

**Carbon Dioxide and Ethylene Gas  
in the Potato Storage Atmosphere  
and their Combined Effect on  
Processing Colour**

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# **Carbon Dioxide and Ethylene Gas in the Potato Storage Atmosphere and their Combined Effect on Processing Colour**

**Barbara J. Daniels-Lake**

## **Thesis**

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## Abstract

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The finished colour of processed potato (*Solanum tuberosum* L.) products is a very important quality characteristic which is attributable to the concentration of reducing sugars in the raw tubers. Many internal and external factors can affect the concentration of these sugars during long-term storage. Ethylene gas, produced by the tubers or from external sources such as pathogens or engine exhaust, is known to increase reducing sugars and darken processing colour. For many years, elevated CO<sub>2</sub> from tuber respiration or external sources was also believed to affect sugars and cause darkening, although the research was somewhat contradictory. Restricted ventilation in potato storage buildings can cause appreciable accumulation of both gases in the storage atmosphere.

The effects of elevated CO<sub>2</sub> and depleted O<sub>2</sub>, with and without trace ethylene (0.5 μL L<sup>-1</sup>), in the atmosphere surrounding potatoes were investigated. Short-term studies (three or nine weeks) using cultivar Russet Burbank stored at 9 °C were conducted during several consecutive storage terms, with evaluation of the processing colour at intervals of three weeks. No responses to elevated CO<sub>2</sub> or depleted O<sub>2</sub> were observed, whereas ethylene darkened colour slightly. However, the colour was darker when tubers were exposed to CO<sub>2</sub> and ethylene together than with ethylene alone. At 0, 0.5, 1.0 and 2.0% CO<sub>2</sub> with 0, 0.25 and 0.5 μL L<sup>-1</sup> ethylene in a 4 × 3 factorial design, the colour darkened as the concentration of either gas increased, except in CO<sub>2</sub> without ethylene where darkening was not observed. Pre-treatment with the ethylene blocking compound, 1-methylcyclopropene prevented darkening attributable to 0.5 μL L<sup>-1</sup> ethylene and to 2% CO<sub>2</sub> plus 0.5 μL L<sup>-1</sup> ethylene.

Long-term studies (December to June) using cultivars Shepody, Innovator and Dakota Pearl in addition to Russet Burbank were subsequently

undertaken, using 2% CO<sub>2</sub> with 0.5 or 10 µL L<sup>-1</sup> ethylene (trace and sprout-inhibiting concentrations, respectively) and evaluations every four weeks. There was little or no change in processing colour in Dakota Pearl, a potato chip cultivar, in response to any of the treatments throughout the storage season. In the three French fry cultivars Russet Burbank, Innovator and Shepody, processing colour was darker in response to either concentration of ethylene at four weeks after the exposure began, although recovery to a lighter colour occurred with increased duration of storage in Russet Burbank and Shepody tubers. Interestingly, darkening in response to 2% CO<sub>2</sub> applied alone was observed after exposure for eight weeks or more in all three French fry cultivars. Darkening attributable to CO<sub>2</sub> and ethylene applied together was observed from the first evaluation after the start of exposure in the three French fry cultivars. This darkening occurred whether or not the cultivar responded to ethylene or CO<sub>2</sub> alone, and was worse than with ethylene alone in all three cultivars, except that Shepody tubers exposed to CO<sub>2</sub> plus 10 µL L<sup>-1</sup> ethylene was the same as with 10 µL L<sup>-1</sup> ethylene alone. The magnitude of darkening varied slightly among cultivars, and was usually more severe as storage duration increased.

This research has provided useful information to help storage managers maintain the physiological condition of stored potato tubers to ensure light processing colour.

**Keywords:** *Solanum tuberosum* L., carbon dioxide, ethylene, storage, processing, fry colour, chip colour, 1-methylcyclopropene.

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# Chapter 1

## General Introduction

### 1.1. The Potato as a Food Crop

The potato (*Solanum tuberosum* L.) is the third most important food crop worldwide, after rice and wheat (CIP 2010). First cultivated for its starchy tubers more than 7000 years ago in the Andean highlands of South America, the potato was introduced to Europe in the 1600's (Hawkes 1990). In the centuries since that time, it has spread throughout Europe and around the globe. At present, potatoes are produced and consumed in virtually every nation (CIP 2006).

Potato tubers provide high quality nutrition, especially food energy, vitamin C, potassium, protein and dietary fibre (Horton and Sawyer 1985; Li et al. 2006). The potato plant produces more food calories per hectare, using less water, than either wheat or rice (Horton and Sawyer 1985; UN-IYP 2008; CIP 2013a). Because of its short production cycle, a crop of potatoes provides food much faster than cereals or legumes. It is useful as a hunger- breaker crop for small holders, for example in East Africa (PC Struik, personal communication). The importance of potato in resolving food insufficiencies in developing nations was recognized by the United Nations, by their declaration of 2008 as the International Year of the Potato (IYP), with aims of

*“...raising the profile of this globally important food crop and commodity, giving emphasis to its biological and nutritional attributes, and thus promoting its production, processing, consumption, marketing and trade.”* (UN-IYP 2008).

Potato tubers are cooked before being eaten, e.g. by boiling or baking or frying. They are a very versatile foodstuff which can be served as the staple food in a meal, as a vegetable accompaniment to the main dish or as one of several ingredients in a mixed dish (Kadam et al. 1991). These mild-flavoured, starchy tubers can be incorporated into traditional dishes from many cultures,

to lend variety and increase the nutritional content of the meal. Potatoes are also made into many prepared or semi-prepared processed products, including frozen par-fried French fries; chilled ready-to-eat or heat-and-serve potato dishes; potato chips (known as crisps in some countries); potato flakes and granules for making instant mashed potatoes or as an ingredient to make snacks or other food items; potato starch for food and industrial uses; ethanol for human consumption and industrial applications including fuel; and feed for livestock and household pets. About half of the annual potato crop in North America and the European Union is processed, mainly into French fries and potato chips (Kirkman, 2007; AAFC 2009; USDA-ERS 2012).

### 1.1.1. Potato Botany

Although the potato was originally domesticated on mountain highlands at tropical latitudes (Hawkes 1990), this plant has been further adapted to a very wide range of climates and growing conditions, ranging from cool temperate regions to tropical lowlands. The edible portion of the potato plant, the tuber, is the fleshy swollen tip of a subterranean branch called a stolon. Potato tubers are therefore stem tissue and have both apical and axillary buds, known as eyes. The eyes are usually dormant while the tuber is growing beneath the potato plant, and remain so for a period of time after the mother plant senesces or the tuber is harvested. The duration of dormancy is a varietal characteristic controlled by the concentrations of endogenous plant growth regulators and specific genetic factors, but it is also influenced by the maturity of the tuber at harvest, the temperature during storage, exposure to light, and exogenous chemicals including sprout inhibitors (Burton et al. 1992; Suttle 2007).

