the largest numbers of bacteria (Hirano and Upper, 1983; Leben, 1965).

Free moisture from dew, fog, or rainfall profoundly influences the number of epiphytes on plants. Free water enables bacteria to move to sources of food, protects bacteria from desiccation, and provides bacteria with nutrients by enabling the diffusion of small compounds from plant cells (Crosse, 1968; Leben, 1965; Lund, 1992). Free water on plant surfaces also promotes microbial activity by delaying host resistance reactions, slowing wound healing, and slowing the desiccation of wounded tissues (Perombelon and Lowe, 1975). Persistent free water inside plant tissues has been associated with the multiplication of saprophytic bacteria that could not grow in the absence of the water (Young, 1974).

C. Bacteria in the Root System of Plants

The microbial ecosystem on root surfaces (rhizoplane) or in the soil mass influenced by root development (rhizosphere) is protected from physical stresses but is profoundly influenced by soil-inhabiting microorganisms (Crosse, 1968). Nutrition required for microbial growth in the soil is usually limited. Regular sloughing of surface cells in the developing root provides nutrition for bacteria that are equipped to survive in the soil or in intimate association with roots. However, the microbes in soils located outside the rhizosphere that do not contain degradable organic matter are relatively inactive (Leben, 1974). Bacteria in this ecosystem are hypobiotic, defined as being in a state of reduced metabolic activity.

The microbial ecosystem in the rhizosphere is usually not the same as that on the phylloplane (Crosse, 1968). Bacteria from the soil may be repeatedly rain-splashed to the plant canopy, but most perish quickly due to physical stress (Crosse, 1968; Leben, 1974). By contrast, phyllosphere epiphytes washed into the soil by rainfall usually cannot compete with soil-borne microorganisms for available nutrition.

D. Changes in Microbial Ecosystems

Plant-associated microbial ecosystems are dynamic over time (Upper et al., 1989) becoming larger and more diverse in wet weather and smaller in dry weather (Hirano and Upper, 1983). The plant is also dynamic, undergoing growth, maturation, senescence, and death. Phyllosphere ecosystems may be profoundly disturbed by severe storms featuring wind, hail, or heavy rainfall; insects that create wounds; or pathogens that infect the plant (Upper et al., 1989). Heavy rainfall or rainfall accompanied by winds greater than 49 km/h (18 mph) can force water through natural openings on plant surfaces into intercellular spaces in tissues (Gottwald et al., 1989). Bacteria from the plant surface or in the rainfall accompany the water as it infiltrates plant tissues. This infiltration also provides a continuous ''bridge'' of water from the leaf surface through stomata into intercellular spaces, which permits the movement of bacteria into the leaf. Water-congested tissues allow a variety of bacteria to grow (Young, 1974). An increase in the epiphytic population on leaves associated with a storm event persists for a period of time, even if the weather is dry and sunny (Hirano et al., 1995). Storms accompanied by hail or strong winds create wounds on plant surfaces (Gottwald et al., 1989), which are ideal infection courts for plant pathogenic bacteria as well as niches for many different types of microorganisms. Additionally, very strong winds, as in tornadoes or other violent storms, can disperse bacteria over large areas (Gottwald et al., 1997).

Crop development favors an increase in the size of plant-associated microbial ecosystems. As vegetables mature, the outer leaves form a canopy that protects inner leaves and stems from exposure to direct sunlight and temperature extremes. The canopy of one row may overlap with that of another, creating shade for everything the lies beneath the canopies. Free moisture tends to persist inside canopies, which favors the survival and growth of microorganisms. Simple plant cell metabolites often become more available for utilization by microbes as the crop matures.

During harvest and handling, vegetables receive various injuries that provide sites for colonization by certain saprophytes as well as various postharvest pathogens. The injured tissues release moisture and metabolites that provide shelter and nutrition for bacteria (King and Bolin, 1989). New bacteria may be introduced into the crop by machinery, containers, workers, or water used in harvest and handling (Goepfert, 1980). How these new bacteria fare on the crop depends on the postharvest environment and, apparently, on the preexisting ecosystem.

E. Plant Pathogenic Bacteria on Vegetables

Plant pathogens attack living plant tissues, deriving nutrients and a shelter in the process. Many plant pathogenic bacteria live on host plants as epiphytes for prolonged periods of time (Leben, 1961). These pathogen populations can initiate disease quickly if the underlying tissues become injured or water-soaked (Young, 1974). During an infection of a host, pathogenic bacteria multiply rapidly. Diseased tissues become congested with water, cells, and slime produced by the pathogen. Leaf spots on bean leaves contain 10^7 to 10^{11} colony-forming units (CFU) per gram fresh tissue weight (Ercolani and Crosse, 1966), whereas bacterial soft rot lesions in tomatoes contain 10^9 to 10^{10} CFU/g (Stall and Hall, 1969). (Note: A CFU equals one bacterial cell or up to several cells that adhere to each other when suspended in water.)

1. Necrotic Lesions

Lesions caused by plant pathogenic bacteria can be necrotic, chlorotic, soft-rotted, sour, corky, or a combination of these characteristics. Necrotic lesions, which range in size from specks to deep corky areas, usually do not expand rapidly or shed large numbers of bacteria. The spread of pathogens from necrotic lesions to new infection courts is unlikely. Most necrotic lesions, however, provide opportunities for invasion of the plant by bacteria and fungi that can spread rapidly in packaged or stored vegetables.

2. Internal Necroses

Necroses largely restricted to the interior of the plant can result from an initial attack of xylem tissues by vascular pathogens such as *Pseudomonas solanacearum*, the cause of bacterial wilt of several genera of the Solanaceae, or *Clavibacter sepedonicum*, the cause of ring rot in potatoes. Vascular lesions tend to expand slowly and do not shed large numbers of cells. Spread of disease from internal necroses among packaged or stored vegetables is unlikely. A second type of internal necrosis develops when weak pathogens infect vascular tissues in the pericarp of tomato (Stall and Hall, 1969) or watermelon fruit (Hopkins and Elmstrom, 1977). Symptoms in tomatoes have led to the name *graywall*, whereas in watermelon the disease was called *rind necrosis*. The appearance of necrosis coincides with a slowing of multiplication of the pathogen such that populations in the affected tissues are smaller than those normally associated with bacterial diseases. These diseases, which are favored by moist, cool weather, do not spread in the field or in storage like typical bacterial diseases. In tomatoes, chilling injury appears to be a major predisposition for the development of graywall (Stall and Hall, 1969).