The potato crop is usually propagated vegetatively, by planting seed tubers saved from the preceding cropping cycle which have broken dormancy and will grow sprouts from the meristematic tissue at their eyes. The sprouts elongate upward, emerging above the soil surface as shoots which develop into potato plants with green leaves, aerial branches and flowers. Meanwhile, beneath the soil surface, stolons branch from the main shoots and swell at their tips into daughter tubers to complete another crop cycle (Struik 2007).

### 1.1.2. Potato Production

Potato production in developed countries is complex and highly mechanized to maximize production efficiencies and yields. However, less-mechanized farmers can also successfully produce potato crops using basic tools. Potato production is actively encouraged in many developing regions, both to provide food for the family and as a source of income for the farmers. In areas where crops can be grown year-round, potato is often chosen as an intervening crop during seasons which are less suitable for other crops (FAO 2007; CIP 2013b). For example, in India, Vietnam and southern China, most of the potatoes are grown during the relatively cool winter season, between two crops of rice or other vegetables which require warmer conditions.

While potato production in developed countries has been declining slightly over the past 20 years, production in developing nations has increased greatly during the same period (Horton and Sawyer 1985; FAO 2007; FAOSTAT 2010). The area under potato cultivation in developing countries now exceeds that in developed nations. For example, statistics for 2008 rank China as first in world potato production, at 69 million MT grown on 4.7 million ha, i.e. approximately 23% of the world crop (FAOSTAT 2010). This reflects the steady increase in potato production in Asia, e.g., mean annual increases in total crop of ca. 4, 5, 11 and 13% per year in China, India, Pakistan and Bangladesh, respectively, from 1997 to 2007 (AAFC 2009; FAOSTAT 2010; CIP 2013a). Increasing production in developing countries is driven, in part, by the preferences of newly-affluent young urban dwellers for a Western-style diet, including processed potato products such as potato-based snacks and French fries eaten in restaurants (FAO 2007).

### 1.1.3. Potato Consumption

In North America and most European countries potatoes have been an important staple food for about two hundred years, eaten nearly every day in most homes. For example, in the USA in 1960, the average per capita consumption of potatoes was ca. 48 kg per year, with 37 kg or more than 75% of these potatoes being purchased as fresh tubers for preparation at home (USDA-ERS 2012).

Today's consumers demand more convenience foods, both in restaurants and at home. This has shifted the emphasis in potato consumption to processed products such as frozen French fries and instant potato flakes. Although the annual consumption of potatoes in the USA reached 63 kg per person in 2001, the share of fresh potatoes has declined to 21 kg per person or only 33.5% of the total (USDA-ERS 2012). In contrast, consumption of frozen French fries increased from ca. 3 kg per person per year in 1960 to more than 26 kg in 2001 (USDA-ERS 2012).

Similar market trends have occurred in other developed countries, including Canada and EU nations (AAFC 2009; FAO 2010). Low-carbohydrate diet trends and substitution with other starchy foods such as pasta or rice have helped to reduce the demand for table potatoes in many developed countries (McGregor 2007). Never-the-less, the per capita consumption of potatoes in Canada, the USA and the European Union remains relatively high, at 75, 56 and 94 kg per person per year, respectively (AAFC 2009).

## **1.2. Potato Storage**

To maintain a year-round supply for consumers and the processing industry, potato tubers are stored for various periods of time before consumption or processing. Diversion of a portion of the crop to storage prevents overloading of the market at harvest time, reduces the need to import potatoes from different climactic zones at other times of the year, and enables year-round operation of processing facilities. Careful management can achieve successful storage of potato tubers for a year or more, if desired. However, in commercial practice the storage term generally ranges from a few weeks to several months.

The duration of storage is strongly influenced by local climate and economic conditions. For example, in temperate climates where the crop is harvested in late summer to fall, much of it is stored for many months to provide a domestic supply until the next crop becomes available in the following summer. In contrast, in regions where the climate permits year-round agriculture the need for long-term storage of potatoes (e.g., more than 3 months) may be minimal. Short-term storage (e.g. several weeks) may

sufficiently distribute the harvest bounty to extend market supplies and avoid overwhelming the marketplace.

The quality of the tubers following a period of storage is very important. To assure high quality tubers after storage, it is necessary to begin with healthy, well-matured tubers of an appropriate cultivar for the intended purpose. However, several other factors also influence their final quality. These include duration of storage; dormancy status and physiological age; diseases and pests; temperature; relative humidity; application of postharvest chemicals and the composition of the atmosphere surrounding the stored tubers (Isherwood 1973; Mazza et al. 1983; van Es and Hartmans 1987a; Burton et al. 1992; Prange et al. 1998).

### 1.2.1. Storage Methods

Below-freezing temperatures are unsuitable for storing raw potato tubers but cool-temperature storage (ca. 3 to 12 °C) keeps the tuber respiration rate relatively low, impairs disease development, and slows physiological ageing (Burton et al. 1992). These effects help to retain good quality in the tubers for all end-uses. In developed countries with temperate climates, storage of potatoes usually involves specialized buildings with automated temperature control, humidification and forced-air ventilation, to help retain tuber quality for fresh use, processing or seed (Burton et al. 1992).

There are a broad range of other storage methods, with the choice dependent upon local circumstances including climate and economics. In-ground storage is the least complex, and is often practical in areas where winter or off-season temperatures are relatively mild. The mature tubers are simply left in place where they grew, and are harvested as needed. However, this method makes the field unavailable for other possible crops, and some tubers may be lost to diseases or pests, or perhaps grow into new plants before they can be eaten.

Heap or clamp storage is another method which is useful in areas of mild winter weather. The harvested tubers are piled up outdoors and covered with straw, earth and/or tarpaulins to exclude light, reduce temperature fluctuations and shed rain. Pit storage is a somewhat similar method, except

that the harvested tubers are placed in a pit dug into the ground, with a covering to exclude light and shed rain. Although water loss from the tubers is usually not problematic in these systems, they have little or no ventilation for the tubers and they may be overwhelmed by adverse weather conditions. Tubers stored in these ways are also quite susceptible to disease, damage by pests or loss to animal or human marauders.

Slightly more complex potato storage systems include potato cellars and above-ground structures such as sheds and passive-evaporation cool stores. These are usually ventilated by natural convection and wind to reduce CO<sub>2</sub> accumulation, but have only limited control of temperature and humidity. Low humidity can occur in many types of above-ground structures, which increases weight loss. Diseases and pests are still problematic, but because the stored tubers are easier to see than in heaps or pits, these issues can be detected earlier and steps can be taken to minimize loss. Seed tubers are often placed in buildings with diffuse light for several weeks before planting. This encourages sprout growth to be short, robust and containing chlorophyll, which hastens emergence and growth in the field.

### 1.2.2. Storage Physiology

Soon after harvest, most of the remaining sucrose photosynthate which was translocated from the haulm is converted to the storage molecule starch. During storage, potato tubers remain alive. Metabolic processes such as cellular respiration continue, gradually consuming the tuber's starch reserves (van Es and Hartmans 1987a,b; Burton et al. 1992). The starch is converted into the disaccharide, sucrose, and the reducing sugars, glucose and fructose (Isherwood 1973; van Es and Hartmans 1987a, b; Burton et al 1992).

As the storage term proceeds, the absolute and relative concentrations of various cellular metabolites such as plant growth regulators, enzymes and carbohydrates shift over time in response to internal cues and external factors such as storage temperature, stresses and disease (Dwelle and Stallknecht 1978; Mazza et al. 1983; Burton et al.1992; Kumar et al. 2004). The tubers age physiologically and eventually pass out of their dormant phase. In non-dormant tubers, starch is broken down more rapidly to provide additional cellular energy and a pool of structural molecules which are utilized to grow

sprouts. The rate of respiration increases and tuber sugar concentrations usually rise (van Es and Hartmans 1987a,b; Davies 1990; Burton et al. 1992). As physiological ageing proceeds to senescence, the tubers develop numerous branched sprouts from many eyes and irreversible senescent sweetening occurs (Burton et al. 1992; Pringle et al. 2009).

Aside from the mild change in flavour which can result when tuber sugar levels rise, sweetening is a significant quality concern for potato processors. During high-temperature processing such as frying, the non-enzymatic Maillard reaction occurs, in which reducing sugars such as glucose and fructose combine with free amino acids to produce bitter-tasting, brown-coloured melanoidin compounds (summarized in Burton et al.1992). In potatoes, the limiting factor determining the quantity of melanoidin compounds formed - and therefore the degree of darkening - is the quantity of reducing sugars in the raw tuber tissue (Denny and Thornton 1940; Shallenberger et 1959; Marques and Añon 1986; Burton et al. 1992; Khanbari and Thompson 1993). When a significant quantity of melanoidins is produced, the finished colour of the processed product is darkened (Denny and Thornton 1940; Shallenberger et al. 1959; Marquez and Añon 1986; Khanbari and Thompson 1993; Kumar et al. 2004). The flavour of the finished products may also be affected.

Although the optimal preferred colour for fry-processed potato products varies somewhat among geographic regions and specific products, it is generally true that light-coloured finished products are more desirable in the marketplace than darker-coloured products. Among French fry and potato chip processors, colour is one of the most important quality attributes of their finished products. Light coloured products usually command the highest price in the marketplace. Processors assess the processing colour of each shipment of tubers upon arrival at the factory, and often pay premium prices for tubers which will yield very light coloured products. The recent discovery of acrylamide in several processed starchy foods including potato products has increased the importance of light colour in processed potato products (Tareke et al. 2002). Acrylamide is a Maillard reaction product formed when the reacting amino acid is asparagine (Tareke et al. 2002; Biedermann-Brem et al. 2003; Williams 2005; Serpen and Gökmen 2009). For all of these reasons the storage of potatoes intended for processing is carefully managed to avoid factors which could increase sugars, darken colour and thereby reduce the

value of the tubers.

Potato tuber respiration is influenced by several external factors. Warm temperatures and stresses such as injury, disease or chilling increase the tuber respiration rate (Dwelle and Stallknecht 1978; van Es and Hartmans, 1987b; Burton et al. 1992; Fennir et al. 2002). Prolonged elevation of the respiration rate during storage can significantly reduce the mass of the tubers, by consuming their dry matter, i.e. sugars and starch. However, increased cellular respiration can also lighten the colour to which sweetened tubers will fry, by consuming some of the accumulated sugars (Isherwood, 1973; Dwelle and Stallknecht 1978; Burton et al. 1992). This response is the basis of the storage strategy known as reconditioning, whereby tubers that have a high sugar content (and would therefore yield dark-coloured products when processed) are stored for a few weeks at a slightly warmer temperature than previously, to improve (lighten) their processing colour. In addition to respiration, the elevated temperature also encourages reconversion of some of the sugars to starch (Burton et al. 1992). However, the warmer temperatures also increase disease proliferation, sprout development and weight loss. Since the elevated sugars in senescent tubers do not usually respond to reconditioning, this strategy is not always appropriate; it must be employed with caution.

### 1.2.3. Potato Sprout Inhibition

When potato tubers are to be stored beyond the end of their natural dormancy period, sprout inhibition becomes desirable. Sprouts are unsightly in the marketplace, they interfere with processing operations, and their growth is accompanied by quality deterioration such as weight loss, wilting and sweetening (Davies 1990; Burton et al. 1992). A low storage temperature (e.g. 3 to 6 °C) delays dormancy break and slows sprout growth, and therefore low temperature storage is used extensively to control potato sprouting (Rastovski 1987; Burton et al. 1992). However, in most cultivars low temperature storage also induces low-temperature sweetening (LTS), i.e. the conversion of starch to sugars in response to chilling stress (Isherwood 1973). While this is usually of little concern for seed or table stocks, LTS can be problematic for processing stocks due to Maillard browning. To minimize LTS, potato tubers intended for processing are usually stored at relatively warm temperatures



(e.g. 8 to 12 °C). However, the warmer storage temperature also hastens dormancy break, aids sprout growth and encourages disease proliferation (Burton et al. 1992).

To control sprouting, particularly for cultivars with rather short dormancy periods and for processing stocks, several chemical sprout inhibitors are available to retard sprout growth and prevent the quality changes associated with sprouting. The most popular of these is chlorpropham [isopropyl N-(3-chlorophenyl) carbamate], which has been widely used for more than a half-century (Marth and Schultz 1952; Burton 1989; Kleinkopf et al. 2003). Maleic hydrazide (diethanolamine salt of 1,2-dihydro-3,6-pyridazinedione) has also been a popular potato sprout inhibitor in many regions since the 1950's (Denisen 1953; Burton et al. 1992; Kleinkopf et al. 2003).