3. Bacterial Soft Rots

The initial symptoms of bacterial soft rot (water soaking and maceration of plant tissues) can develop within 6 to 8 h after inoculation. The lesions enlarge rapidly, eventually shedding enormous numbers of bacteria suspended in a combination of cellular fluid and bacterial slime. This "ooze" spreads the pathogen from infected to adjacent and nearby vegetables in packages or bulk storage. In tomatoes, secondary spread from lesions to adjacent fruit may occur within 24 h (Bartz, unpublished).

Soft rots involve the production of large volumes of extracellular enzymes that break down pectins in the middle lamellae and cell walls of succulent plants (Lund, 1992). The cytoplasm does not appear to be directly attacked (Kelman, 1979). However, as the cell wall is weakened, turgor causes the cell membrane to tear, which releases cell contents. Bacteria grow rapidly in the released material and produce additional liquid in the form of slime.

The fluid released from soft rot lesions may predispose plant tissues to the disease by restricting the movement of oxygen. Tissue anoxia prevents the development of certain resistance reactions and increases the permeability of cell membranes (Perombelon and Lowe, 1975). Potato tubers, for example, are highly resistant to bacterial soft rot when growing or stored in an aerobic environment at moderate temperatures. If the tuber surfaces are covered with water for as little as 2.5 h at 21°C, however, internal tissues become anaerobic and highly susceptible to bacterial soft rot (Burton and Wigginton, 1970). The anaerobic environment in lenticels on the surface of wet, healthy tubers allows spores of the obligate anaerobe *Clostridium* spp. to germinate (Lund, 1979). Pectolytic strains of these clostridia cause a rapidly spreading soft rot that is usually accompanied by strong odors and heavy slime production.

The potential sources of soft rot bacteria include the soil, water, and plant debris. Strains of *Erwinia* spp. that cause soft rots have been isolated from plant roots, plant surfaces, pores on the surfaces of root crops, surface water, rainfall, snowfall, and ocean spray (France et al., 1985; McCarter-Zorner et al., 1985). Populations of *Erwinia* spp. found on healthy plants or in the environment are usually small, but these bacteria can multiply rapidly in wounds or infection courts. Puncture wounds on tomato leaves supported initial growth and then survival of *E. carotovora* subsp. *carotovora* for several weeks (Bartz and Concelmo, 1989). Thus, leaves damaged by insects or storm events could provide inocula for the fruit. Strains of soft-rotting *Pseudomonas* spp. and *Clostridium* spp. can usually be directly isolated from the soil even in the absence of an actively growing crop (Crosse, 1968; Lund, 1992). However, large populations develop in the soil in association with certain vegetable crops, particularly under the crop canopy.

4. Slime, Stains, and Discoloration

A nonspecific spoilage in fresh-cut vegetables can accompany the development of large populations of weakly pathogenic or saprophytic bacteria (King and Bolin, 1989). Saprophytes, by definition, do not attack living plant tissues; but the distinction between saprophytic and pathogenic is blurred when tissues become stressed. Severe water congestion can cause tissue membranes to leak minerals and metabolites that support the growth of pathogens as well as saprophytes (King and Bolin, 1989; Young, 1974). Pathogens and weak pathogens, however, should be better adapted to growth on stressed tissues than true saprophytes. For example, Robbs et al. (1996) isolated several different bacteria from spoiled celery sections; inoculation of fresh celery sections with strains identified as pectolytic pseudomonads (and therefore likely pathogens) led to severe damage, whereas inoculation with nonpectolytic bacteria produced responses ranging from no effect to tissue darkening and water soaking.

Certain *Leuconostoc* spp. and *Lactobacillus* spp. may qualify as common weak pathogens. These ''lactic-acid'' bacteria are residents on many vegetables (Goepfert, 1980; Lund, 1992) and are responsible for the fermentation of brined vegetables (Samish et al., 1963). However, Conn et al. (1995) described a sour rot type decay of tomatoes that was caused by *L. mesenteroides*. Bartz et al. (1995) isolated both *L. mesenteroides* and a species of *Lactobacillus* from lesions on tomatoes that appeared to have sour rot caused by the fungus *Geotrichum candidum*. Both of these lactic acid bacteria appear to be fastidious and do not grow well or at all on the common media used for isolating plant pathogens (Conn et al., 1995). Consequently, lesions caused by lactic acid bacteria may have been confused in the past with sour rot. Lactic acid bacteria were also implicated in spoilage of fresh cut celery where cells, typical in shape for *Leuconostoc* and *Lactobacillus* spp., were observed in a complex of bacteria in spoiled segments (Robbs et al., 1996).

5. Bacteria Responsible for Soft Rots

Strains of pectolytic *Erwinia* spp. or *Pseudomonas* spp. cause most of the decay damage found in stored vegetables. The ''soft rot Erwinia group'' includes *E. carotovora* subsp. *carotovora*, *E. c. atroseptica*, and *E. chrysanthemi*, whereas the pectolytic pseudomonads include *Pseudomonas marginalis*, pectolytic strains of *P. fluorescens*, *P. viride-flava*, and *P. cepacia*. Additionally, certain *Clostridium* spp. cause soft rot in potato tissues stored in an anaerobic environment (Lund, 1992). *Bacillus* spp. have been associated with a soft rot of potatoes at >30°C (Lund, 1992), and a strain of *B. subtilis* caused a rapid soft rot of tomatoes stored at 33°C (Volcani and Wahl, 1954). Pectolytic strains of *Xanthomonas* spp., identified as species *campestris*, and of *Cytophaga* spp. were isolated from decayed tomato, bell pepper, papaya, and cucumber sampled from commercial markets (Liao and Wells, 1987). These bacteria caused soft rot in an array of inoculated vegetables, but their aggressiveness relative to that of members of the soft rot *Erwinia* group is unclear.

Most of the more aggressive soft-rotting pseudomonads are ''fluorescent,'' a designation derived from a pigmented siderophore produced by cultures growing on iron-deficient media (Lund, 1992). The siderophore, which chelates iron for use by the bacterium, fluoresces green to yellow-green under long-wave ultraviolet light. The pectolytic pseudomonads are strict aerobes and would not be expected to thrive in low-oxygen environments. Growth in an anaerobic environment is possible, however, if nitrate is present.