More recently, in response to pressure from consumers for reduced use of pesticides and lower-toxicity active ingredients, several 'alternative' sprout inhibitors have been identified. These include carvone, clove oil, mint oils, dimethylnaphthalene, diisopropylnaphthalene, hydrogen peroxide, unsaturated ketones, and ethylene gas (Hartmans et al. 1995; Prange et al. 1998; Afek et al. 2000; Kleinkopf et al. 2003; Knowles and Knowles 2008). While each of these has been shown to reduce or delay sprouting, the modes of action, durations of effectiveness, application methodologies and suitability for particular purposes vary among the compounds. The availability of these sprout inhibitors also varies significantly, as each must be approved for use by the appropriate national or regional authorities.

### **1.3. Carbon Dioxide**

Carbon dioxide (CO<sub>2</sub>) is a naturally-occurring gas, present at ca. 0.04% in the ambient atmosphere. It is the source of carbon for the carbohydrates produced by plants during the photosynthetic capture of light energy in the Calvin cycle, and it is released by all living cells during cellular respiration of those carbohydrates (summarized in Salisbury and Ross 1978a,b). Production of CO<sub>2</sub> during respiration is accompanied by consumption of oxygen (O<sub>2</sub>) at an equal rate, as the enzymes of glycolysis and the Krebs cycle oxidize glucose to convert ADP to ATP for cellular energy.

In air-tight storage rooms, cellular respiration by the plant products stored there can significantly alter the proportions of CO<sub>2</sub> and O<sub>2</sub> in the headspace of the room if ventilation is restricted for a period of time. This phenomenon is used to great advantage in the commercial controlled-atmosphere storage of many fruit crops. For example, the ripening and subsequent softening of stored apples is delayed when the concentrations of oxygen and CO<sub>2</sub> deviate significantly from ambient conditions such as those which result from the respiration of the apples in an enclosed space (Kidd and West 1927, 1933). Burg and Burg (1967) found that CO<sub>2</sub> is a competitive inhibitor of ethylene binding, and suggested this was why it delayed ripening of climacteric fruits. However, elevated CO<sub>2</sub> also stimulates ethylene production in many plants including stored potato tubers (Creech et al. 1973; Mattoo and White 1991).

Elevated CO<sub>2</sub> (10 to 100%) is useful in controlling insects and diseases in stored nuts, grains and some fruits (summarized in Kader 1992). Enhanced CO<sub>2</sub> in the atmosphere surrounding growing green plants increases their rate of photosynthesis and thereby enhances growth (Farquhar et al. 1980; Salisbury and Ross 1978a; Yin and Struik 2009).

### 1.3.1. CO<sub>2</sub> and Stored Potatoes

Although the respiration rate of well-stored, dormant potato tubers is rather low (CO<sub>2</sub> output of 2-4 mL kg<sup>-1</sup> h<sup>-1</sup>; van Es and Hartmans, 1987b), several factors (e.g. warm temperatures, stress, injury, physiological age, ethylene) can cause the respiration rate to increase. Respired CO<sub>2</sub> in a bin of stored tubers will accumulate quickly if not removed by ventilation (Schaper and Varns 1978). CO<sub>2</sub> concentrations which greatly exceed ambient levels can easily occur in potato storage bins, accompanied by depletion of O<sub>2</sub>. Observations of 1 to 4% CO<sub>2</sub> in the storage headspace are not unusual, with levels exceeding 10% reported occasionally (Schaper and Varns 1978; Mazza and Siemans 1990).

Exposure to moderate or high concentrations of CO<sub>2</sub> (3 to 30%) both stimulates respiration in potato tubers (Day et al. 1978; Perez-Trejo et al. 1981) and inhibits tuber respiration (Wills et al. 1979). These effects persist for several days after exposure, although the magnitude of the responses varies

somewhat depending on temperature. Wiggington (1974) found that elevated CO<sub>2</sub> (5, 10 and 15%) reduces suberization. Elevated CO<sub>2</sub> either increases or inhibits sprouting, depending on the maturity of the tubers (Schouten 1993). Elevated CO<sub>2</sub> in combination with rather low O<sub>2</sub> concentrations, i.e. classical controlled atmosphere conditions, inhibits sprouting (Khanbari and Thompson 1994, 1996). Exposure to CO<sub>2</sub> concentrations above 10% can cause tissue necrosis (Burton et al. 1992).

### 1.3.2. CO<sub>2</sub> and Processing Colour

For many years it has been widely believed within the potato processing industry that accumulated CO<sub>2</sub> in the storage atmosphere causes processing colour to darken. Limiting the CO<sub>2</sub> concentration in the storage atmosphere below 1 or 2% CO<sub>2</sub> has often been recommended (e.g. Rastovski 1987; Schaper et al. 1993). However, the research findings on this topic are somewhat confusing. Denny and Thornton (1941) found that exposure to 2 to 5% CO<sub>2</sub> prevents LTS. Blankson (1988) reported that 2 to 3% CO<sub>2</sub> has little effect on potato chip colour of several cultivars, but at a higher concentration (13%) the reducing sugar concentrations increase. Mazza and Siemens (1990) found that as little as 0.5% CO<sub>2</sub> results in darkening of potato chip colour. Schouten (1993) found that 3, 6 and 9% CO<sub>2</sub> does not affect potato chip colour of tubers during suberization at 18 °C, but during suberization at 12 °C or during later storage at 6 °C the same concentrations of CO<sub>2</sub> significantly darken colour.

Despite these conflicting findings, or perhaps because of them, many storage operators now monitor the CO<sub>2</sub> concentration in the atmosphere of their potato rooms with the goal of protecting processing colour. Automated equipment engages the ventilation system when the CO<sub>2</sub> concentration passes a selected threshold, usually 0.5 to 1%, v/v (R Andrews, Crop Systems Ltd, A Sardo, Xeda Corp, J Walsh, McCain Foods Limited, personal communications; Pringle et al. 2009).

## 1.4. Ethylene

Although the IUPAC systematic nomenclature for this 2-carbon alkene

has been designated as 'ethene' since 1993 (IUPAC 1993), the common name 'ethylene' persists in industry and agriculture, and will be used here. Ethylene has long been recognized as an important plant growth regulator in virtually all plants including potato (Huelin and Barker 1939; Abeles et al. 1992; Reid 1995). It is essentially non-toxic to mammals including humans (e.g. mouse  $LC_{50}$  is  $950,000 \mu\text{L L}^{-1}$ , O'Neil et al. 2006), but even very low concentrations ( $0.1$  to  $1 \mu\text{L L}^{-1}$ ) can have dramatic effects on plants and plant parts including potato tubers (Abeles et al. 1992; Reid 1995).