Soft rot bacteria are considered wound pathogens although *E. c. carotovora* and *E. c. atroseptica* can invade lenticels on potatoes that are stressed for oxygen (Lund, 1979; Perombelon and Lowe, 1975). Soft rot bacteria forced into tomatoes by an infiltration of the stem scar or of the corky ring that surrounds the attached stem can directly attack nonwounded fruit tissues, causing lesions that originate inside the fruit (Bartz and Showalter, 1981). Certain strains of pectolytic *Pseudomonas* spp. directly infect broccoli florets through production of a biosurfactant (Hildebrand, 1989). The surfactant was suggested to enable *P. marginalis* to enter stomata and, then attack cells below the epidermis. Certain surfactants, however, increase electrolyte leakage from treated tissues, which should increase the food available to the pathogen (Bartz and Kelman, 1984).

6. Bacteria That Produce Slime, Stains, or Discoloration

Many different bacteria appear to be capable of growing on vegetables in storage, particularly if the vegetable is wet, senescing, or fresh-cut. Growth of bacteria, particularly *L. mensenteroides*, leads to an accumulation of thick slime (King and Bolin, 1989). Growth of pigmented bacteria such as *Serratia marcescens* or *Xanthomonas* spp. produces red or yellow colors, respectively. The plant's response to bacterial growth can involve an oxidation of phenolic compounds or production of ethylene. Oxidized phenolic compounds turn plant tissues brown to black, whereas green plant tissues usually turn yellow in response to ethylene.

II. FOODBORNE PATHOGENIC MICROORGANISMS IN FRESH FRUITS AND VEGETABLES

A. Introduction

Microorganisms bacteria, viruses, and parasites that are pathogenic to humans (clinical pathogens) can profoundly influence the postharvest life of vegetables. Human pathogens have been found not only in fresh vegetables in the marketplace but also associated with outbreaks of illness (Fain, 1994; Lund, 1992; Robinson, 1996). An increased risk for pathogen development on fresh vegetable products has accompanied the popularity of ready-to-eat salads, fresh-cut fruits and vegetables and sprouted seeds. The production of these items includes handling steps that increase not only the opportunity for fruits and vegetables to become contaminated but also the chance for the offending microorganism to multiply.

The number of cases of illness caused annually by food-borne pathogens is difficult to determine (Fain, 1994; Robinson, 1996). Estimates of the cost of food-borne illnesses range from over $5 billion to over $22 billion annually for U.S. citizens alone (Robinson, 1996). The numbers of cases of ''intestinal flu'' is greatly underreported for two reasons. First, the majority of infections are so mild (self-limiting) that the patient recovers fully without visiting a physician. Second, health professionals usually treat the major symptom of food-borne illness, which is diarrhea, without identifying the cause.

An estimated 2% to 3% of all food-borne illnesses lead to serious complications such as septicemia, meningitis, kidney failure, reactive arthritis, etc. (Robinson, 1996). Persons with suppressed, underdeveloped, or declining immune systems—such as children, senior citizens, and persons with underlying health problems—are most at risk.

Most food-borne pathogens apparently do not normally live on or in plants and, thus, qualify as casuals. However, several will multiply on vegetables stored at room temperatures, a few will multiply on refrigerated vegetables and most have the ability to survive on vegetables for several days. The following list of microorganisms found in fresh fruits and vegetables represents outbreaks and surveys reported through 1997. The number of outbreaks linked to fresh fruits and vegetables, particularly seed sprouts, has increased greatly since then. A recent review (through 2000) of such outbreaks has been posted on the website of the U.S. Food and Drug Administration (Institute of Food Technologists, 2001).

B. *Listeria monocytogenes*

L. monocytogenes is widely distributed in soil, surface water, decaying vegetation, silage, sewage, and feces of animals and humans (Holt et al., 1994). Ingestion of the pathogen by humans with relatively inactive immune systems can lead to septicemia, meningitis and stillbirths or miscarriages with an overall fatality rate of 20% to 40% (Robinson, 1996). Hofer (1975), who first associated *L. monocytogenes* with fresh vegetables, isolated three strains from fresh lettuce in Brazil. Since that report, numerous investigators have focused on fresh vegetables as potential sources of the pathogen (Harvey and Gilmour, 1993; Heisick et al., 1989a; Lin et al., 1996; Sizmur and Walker, 1988; Velani and Roberts, 1991). Schlech et al. (1983) linked contaminated vegetables with human illness. A large listeriosis outbreak in Nova Scotia, Canada, in 1981 was traced to coleslaw prepared from stored cabbage. The cabbage crop had been fertilized with manure from sheep that contained the same strains of *L. monocytogenes* as found in stools from infected patients.

L. monocytogenes has been detected in fresh vegetables in many different countries, including the United Kingdom (McLauchlin and Gilbert, 1990; Sizmur and Walker, 1988; Velani and Roberts, 1991), France (Bind, 1989; Catteau, 1990; Lainé and Michard, 1988), Germany (Beckers et al., 1989; Breer and Schopfer, 1989), Taiwan (Wong et al., 1990), Switzerland (Ryser and Marth, 1991), Spain (de Simon et al., 1992), Northern Ireland (Harvey and Gilmour, 1993), and the United States (Heisick et al, 1989b; Ryser and Marth, 1991). The percentage of the samples found to be contaminated with the pathogen ranged from 3% (Beckers et al., 1989) to 30.3% (Heisick et al, 1989b). In the latter study, the highest incidence was among radishes, whereas an average 25.8% of potato samples were positive. By contrast, the bacterium was not detected in samples of broccoli, carrots, cauliflower, and tomatoes.

Vegetable salads have been implicated in listeriosis acquired in hospitals. Ho et al. (1986) reported that 23 patients in eight hospitals in the Boston area appeared to have acquired listeriosis from eating raw celery, tomatoes, and/or lettuce over a 2-month period in 1979. Allerberger and Guggenbichler (1989) linked organically grown vegetables with 28 infections (24 newborn infants and 4 adults) in a hospital in Austria in 1986. The linkage between the infants and the vegetables was not detailed. Bending and Strangeways (1989) isolated *L. monocytogenes* from prepared salads at St. James's Hospital in London. Houang et al. (1991) checked 256 green salad plates prepared in the Queen Charlotte's and Chelsea Hospital in London from April 1989 to February 1990 and failed to detect *L. monocytogenes*. Thus, salads prepared in hospital kitchens appeared to transmit *L. monocytogenes* to patients, but use of appropriate washing and storage conditions, as in the latter report, yielded salads that were free of the pathogen.