Plant responses to ethylene include the classical triple response of seedlings (short radially-enlarged hypocotyl, retention of the hypocotyl hook, and abnormal geotropic response; Abeles et al. 1992), induction of senescence, abscission of leaves and petals, germination of seeds, ripening of fruits, and increased respiration rate (Rychter et al. 1979; Yang 1985; Abeles et al. 1992; Reid 1995). In many species ethylene influences organ development, flowering, climacteric responses (autocatalytic increases in ethylene production during fruit ripening) and responses to external stimuli such as gravity or photoperiod. Ethylene also interacts with other plant growth regulators in complex ways which are not yet completely understood (McGlasson 1985; Reid 1995; Reid and Howell 1995; Schaller 2012).

#### 1.4.1. Ethylene and Potatoes

Like most plant species and their parts, potato tubers are capable of producing ethylene, although the rate of production is usually very low (ca.  $0.001 \text{ mg kg}^{-1} \text{ hr}^{-1}$ ; Poapst et al. 1968; McGlasson 1969; Burton and Meigh 1971; Creech et al. 1973; Cvikrová et al. 1994). However the rate of production increases in response to various stresses, including injury, chilling, and disease (Creech et al. 1973; Burton et al. 1992; Korableva and Ladyzhenskaya 1995).

Exposure of potato tubers to  $1$  to  $100 \mu\text{L L}^{-1}$  of exogenous ethylene stimulates respiration and alters sugar metabolism (Huelin and Barker 1939; Haard 1971; Reid and Pratt 1972; Isherwood 1973; Day et al. 1978; Parkin and Schwobe 1990; Schwobe and Parkin 1990). This can affect tuber quality, particularly processing quality. French fry and potato chip colour can be darkened severely by exposure to ethylene gas (Haard 1971; Parkin and

Schwobe 1990; Prange et al. 1998; Daniels-Lake et al. 2005), although the degree of darkening depends upon the concentration and the exposure protocol (Daniels-Lake et al. 2005, 2006). Abrupt exposure of cool-stored tubers to  $4 \mu\text{L L}^{-1}$  ethylene gas causes a sharp darkening of processing colour in most cultivars (Prange et al. 1998; Daniels-Lake et al. 2006). In contrast, gradual introduction of ethylene, i.e. commencing as soon as possible after harvest during the relatively warm suberization period at an initial gas concentration of 0.1 or lower and then increasing the concentration to  $4 \mu\text{L L}^{-1}$  in five to eight steps at weekly intervals, has little or no effect on the processing colour of many cultivars (Daniels-Lake et al. 2006).

Ethylene also affects the sprouting of potato tubers, but in two rather different ways. A brief exposure to ethylene shortens tuber dormancy, overcomes apical dominance and promotes sprouting, whereas prolonged exposure delays sprouting and inhibits sprout elongation (Haard 1971; Hughes et al. 1973; Rylski et al. 1974; Minato et al. 1979; Timm et al. 1986; Prange et al. 1998). The responses to long-term exposure make ethylene useful as a potato sprout inhibitor (Prange et al. 1998), while the effect on apical dominance has been found to improve field performance and stem number in many cultivars when seed tubers are treated with ethylene during storage (Pruski et al. 2006).

Responses to ethylene are dose-dependent in potato tubers (Daniels-Lake et al. 2005, 2006). Although threshold ethylene levels have not been determined for most ethylene responses in potato tubers, for some effects a saturation level has been proposed. For example, Daniels-Lake et al. (2005) suggest that for many cultivars the sprout inhibition response is saturated between 4 and  $10 \mu\text{L L}^{-1}$ , whereas the negative effect on fry colour is saturated at ca.  $1 \mu\text{L L}^{-1}$ . Reid and Pratt (1972) found that the effect of ethylene on potato tuber respiration is saturated at  $2.0 \mu\text{L L}^{-1}$ . These variations suggest that the different observed responses may be associated with separate receptor sites or response mechanisms.

#### 1.4.2. Ethylene in the Storage Atmosphere

The concentration of ethylene in the atmosphere of well-ventilated commercial potato storage facilities is usually relatively low (e.g. 0.04 to 0.15

$\mu\text{L L}^{-1}$ , P Bethke, University of Wisconsin/USDA, J Walsh, McCain Foods Limited, personal communications). Higher concentrations are entirely possible, such as when ventilation is restricted and/or ethylene production is increased by stress.

In addition to production by the tubers, there are several other potential sources of ethylene in the storage environment, including tuber pathogens (Arshad and Frankenberger 2002), ripening fruit stored nearby, and exhaust from fuel-burning equipment such as forklifts, heaters and vehicles used inside the facility or left with the engine running near ventilation intake openings (summarized in Abeles 1992). For example, concentrations exceeding  $10 \mu\text{L L}^{-1}$  have been observed when propane-powered equipment was used in a building which also contained stored potatoes (S Johnson, University of Maine, personal communication). The exhaust from heaters used for chlorpropham application can contribute significant quantities of ethylene to the storage atmosphere (Dowd 2004). For this reason, in recent years most chlorpropham applicators have altered their equipment to prevent this occurrence and/or shortened the period of time without fresh air introduction after the chlorpropham is applied (T Hoffman, Certis, A Briddon, British Potato Council, personal communications).

Since potato tubers are quite sensitive to ethylene, even relatively low concentrations can negatively affect stored tubers. However, in the past the concentration of ethylene in potato storage facilities was not usually monitored, because its significance was not widely recognized and because doing so required sophisticated laboratory equipment which was not usually available to commercial storage operators. More recently, interest in ethylene as a sprout inhibitor and reports of ethylene in chlorpropham fog during application, coupled with a better understanding of its effects and development of more user-friendly ethylene measuring equipment, have encouraged measurement of this important gas in many facilities (R Andrews, Crop Systems Ltd, T Hoffman, Certis, personal communications).

### **1.5. Interaction between CO<sub>2</sub> and Ethylene**

CO<sub>2</sub> was long believed to inhibit ethylene action in many crops (Burg and Burg 1967; Kidd and West 1927, 1933). It was often used in research

trials before the discovery of specific ethylene inhibitors such as silver ions, silver thiosulphate, norbornadiene, aminoethoxyvinylglycine (AVG) and 1-methylcyclopropene (1-MCP). However, more recent studies have found that many of the supposed inhibitions of ethylene effects by CO<sub>2</sub> are in fact directly attributable to CO<sub>2</sub>, i.e. effects that are unrelated to possible CO<sub>2</sub> blocking of ethylene binding sites (e.g. inhibition of respiration, changes in cell pH, effects on photosynthesis and stomatal aperture; summarized in Abeles et al. 1992; and in Reid 1995). In other situations where one gas was believed to enhance the effect of the other, the effects may instead be attributable to both in an additive manner but with different modes of action (e.g. seed germination, root elongation, cotyledon growth).

#### 1.5.1. CO<sub>2</sub> and Ethylene and Potatoes

Managing the storage of potatoes for processing is a complex and challenging task. Several other consequences in addition to processing colour must be considered, including weight loss, wilting, disease development, sprouting and nutritional value. Management practices which favour one of these may be detrimental to another. Factors which can be controlled, i.e. temperature, humidity and ventilation, plus the effects of physiological ageing, cultivar differences, storage duration and intended use must be included in the management plans. In addition, external factors which are beyond the control of the manager, such as outdoor temperatures, utility costs, and market demand, can add further complications.

One of the most important tools which storage managers need is a good understanding of how the tubers respond to these variables in the storage environment. Research has contributed greatly to this understanding over the past several decades. It is clear that exposure to ethylene gas can negatively affect the processing colour of stored potatoes. Although the effect on processing colour of accumulated CO<sub>2</sub> in the storage atmosphere is not entirely clear, the published research suggests that it does affect processing colour in at least some circumstances. However, what happens when these two gases are present simultaneously at active concentrations in the storage atmosphere? It is reasonable to think that each gas would still affect potato tubers when the other is present, but to what extent? Do they interact, either negatively or positively? Are all cultivars affected in the same manner, or to

the same degree? Do other factors influence the responses to these gases? The overall aim of the project reported here was to address these questions, using a systematic series of research trials.

## 1.6. The Research Project

### 1.6.1. Overall Objectives of the Research

Because finished colour is such an important quality attribute of stored potatoes destined for processing, additional insights on and clarification of the factors which can influence colour would assist the potato industry to provide high quality products at a reasonable price and in a profitable manner. The market preference for relatively light-coloured processed potato products confers economic value to the potential of raw tubers to yield a light colour when processed after storage. Retaining that potential from harvest until processing is therefore a significant issue for potato storage managers.

At present, although it is widely believed that CO<sub>2</sub> can darken colour, the effect is not clearly defined. While the effects of ethylene gas appear to be more straightforward, many questions remain. The possibility of interactions should be explored. This project investigated the relationships between these two gases in terms of processing colour, and attempts to improve our understanding of the response of potato tubers to these gases.

### 1.6.2. Research Hypotheses

H<sub>0</sub>: Accumulated carbon dioxide and ethylene gases, present alone or together in the atmosphere surrounding stored potato tubers, have no effect on the processing colour of those tubers.

H<sub>1</sub>: Accumulated carbon dioxide in the storage atmosphere affects the processing colour of stored potatoes.

H<sub>2</sub>: Accumulated ethylene in the storage atmosphere affects the processing colour of stored potatoes.

H<sub>3</sub>: Carbon dioxide and ethylene in the storage atmosphere interact in some way to affect the processing colour of stored potatoes



more than either gas alone.

These hypotheses were tested using a series of research trials which addressed the questions outlined in Section 1.6.3, below. If  $H_0$  is rejected on the basis of the results of these trials, then one or more of  $H_1$ ,  $H_2$  and  $H_3$  must be accepted.

### 1.6.3. Research Questions to be Addressed

The research described in this Thesis was focussed on the following questions:

1. Is elevated  $CO_2$  in the storage atmosphere truly a cause of darkening of processing colour in stored potato tubers?
2. Does ethylene gas play a role in the response to elevated  $CO_2$ ?
3. Can the responses to  $CO_2$  and ethylene be prevented or reduced?
4. Are there threshold concentrations of  $CO_2$  and ethylene in potato storage atmospheres, below which darkening does not occur?
5. Do different potato cultivars respond to  $CO_2$  and ethylene in the same manner?
6. Does time in storage, i.e. tuber physiological age, play a role in the responses to  $CO_2$  and ethylene?

### 1.6.4. General Approach and Methodology

The first two years of research in this project (2001-02 and 2002-03 storage seasons) were partially funded by McCain Foods Limited (McCains), a major global French fry producer based in Florenceville, New Brunswick, Canada. The potato industry in general, and McCains in particular, wanted a better understanding of the effects of  $CO_2$  in the storage atmosphere on fry colour of the stored tubers, because the industry guidelines in place at that time were producing variable results and the literature seemed somewhat contradictory.

All trials in this project were conducted at the Agriculture and Agri-Food Canada potato postharvest research facility at the Atlantic Food and Horticulture Research Centre in Kentville, Nova Scotia, Canada. In order to

focus the early investigations clearly, only a single cultivar was studied, i.e. Russet Burbank, a widely-used French fry cultivar. The earliest trials were of short duration, i.e. three or nine weeks, with several replications of tuber material, evaluations at intervals of three weeks, and repetition of the trials within each year. Later work included additional cultivars, and extension of individual trials throughout the Fall to Spring potato storage season.

The tubers used for this research project were sourced from several commercial producers across the Maritime Provinces of Canada, ensuring that the findings would be applicable to “real-world” material. Numerous lab-scale research chambers were employed, the atmosphere in each amended with compressed gases to create the applied treatments. The evaluations focussed primarily on the fry colour of the tubers, assessed after storage for specific periods of time under the various storage atmospheres. Assessments of other characteristics, e.g. potato chip colour, sprout development, sugar content, etc., were included as appropriate in some trials. All of these factors together enabled robust experimental designs and informative statistical analyses of the resulting data. The specific details and findings of each trial are provided in the following chapters.

At an early stage in this project, it was apparent that something more than CO<sub>2</sub> was responsible for the changes in fry colour which were sometimes observed in commercial situations. Based upon the author’s previous research work with ethylene gas as a potato sprout inhibitor, it seemed logical to investigate ethylene as a possible contributing factor. Soon it became clear that ethylene was indeed involved. The subsequent investigations have continued in various directions, and for several years after the original industrial partner’s involvement ended.

## **1.7. Outline of Thesis**

Chapter 1, the General Introduction, provides some background on the potato and the issues surrounding potato storage, processing colour and the composition of the atmosphere surrounding the stored tubers. Chapters 2, 3 and 4 describe research which used a single cultivar, Russet Burbank, to identify and begin to understand the interaction of CO<sub>2</sub> and ethylene.

Chapter 2 deals with the question of whether the presumed effect of CO<sub>2</sub> on processing colour is due to CO<sub>2</sub> accumulation, O<sub>2</sub> depletion or something else. Chapter 2 also introduces the interaction of CO<sub>2</sub> and ethylene gas. Chapter 3 describes use of the ethylene-blocking compound, 1-MCP, to mitigate the effect of the CO<sub>2</sub> plus ethylene interaction. Chapter 4 investigates the effect of different concentrations of the two gases.