In general, *L. monocytogenes* is seldom found in facilities that process and handle fresh fruits and vegetables. By contrast, the bacterium has been found in many facilities that process dairy or meat products (Cotton and White, 1992; Klausner and Donnelly, 1991; Pociecha et al., 1991) as well as in domestic kitchens (Cox et al., 1989). During a year-long study in Northern Ireland, Harvey and Gilmour (1993) failed to isolate the pathogen from salads and mixed vegetables produced by one processor. Distinct and identical strains, however, were found in products from two of the three other processors in the survey. Since all four processors likely purchased the same raw vegetables, product contamination must have occurred within the establishments. Several workers have concluded that most of the contamination of foods by *Listeria* occurs within a processing facility (Boerlin et al., 1991; Busse, 1990), since high populations are rarely found in the raw material. Indeed, Lainé and Michard (1988) reported a case where serotype 1/2a was regularly found in shredded cabbage and on shredders in the processing line but not in the intact cabbage heads.

Certain vegetables support growth of *Listeria* spp. better than others. *L. monocytogenes* was not detected in tomatoes by Farber et al. (1989), or in a total of 92 samples of broccoli, carrots, cauliflower, and tomatoes by Heisick et al. (1989b). However, depending on storage temperature, the bacterium grew on many of these vegetables in laboratory tests. Populations of *L. monocytogenes* increased in whole tomatoes stored at 21°C but not at 10°C (Beuchat and Brackett, 1991). By contrast, the organism failed to survive in chopped tomatoes stored at those temperatures but grew in refrigerated low-acid raw salad vegetables such as lettuce, broccoli, asparagus, and cauliflower. Sizmur and Walker (1988) reported that a naturally occurring population of *Listeria* spp. in lettuce-based salads increased roughly twofold during storage at 4°C for 4 days. Steinbruegge et al. (1988) confirmed that *L. monocytogenes* was able to grow on shredded lettuce stored at different temperatures, but over a 14-day storage interval the population increases were modest, ranging from about 1 $\log_{10}$ unit at 5 and 25°C to 3 $\log_{10}$ units at 12°C. By contrast, lettuce juice stored at 5°C supported larger increases in populations. Populations of *L. monocytogenes* on fresh asparagus, broccoli, and cauliflower stored in air or a controlled atmosphere (CA) at 15°C increased by about 4 $\log_{10}$ units within 6 days (Berrang et al., 1989b). However, during storage at 4°C for 14 days, populations on asparagus increased by about 1 $\log_{10}$ and decreased on broccoli and cauliflower by about 0.5 $\log_{10}$. The CA treatment had no detectable effect on growth of the bacterium but increased the shelf life of the vegetables considerably. Populations of *L. monocytogenes* decreased in inoculated whole and shredded carrots stored at 5 and 15°C in an atmosphere of 3% O_2 plus 97% N_2 (Beuchat and Brackett, 1990b). Heat labile antibacterial compounds were detected in the shredded carrots. With shredded cabbage stored at 5°C, however, the population of *L. monocytogenes* increased over the initial 25 days and then decreased slightly by 64 days (Beuchat et al., 1986). Conner et al. (1986) found that raw cabbage juice stored at 4°C would not support growth of *L. monocytogenes*, but the organism survived for long periods of time. Beuchat et al. (1986) reported that *L. monocytogenes* was unable to grow on heat-sterilized cabbage at 5°C and suggested that the heat treatment either decreased the availability of certain essential nutrients or resulted in the formation of inhibitory compounds. By contrast, the bacterium grew in heat-sterilized but nonclarified cabbage juice stored at 30°C. The sensitivity of *L. monocytogenes* to high temperatures increased as the pH of clarified cabbage juice decreased from 5.6 to 4.0. These authors concluded that fermented vegetables receiving minimal heat processing before marketing pose little threat to public health.

The survival of *L. monocytogenes* in lightly processed vegetables appears to be affected by the pH of the product. George and Levett (1990) noted that the bacterium became undetectable in inoculated coleslaw at pH 4.0 within 5 days of storage at 4, 15, or 25°C. Populations also declined when the inoculated coleslaw was adjusted to pH 5.0. However, at pH 6.0, populations declined during a 25-day storage period at 4 and 15°C; but at 25°C, populations increased quickly and remained high.

C. *Salmonella* spp.

Salmonelloses are characterized by mild to severe diarrhea with complications that can include septicemia, reactive arthritis, and death (Robinson, 1996). This disease is usually linked to the consumption of contaminated meat, eggs, or dairy products. However, *Salmonella* spp. have been isolated from an array of vegetables collected in The Netherlands (Tamminga et al., 1978), Italy (Ercolani, 1976), Spain (Garcia-Villanova Ruiz et al., 1987), Thailand (Jerngklinchan and Saitanu, 1993; Rasrinaul et al., 1988), and the United States (Wells and Butterfield, 1997).

Several large outbreaks of salmonellosis have been traced to fresh vegetables. In 1988, raw mung bean sprouts were the source for 143 confirmed cases in the United

Kingdom and additional cases in Sweden (O'Mahony et al., 1990). *Salmonella saint-paul* was the primarily causal agent in these two outbreaks, although *S. havana* and *S. muenchen* were also isolated in Sweden. Cantaloupes were probable sources for multistate outbreaks of salmonellosis in the United States in 1990 (Ries et al., 1990) and 1991 (CDC, 1991). In 1990, an outbreak caused by *S. chester* covered 30 states and produced approximately 25,000 confirmed cases, with two deaths (Ries et al., 1990). In 1991, a total of 185 confirmed cases in 23 U.S. states and 56 cases in two Canadian provinces were caused by *S. poona* (CDC, 1991). Previously, *S. miami* and *S. bareilly* were responsible for two outbreaks linked to precut watermelon (Gayler et al., 1955), whereas *S. oranienburg* and *S. javiana* were responsible for more recent outbreaks attributed to consumption of watermelons (Blostein, 1991; CDC, 1979). In 1992 and 1993, raw tomatoes contaminated with *S. javiana* and *S. montevideo*, respectively, led to multistate outbreaks of salmonellosis (Hedberg et al., 1994; Wood et al., 1991). Since 1995, four outbreaks of salmonellosis in the United States have been traced to contaminated alfalfa sprouts (Tamplin, personal communication).