Chapters 5 and 6 expand the scope to include additional cultivars and continuous exposure to these two gases over a longer time-frame. Chapter 5 compares the response of three other cultivars with Russet Burbank, while Chapter 6 looks at the same four cultivars but with ethylene raised to the concentration used for sprout inhibition.

Chapter 7, the General Discussion, pulls all of these results together, and explores the broader implications of this new information, with particular reference to the potato processing industry.

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## Chapter 2

### Carbon Dioxide and Ethylene: A Combined Influence on Potato Fry Colour\*

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#### Abstract

For many years, the accepted wisdom among potato storage researchers and industry personnel linked the accumulation of CO<sub>2</sub> in the storage atmosphere to darkening of potato fry colour. Dark fry colour is undesirable in the potato processing industry, as consumers prefer light-coloured finished products. Previous research to elucidate the effect of CO<sub>2</sub> has presented conflicting results. In three consecutive years of storage trials, the effects of elevated CO<sub>2</sub> concentrations, reduced O<sub>2</sub> concentrations and ethylene gas on the fry colour and sugar content of 'Russet Burbank' potato (*Solanum tuberosum* L.) tubers were evaluated. The potatoes were stored in modified atmosphere chambers and selected atmosphere mixtures were supplied from compressed gas cylinders. Four 3-week trials were conducted in 2002 and two 9-week trials were conducted in each of 2003 and 2004. Fry colour and tuber sugars were assessed at the start of each trial and after several weeks of exposure to the treatment atmospheres. Compared with untreated controls, increased CO<sub>2</sub> alone or in combination with decreased O<sub>2</sub> had little or no effect on fry colour or tuber sugars. During the second and third years, only selected treatments were repeated, with or without the addition of 0.5 µL L<sup>-1</sup> ethylene gas. Ethylene is known to affect potato fry colour and reducing sugars. In 3 of 4 trials, tubers exposed to ethylene alone had darker fry colour and higher reducing sugars compared with controls. Applied treatments had little or no effect on fry colour or sugars in the fourth trial. Interestingly, in the same 3 of 4 trials, fry colour of tubers exposed to both elevated CO<sub>2</sub> and ethylene gas was not only darker than controls but also darker than tubers treated with ethylene alone. Similarly, reducing sugar concentrations were higher in tubers exposed to both ethylene and CO<sub>2</sub> than

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with ethylene alone. No similar interaction between ethylene and oxygen concentration was observed. The results suggest a synergistic negative effect of trace ethylene and elevated CO<sub>2</sub> on fry colour which may explain the apparently contradictory findings of some published research examining the effects of CO<sub>2</sub> on potato fry colour.

## 2.1. Introduction

Fry colour is an important quality characteristic in processed potato products such as French fries and potato chips. The light fry colour preferred by consumers is produced when reducing sugar concentrations in the raw tubers are low (Mazza 1983; Burton et al. 1992). Researchers and industry experts have long believed that the storage atmosphere can provoke increases in reducing sugars and darken fry colour. Tuber respiration can deplete O<sub>2</sub> and raise CO<sub>2</sub> concentrations in the atmosphere surrounding the tuber, particularly when ventilation is restricted. For this reason most of the fry colour research to date has focused on increases in CO<sub>2</sub> and, to a lesser extent, decreases in O<sub>2</sub>.

Although early work by Denny and Thornton (1940) showed that 5% CO<sub>2</sub> prevents accumulation of reducing sugars during storage, Blankson (1988) found that CO<sub>2</sub> concentrations up to 2-3% have little effect on reducing sugar concentrations, whereas higher concentrations of CO<sub>2</sub> (up to about 13%) cause reducing sugars to rise substantially. Most research has shown that tubers stored with elevated CO<sub>2</sub> concentrations (0.5 to 15%) have higher reducing sugars and/or darker fry colour than tubers stored at ambient concentrations of CO<sub>2</sub> (Mazza and Siemens 1990; Schouten 1993a; Khanbari and Thompson 1994, 1996). Interestingly, recent extensive monitoring of several commercial storage buildings through a storage season found no correlation between the measured CO<sub>2</sub> concentrations and the fry colour changes observed (J Walsh, unpublished data).

Depleted O<sub>2</sub> concentrations accompany CO<sub>2</sub> accumulation in potato stores. Very low O<sub>2</sub> atmospheres (1 to 3%) have been shown to both lower reducing sugar concentrations (Harkett 1971; Sherman and Ewing 1983) and to darken fry colour (Khanbari and Thompson 1994; Schouten 1993b). Schwobe and Parkin (1990) found the effect varied among cultivars. However,

the influence of more moderate O<sub>2</sub> depletion on potato fry colour has not been reported.

Ventilation with external air to control temperature and humidity in the store is generally assumed to restore CO<sub>2</sub> and O<sub>2</sub> to ambient concentrations (Smith 1967; Rastovski 1987a; Burton et al. 1992). However, peak CO<sub>2</sub> concentrations measured in ventilated potato stores range from 0.6 to 14% (Mazza and Siemens 1990; Schaper et al. 1993). Rastovski (1987b) and Schaper et al. (1993) recommend that the CO<sub>2</sub> concentration within potato stores should be maintained below 1%.

Based on previous work with potatoes and ethylene gas (Prange et al. 1998; Daniels-Lake et al. 2005), it was hypothesized that ethylene may be involved in the fry colour darkening previously reported to be associated solely with elevated CO<sub>2</sub>. Exposure to low concentrations of ethylene (0.4 to 40 µL L<sup>-1</sup>) is known to increase reducing sugar concentrations and darken potato fry colour (Prange et al. 1998; Daniels-Lake et al. 2005). The response varies among cultivars (Haard 1971; Prange and Daniels-Lake, unpublished data) and darkening is concentration-dependent below about 4 µL L<sup>-1</sup> (Daniels-Lake et al. 2005). Ethylene is a metabolic product of potato tubers (Poapst et al. 1968; Suttle 2003) and the rate of production increases in response to stress (Poapst et al. 1968; McGlasson 1969; Creech et al. 1973; Korableva and Ladyzhenskaya 1995). Numerous potato storage pathogens also produce ethylene (summarized in Arshad and Frankenberger 2002b). The ethylene gas can accumulate to metabolically-significant concentrations around the tuber, particularly when ventilation is restricted. However an interaction of ethylene with either elevated CO<sub>2</sub> or decreased O<sub>2</sub> atmospheres, and its potential to influence potato fry colour or reducing sugars, have not been well examined. Duncan and Kraish (1999) speculated on a possible interaction, but no evidence was provided.