The *Salmonella* spp. can multiply or survive on many different types of vegetables such as fresh watermelon cubes (Escartin et al., 1989), sections of rind-free cantaloupe, watermelon, and honeydew melons (Golden et al., 1993), and fresh-cut tomatoes (pH 3.99 to 4.37) (Asplund and Nurmi, 1991). A strain of *S. montevideo* isolated from an infected patient grew on the surface of tomatoes stored at 20°C and in chopped tomatoes (pH 4.1) (Wei et al., 1995; Zhuang et al., 1995). Thus, certain species of *Salmonella* are either not sensitive to the acidulants in tomatoes or not greatly affected by the pH of the vegetable (down to at least pH 4.0).

D. *Escherichia coli*

This bacterium is a common inhabitant of the intestines of warm-blooded animals. Certain strains, however, produce toxins that cause diarrhea and other illnesses in people. Based on their effects on humans, pathogenic strains of *E. coli* are classified as enteropathogenic, enteroinvasive, enterotoxic, or enterohemorrhagic (Carlson, 1991). Fresh vegetables have been the source of pathogenic strains in several outbreaks (Fain, 1994). For example, an outbreak of travelers' diarrhea (caused by enterotoxic strains) afflicted 59 participants at a conference in Mexico City in 1974 (Merson et al., 1976). A salad containing raw vegetables was the probable source. Although travelers' diarrhea is usually associated with developing countries, tourists in the United States have contracted the disease (Fain, 1994). Two separate outbreaks in Rhode Island and New Hampshire involving 47 airline passengers and 78 lodge guests, respectively, were traced to salads containing various vegetable ingredients (Mintz, 1994). Iceberg and romaine lettuce, endive, and shredded carrots were served to airline passengers, whereas the lodge guests had onions, carrots, zucchini, broccoli, mushrooms, and tomatoes (CDC, 1994).

A recently identified group of strains of *E. coli* produce a toxin similar to the Shiga toxin (now called verotoxin) produced by *Shigella dysenteriae* (Cliver and Atwill, 1997). The most prominent verotoxin producer is strain O157:H7, which was responsible for the "hamburger disease" outbreak in the Pacific Northwest area of the United States in 1992. These enterohemorrhagic strains can cause bloody diarrhea or kidney failure. An infectious dose for an average human has been estimated at less than 50 cells and perhaps with certain individuals as few as 5 cells. Outbreaks of illness caused by these strains are usually associated with undercooked beef (Cliver and Atwill, 1997; Fain, 1994; Robinson, 1996).

However, dairy products, vegetables and nonpasteurized apple juice are also possible sources.

Most outbreaks of *E. coli* O157:H7 associated with fresh fruits or vegetables involve cross-contamination by undercooked beef or dairy products (Cliver and Atwill, 1997; Fain, 1994). For example, an outbreak in the Pacific Northwest was associated with cantaloupe from salad bars (Anonymous, 1993). The cantaloupe appeared to have been in contact with a meat food, such as beef. In 1994, raw broccoli and other raw salad bar items served at the University of Texas appear to have been cross-contaminated by raw ground beef (Barnett et al., 1995). Lettuce implicated in an outbreak in northwestern Montana in 1995 was suspected of having been cross-contaminated by raw ground beef. However, strains recovered from the beef could not be linked by pulsed-field gel electrophoresis with strains isolated from the lettuce (CDC, 1995). Vegetables can also be cross-contaminated by contact with other types of meat, since *E. coli* O157:H7 occurs naturally in sheep, deer, and possibly other ruminants (Cliver and Atwill, 1997).

Infected food handlers have also been responsible for the contamination of fresh vegetables by *E. coli* O157:H7. In Idaho in 1995, 13 confirmed and 8 probable cases were traced to the consumption of chicken-based Caesar salads at a single restaurant (Anonymous, 1995b). An apparently healthy food handler who was shedding the pathogen contaminated romaine lettuce in the salad. Direct contamination of produce by cattle manure appeared to be responsible for at least three outbreaks of O157:H7 (Besser et al., 1993; CDC, 1996; Steele et al., 1982). Fresh cider prepared from ''windfalls'' or ''drops,'' which are apples harvested from the floor of an orchard, was linked to diarrhea and uremic syndrome in people who had consumed the cider. Probable sources of contamination were cattle that grazed in nearby pastures or the orchard. In contrast, white radish sprouts were the probable source of *E. coli* O157:H7 responsible for roughly 10,000 illnesses in Japan in 1996. How the radish seed, the probable initial source of O157:H7, became contaminated is unknown.

Pathogenic strains of *E. coli* can multiply outside their animal or human hosts (Cliver and Atwill, 1997). Packaging treatments or storage in a modified atmosphere (MA) showed no inhibitory effect on the growth of O157:H7 on shredded lettuce or sliced cucumber stored at 12 and 21°C (Abdul-Raouf et al., 1993). However, growth did not occur on shredded carrots held at the same temperatures. Populations of O157:H7 remained constant on inoculated cubes of cantaloupe and watermelon stored at 5°C over a 34-h storage period, but when the storage temperature was increased to 25°C, populations of the bacterium increased. Growth was observed on the rind of melons stored under high relative humidity at 25°C for 14 to 22 days (del Rosario and Beuchat, 1995). Zhao et al. (1993) reported that *E. coli* O157:H7 survived 20 days in refrigerated (8°C) apple cider with a $\text{pH} < 4.0$, but when 0.1% of the preservative sodium benzoate was added, survival was less than 7 days. Strains of *E. coli* that produce verotoxin are more acid-tolerant than are nonproducers of toxin (Cliver and Atwill, 1997). Under certain conditions, strain O157:H7 will survive exposure to a pH as low as 2.0.

E. *Shigella* spp.

Shigellosis—caused by *S. sonnei*, *S. flexneri*, and *S. dysenteriae*—can result from the consumption of contaminated salad vegetables (Fain, 1994). Lettuce from salad bars that had been contaminated with *S. sonnei* was responsible for two outbreaks occurring simultaneously on two university campuses in Texas (Martin et al., 1986). Another shigellosis outbreak caused by *S. sonnei* involved 347 cases (Davis et al., 1988). Shredded lettuce served at restaurants was traced to a single facility where a worker was the source of contamination. An outbreak (1994) in several European countries—including Norway, Sweden, and the United Kingdom—was also caused by the contamination of iceberg lettuce by *S. sonnei* (Frost et al., 1995; Kapperud et al., 1995). A total of 110 confirmed cases were reported in Norway alone.

Fresh green onions have been linked to shigellosis in the United States. Two midwestern outbreaks of disease caused by *S. flexneri* were traced to a single Mexican farm where the Californian shippers obtained most of their green onions (Cook et al., 1995). Contamination was believed to have occurred during harvest or packing.

Shigella spp. can multiply on sliced vegetables and fresh fruits. *S. sonnei* survived on lettuce for at least 3 days at 5°C, but when the lettuce was stored at 22°C, populations increased by more than 1,000-fold (Beuchat, 1996; Davis et al., 1988). Satchell et al. (1990) reported that *Shigella* spp. multiplied on shredded cabbage stored at room temperature. Substantial population increases were detected within 4 to 6 h after freshly cut cubes of papaya, jicama, and watermelon were contaminated with *S. sonnei*, *S. flexneri*, or *S. dysenteriae* and then stored at room temperature (Escartin et al., 1989).

F. Other Pathogenic Bacteria, Viruses, and Parasites

Pathogenic strains of *Aeromonas* spp., *Campylobacter* spp., *Yersinia enterocolitica*, *Staphylococcus aureus*, *Bacillus cereus*, *Clostridium botulinum*, and *C. perfringens* have been isolated from fresh vegetables. *Aeromonas* spp. are psychrotrophic and found naturally in fresh and saline water, brackish water, and sewage (Callister and Agger, 1989). Pathogenic strains of *A. hydrophila* have been isolated from raw seafood, poultry, and fresh produce such as parsley, spinach, celery, alfalfa sprouts, broccoli, lettuce, and kale. Berrang et al. (1989a) found *A. hydrophila* at 10^6 CFU/g fresh tissue weight in fresh asparagus, broccoli, and cauliflower that had been stored in CA at 4°C for 2 weeks. Robbs et al. (1996) detected *A. caviae*, a member of the "hydrophila group," in six of seven samples of lightly processed celery taken from a fresh celery packinghouse. Three out of 14 freshly harvested plants also contained this bacterium.

Campylobacter enteritis in humans, caused by *C. jejuni* or *C. coli*, can develop from consumption of raw vegetables and fruits that have been cross-contaminated by contact with poultry or other meats (Harris et al., 1986). *C. jejuni* can survive on sliced watermelon and papaya for a sufficient time to pose a risk to consumers (Castillo and Escartin, 1994).

Pathogenic *Yersinia enterocolitica* has been isolated from raw vegetables including grated carrot (Catteau et al., 1985; Darbas et al., 1985). Although contaminated vegetables have not been linked to illness caused by *Y. enterocolitica*, the isolation of this pathogen from raw salad vegetables is a reason for concern. The bacterium is psychrotrophic and can grow on fresh lettuce and other salad ingredients in cold storage.

Outbreaks of food-borne illness caused by *Staphylococcus aureus* have been traced to ready-to-eat vegetable salads (Houang et al., 1991). Food handlers, who were carriers of the bacterium, apparently contaminated the salads.

Spores of pathogenic *Bacillus cereus*, *Clostridium botulinum*, and *C. perfringens* in the soil can contaminate vegetables (Roberts et al., 1982). However, these bacteria pose no threat unless the produce is handled in a manner that enables spore germination and growth of vegetative cells. In 1973, an outbreak of gastrointestinal illness occurred in the United States following consumption of home-grown sprouts of soybean, mustard, and cress seeds that were contaminated with *B. cereus* (Portnoy et al., 1976). Botulism has been linked to consumption of coleslaw prepared from shredded cabbage that was subsequently stored in modified-atmosphere packaging (MAP) (Solomon et al., 1990). Petran et al. (1995) reported that packaged shredded cabbage stored in an atmosphere of reduced oxygen supported the germination of spores of *C. botulinum.* Toxin formed within 4 to 6 days in vented packages of the cabbage stored in MA at 22 to 25°C. Toxin also formed in nonvented packages of shredded cabbage stored at 21°C for 7 days. Toxin formation by *C. botulinum* has occurred in fresh-cut or prepared raw vegetables that remained visibly acceptable for consumption (Lund, 1992).

Fresh vegetables can also be the source of food-borne illness caused by viruses and parasites. These pathogens share certain features of food-borne bacteria but lack others. As with bacteria, the contamination of vegetables with viruses and parasites is often from contaminated water, cross-contamination with animal products, animal wastes, or infected workers. However, unlike most of the bacteria, viruses and parasites cannot multiply outside of their hosts. Enteroviruses—such as poliomyelitis, ECHO, and coxsackie viruses—can survive in soil for 150 to 170 days, depending on the pH, moisture content, and temperature (Bagdasargan, 1964). Therefore these viruses should be able to survive on radishes, tomatoes, and lettuce stored at 6 to 10°C for periods exceeding the postharvest life of the vegetables. Badawy et al. (1985) demonstrated that rotavirus survived on lettuce, radishes, and carrots for 25 to 30 days at 4°C but only 5 to 25 days at room temperature. Refrigeration appeared to promote the survival of viruses. Hepatitis A virus and Norwalk virus are the most commonly documented viral agents associated with disease outbreaks due to consumption of contaminated produce (Fain, 1994). These viruses have been isolated from infected individuals as well as sewage and untreated wastewater used for crop irrigation (Beuchat, 1996). Hedberg and Osterholm (1993) examined 14 viral gastroenteritis outbreaks. Salads were implicated in five of these 14 outbreaks and an infected food handler was associated with eight. Griffin et al. (1982) traced Norwalk gastroenteritis to food handlers who appeared healthy during the preparation or serving of implicated foods but became sick afterwards. Beuchat (1996) indicated that 74% of the 39 Norwalk-like viral gastroenteritis outbreaks investigated during the period 1983 through 1991 were traced to infected food handlers, and contaminated salad items were implicated in 12 of the 39 outbreaks. Frozen strawberries were responsible for a multistate outbreak of hepatitis A in 1990 that involved 900 students, teachers, and staff in Georgia and Montana as well for 130 cases among Michigan schoolchildren that occurred in 1997. Epidemiological studies indicated that the 1990 hepatitis A outbreak was most likely due to contamination from an infected picker. Outbreaks of hepatitis A infections have been associated with frozen raspberries (Reid and Robinson, 1987), commercially distributed lettuce (Rosenblum et al., 1990), and uncooked diced tomatoes served at a restaurant (Williams et al., 1995).

Vegetables contaminated with parasites also lead to disease. Many of the parasitic infections have been acquired through person-to-person transmission or by ingestion of water, ice, or food that has been contaminated by feces (Barnett et al., 1995). *Giardia lamblia* was identified as the causal agent of an outbreak of intestinal ''flu'' among employees of a large corporation (Mintz et al., 1993). Raw vegetables served in the company's cafeteria were the probable source of the parasite, whereas an apparently healthy food handler appeared to have contaminated the vegetables. In 1995, strawberries contaminated with *Cyclospora cayetanensis*, an enteric coccidian parasite, were the cause of a September outbreak in Florida involving 123 confirmed and 399 probable cases (Anonymous, 1995a). In 1996, another *Cyclospora* outbreak occurred in the eastern United States. Raspberries imported from Guatemala were implicated as the source of infection (Herwaldt and Ackers, 1997). The berries may have been contaminated in the field when untreated water was used to prepare pesticide sprays. A second outbreak of *Cyclospora* linked to raspberries from Guatemala occurred in 1997, which led producers to voluntarily suspend shipments to the United States. Outbreaks of cryptosporidiosis caused by *Cryptosporidium parvum*, a second enteric coccidian parasite, occurred in Maine in 1993 (160 primary cases) and in New York in 1995 (20 confirmed and 11 suspected cases) (CDC, 1997; Millard et al., 1994). Both outbreaks were traced to fresh-pressed apple cider. In the 1993 outbreak, the orchard was adjacent to an area grazed by cattle whose stools contained the organism and windfall or dropped apples had been included in the raw material (Millard et al., 1994). *Cryptosporidium* oocysts were detected in the stools of some patients, in the apple cider, on the cider press, and in the fecal sample from a calf on the farm that supplied the apples. *Cryptosporidium* oocysts have also been detected in cilantro leaves and roots, as well as lettuce, carrots, cucumbers, radishes, and tomatoes grown in Costa Rica (Monge and Chinchilla, 1996). The source of the oocysts was thought to be irrigation water that was drawn from rivers, whereas direct contamination by animal feces was eliminated as a possible source. *Cryptosporidium parvum* is considered a waterborne pathogen (Cliver and Atwill, 1997). An effective dose producing disease in 50% (ED_{50}) of healthy human volunteers was produced by 132 oocysts, whereas 30 were sufficient to induce the disease in at least one person. Thus, the contact of fresh vegetables with contaminated water could easily lead to an outbreak of cryptosporidiosis if the vegetables were consumed raw.

III. CONTROLLING BACTERIAL POPULATIONS ON VEGETABLES

A. Introduction

Bacterial populations on vegetables have been controlled through exclusion, chemical treatments, and physical treatments. The goal with all treatments has been to prevent contamination, since there is no reliable way to decontaminate raw vegetables (Fain, 1994). This concept is also true with plant pathogens. Wash treatments can reduce the microbial load on a fresh vegetable (Abdelnoor et al., 1983), but not eliminate the microbes completely (Goepfert, 1980, Lund, 1992). The exclusion of clinical or plant pathogens from vegetables, the most reliable way to control microbial populations of fresh vegetables, is accomplished by the use of sanitation and hazard analysis critical control points (HACCP) systems. These topics are covered in Chapter 23.

B. Chemical Treatments

Treatment of vegetables with certain chemicals may provide partial control of microbial growth. The use of oxidizing chemicals to control microbial populations on vegetables is discussed in Chapter 23. Populations of *S. montevideo* on the surface of tomatoes were eradicated completely by immersion of the fruit into a 15% aqueous solution of trisodium phosphate for 15 s (Zhuang and Beuchat, 1996). However, bacteria embedded in core tissues were not affected. Washes of freshly harvested vegetables with solutions of sodium carbonate or sodium bicarbonate remove bacteria from vegetable surfaces. Additionally, residual carbonate left in wounds or other potential niches for survival of microbes may inhibit bacterial development (Corral et al., 1988). Immersion or wash treatment with organic acids can also reduce bacterial populations on the surface of vegetables by removal and toxic action. Potassium citrate or tartrate at 100 mM and pH 3.0 were bactericidal to two different plant pathogens (Sands and McIntyre, 1977). The application of an aqueous solution of 30 mM tartrate (pH 3.0) to cowpea leaves caused a 93% reduction in the number of lesions that developed after leaves were inoculated with *Pseudomonas syringae*. Immersion of potato tubers that had been inoculated with *E. carotovora* subsp. *carotovora* in 1% solutions of acetic or citric acids reduced the subsequent development of bacterial soft rot to 45% or 35%, respectively, of inoculated control tubers (Bartz and Kelman, 1986). When these wash treatments were combined with a 2-h air-dry treatment, bacterial soft rot was reduced to 54% or 14% of control values for acetic or citric acid, respectively. The other organic acids tested, ascorbic and malonic, were less effective than citric acid.

Florida citrus packinghouses were required by quarantine regulations for citrus canker to sanitize fruit with chlorine or sodium orthophenylphenate (SOPP) (Brown and Schubert, 1987). Fruit contaminated with *Xanthomonas campestris* pv. *vesicatoria*, a surrogate for the citrus canker pathogen, were disinfected by 2% SOPP during a 30-s wash treatment. The wash treatment involved brushes that removed loose wax particles, sooty mold, and other organic matter from the fruit, which appeared to improve the efficacy of the SOPP. Earlier treatments involved keeping the fruit moist with SOPP in a soap formulation for 45 s or in a water drench for 60 s.

C. Irradiation

The treatment of various produce with ionizing irradiation such as gamma rays was reported to be effective for killing microorganisms in many food products, including fresh fruits and vegetables (Monk et al., 1995). Packaged endive (Langerak, 1978), shredded carrots (Boisseau et al., 1991; Scandella and Foures, 1987), red and green chicory mix (Scandella and Foures, 1987), and apple slices (Hanotel et al., 1990) have been successfully treated with irradiation to reduce total bacterial counts, yeasts, and molds. Nguyen-the and Carlin (1994) suggested that irradiation at doses lower than 2 kGy is generally more efficient than chemical treatment for lightly processed fresh vegetables; the total microbial counts can be reduced by 3 to 4 $\log_{10}$ units. The irradiation apparently did not affect the quality of the vegetables. However, Kader (1986) noted that >1.75 kGy was needed to control postharvest decays of fresh fruits and vegetables, whereas the exposure to 1.0 to 3.0 kGy led to softening and "off" flavors in certain commodities. Maxie et al. (1971) argued that irradiation had few benefits over conventional precooling and cold storage for controlling postharvest decays. Several types of whole fruits tested were softened by dosages below those required to kill decay fungi. These authors further noted that irradiation facilities are expensive to construct and maintain and, as a result, a large volume of produce harvested more or less continuously is required for the treatment to be economically feasible.

D. Controlled/Modified Atmospheres

Modified atmosphere packaging (MAP) has been applied to control microbial growth on fresh produce (Hotchkiss and Banco, 1972). However, in most reports, MAP prolonged the shelf life of the fruit or vegetable but did not affect the survival or growth of the pathogen. Moreover, low O_2/high CO_2 packing would not appear to have much effect on plant pathogenic bacteria although vegetables stressed by anoxia would likely be more susceptible to decay than those stored in ample O_2. Growth of *L. monocytogenes* on asparagus, broccoli, and cauliflower was not affected when these vegetables were stored at 4 or 15°C in 3% CO_2, 18% O_2, plus 79% N_2, although the shelf life of the vegetables was extended (Berrang et al., 1989b). *L. monocytogenes* was also shown to grow well on shredded lettuce packaged in air or 97% NO_2 plus 3% O_2 (Beuchat and Brackett, 1990a), and on shredded cabbage packaged in air or 70% CO_2 plus 30% N_2 (Kallander et al., 1991). Similar observations were reported for the growth of *Aeromonas* spp. on fresh vegetables (Berrang et al., 1989a).

E. Refrigeration and Drying Surfaces

Cooling vegetables to near 0°C as soon as possible after harvest is often the best way to control bacterial growth on vegetables (Lund, 1992). The management of product temperature after harvest is so critical to the control of postharvest decays that other treatments were considered by Sommer (1982) to be ''supplements'' to refrigeration. Refrigeration inhibits bacterial development in several ways. Cold storage slows the growth of all microorganisms including those that continue to multiply at $\leq$5°C. Refrigeration helps to keep vegetables fresh, which makes them more resistant to spoilage and decay.

With certain vegetables, cold temperatures may induce host resistance to spoilage. Carrots stored at 2°C for 3 days were much more resistant to bacterial soft rot than those stored at 20°C (Segall and Dow, 1973). Production of phenolic compounds such as 3-methyl-6-methoxy-8-hydroxy-3,4-dihydroisocoumarin was cited as a reason for the increased resistance. This chemical is not found in freshly harvested carrots but can be isolated from refrigerated carrots.

Refrigeration of vegetables to temperatures below 5°C inhibits the development of mesophilic but not psychrotrophic bacteria. However, the temperature distinction between these groups of bacteria is not always clear. For example, the minimum growth temperature for *E. c. atroseptica*, cause of bacterial soft rot in potato and other vegetables, has been variously reported as 1 to 2.8 or 3.0°C, whereas that for *E. c. carotovora* was 4 or 6°C (Lund, 1979). Soft rotting of potatoes has been reported to occur at temperatures as low as 4°C (Lund, 1979) and of potato tissues at 6°C (Knowles et al., 1982). However, Robbs et al. (1996) found that two strains of *E. c. carotovora* were unable to cause soft rot in celery sections stored at 5°C for 14 days. By contrast, strains of pectolytic pseudomonads have been isolated from soft-rotted celery that was stored at 0.4 to 1.0°C (Brocklehurst and Lund, 1981).

Certain vegetables are cold sensitive (Mitchell, 1992). Storing these vegetables under refrigeration can lead to chilling injury, which is manifested by visible damage as well as increased susceptibility to decay and spoilage. The safe minimum storage temperature for cold sensitive vegetables such as green tomatoes (about 12.5°C) will not completely prevent the development of soft rot. However, the initial multiplication of the casual agent will be slowed significantly, which delays the development of lesions (Bartz et al., 1991). Additionally, slowing the multiplication of the bacteria may allow tissues surrounding inoculated wounds to develop barriers to infection. Perombelon and Lowe (1975) characterized the onset of bacterial soft rot at wound sites on potato tubers as a race between bacterial multiplication and host resistance reactions. If a pathogen density large enough to initiate tissue maceration occurred before the wound healed, then a lesion would form. With green tomatoes, the development of a critical density in wounds before about 3 days was associated with the appearance of lesions (Bartz, 1981). If a critical density was not achieved within 3 days, the bacterium remained viable in the wound but lesions did not develop until after the fruit had ripened. Chilled tomatoes, however, were much more prone to develop soft rot than nonchilled fruit (Bartz et al., 1991). Minimizing populations on potato tubers at harvest or during initial handling slows the development of bacterial soft rot (Bartz and Kelman, 1984). If tuber surfaces dry before lesions have become established, then soft rot may not develop (Perombelon and Lowe, 1975).

Refrigeration may also remove free water from vegetable surfaces. Free moisture promotes the growth of psychrotrophic bacteria even when the vegetable is stored near 0°C. The absence of free moisture usually deprives bacteria of easy access to plant cell contents. The presence of free moisture on vegetables stored at high temperatures often leads to rapid spoilage and decay. The removal of moisture from the surfaces of freshly washed potatoes can be accomplished by blowing heated air over the product (Ruehle, 1940). However, Wardowski et al., (1987) noted that less expensive ways to dry citrus included sponge rolls or bristle brushes that rub against "flick bars." High-speed air also will break up water films on product surfaces, whereas fresh-cut salads can be "dewatered" in a special centrifuge (Cothers, 1992).

Use of a combination of practices appears to be the best way to control bacterial populations on vegetables. Sanitation and HACCP plus refrigeration (see Chap. 23) offer the best current combination for limiting bacterial development.

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