Trials were initiated in January, 2002 at the postharvest physiology facilities at Agriculture and Agri-Food Canada's Atlantic Food and Horticulture Research Centre (AFHRC) in Kentville, Nova Scotia, Canada, to elucidate the effects of CO<sub>2</sub> and O<sub>2</sub> on potato fry colour and tuber sugars. A low concentration of ethylene gas was included in the 2003 and 2004 trials to identify possible interactions among ethylene, O<sub>2</sub> and CO<sub>2</sub>.

## 2.2. Materials and Methods

### 2.2.1. Experimental Material

Trials were conducted during three consecutive years, i.e. January to June of 2002, 2003 and 2004, using commercially-grown 'Russet Burbank' potatoes harvested in mid-October of each preceding growing season. Within each year, potatoes were sourced from eight (2002) or four (2003, 2004) different potato growers located in New Brunswick, Canada. After arrival at AFHRC, the potatoes were held for four weeks at 13 °C to permit suberization and wound healing, gradually cooled to 9 °C over four weeks, and dipped in early December in a 1% a.i. water emulsion of chlorpropham (Sprout-Nip EC, isopropyl n-(3-chlorophenyl) carbamate, 320 g L<sup>-1</sup> a.i., Stanchem Inc., Etobicoke, Ontario, Canada) to control sprouting. Samples of 10 tubers (about 2 kg) were placed in mesh bags and stored at 9 °C in 0.1 m<sup>3</sup> ventilated aluminum chambers (constructed locally) during the trials. Each atmosphere was delivered to two chambers. Samples from half of the potato sources were assigned to each of a pair of chambers according to the statistical design. One (2002) or three (2003, 2004) samples from each of the assigned sources were placed in each chamber at the start of each trial. Relative humidity within the chambers was maintained at 95 to 99% throughout the trials.

### 2.2.2. Modified Atmosphere Treatments

In 2002, four 3-week trial repetitions were conducted consecutively, beginning in February, March, April and June. In each trial, modified atmosphere treatments of 21, 20.5 or 19% O<sub>2</sub> with 0, 0.5 or 2% CO<sub>2</sub> in a factorial design were maintained in the chambers for 3 weeks. In addition, unventilated (sealed) chambers simulated conditions in a poorly-ventilated potato storage building.

In 2003 and 2004, two 9-week trial repetitions were carried out in each year, i.e. January to March (January trial) and April to June (April trial). Modified atmospheres of 21 or 19% O<sub>2</sub> with 0 or 2% CO<sub>2</sub>, with or without the addition of 0.5 µL L<sup>-1</sup> ethylene gas, were applied in a factorial design. In addition, sealed chambers, with or without 0.5 µL L<sup>-1</sup> ethylene, were also



employed. In 2004, the 21% O<sub>2</sub> and the sealed without ethylene treatments were not included, due to space limitations.

In all trials during all years, chambers flushed with compressed air (medical-quality air, Praxair Ltd, Dartmouth, Nova Scotia, Canada) held control samples in all trials. Chambers flushed with medical air plus 0.5  $\mu\text{L L}^{-1}$  ethylene held ethylene check samples (2003 and 2004 only).

The desired atmospheres were achieved by flushing the chambers for 30 min every six h with selected gas mixtures supplied from compressed gas cylinders (Praxair Ltd, Dartmouth, Nova Scotia, Canada), delivered at 1.5-1.8 L min<sup>-1</sup> through 3.2 mm OD nylon tubing (Cole Parmer, Labcor Technical Sales Inc, Anjou, Quebec, Canada). The ventilation schedule was managed by a multi-channel timer (ChronTrol, Labcor Sales, Anjou, Quebec, Canada). In the chambers designated 0% CO<sub>2</sub>, small paper bags containing hydrated lime (Graymont (QC) Inc, Marbleton, Quebec, Canada) scrubbed the ambient and respired CO<sub>2</sub>. Atmospheres were checked several times per week using an O<sub>2</sub>, CO<sub>2</sub> gas analyser (ICA40, International Controlled Atmosphere, Tonbridge, Kent, UK in the 2002, 2003 and January 2004 trials; Checkpoint, PBI Dansensor America, Glen Rock, New Jersey, USA in the April 2004 trial). Chamber atmosphere compositions were corrected when necessary by additional flushing with the compressed gases. At 3-week intervals all chambers were opened briefly to remove samples for fry colour and sugar evaluations, which returned the chamber atmospheres to ambient concentrations. The modified atmospheres were subsequently re-established within several hours after the chambers were re-closed.

Ethylene was distributed to the chambers either from a separate cylinder through a gas distribution board built on-site (2003 January trial and throughout 2004) or included in the cylinder premix (2003 April trial). The ethylene concentration in the chambers was 0.5  $\mu\text{L L}^{-1} \pm 0.15 \mu\text{L L}^{-1}$ . Ethylene was monitored automatically using a Shimadzu 8A gas chromatograph (Mandel Scientific, Guelph, Ontario, Canada) with a PI-52-02A photo-ionization detector (HNU Systems, Newton, Massachusetts, USA), a 2 m stainless steel column hand-packed with 60/80 mesh alumina and nitrogen carrier gas, at 105 °C injector, 100 °C column and 120 °C detector temperatures. Atmosphere samples were drawn sequentially from the chambers by a sample-and-return system built on-site using a computer-

controlled sequencer (Sciometric Instruments, Ottawa, Ontario, Canada), and delivered to a six-port rotary valve (Valco Instruments, Houston, Texas, USA) on the GC injection port. Each chamber was sampled at 2 h intervals, 24 h a day throughout the trials. The ethylene concentration in the chambers was corrected when necessary by manual adjustment of needle valves (Nupro, Mandel Scientific, Guelph, Ontario, Canada) on the gas distribution board, except in the April 2003 trial when corrections were made by additional flushing with the premixed gases.

### 2.2.3. Evaluations

Potato fry colour and sugars were evaluated upon arrival at AFHRC in October of each year, at the start of each trial and after 3 (all years), 6 and 9 (2003 and 2004) weeks of treatment. One sample from each source × treatment combination was assessed at each evaluation date. To evaluate fry colour, a 5 cm disk was cut from the middle of an 8 mm-thick central longitudinal slice from each of the tubers in a sample. The disks were fried at 190 °C in canola oil (Maple Leaf Foods, Moncton, New Brunswick, Canada) for 2.5 min, drained for 1 min, and the excess oil absorbed on paper toweling. After cooling to room temperature, the colour of each disk was measured using an Agtron reflectance colourimeter (model M35-D, Agtron Inc, Sparks, Nevada, USA) on the green setting and calibrated using Agtron standard reflectance discs #00 (black) as zero and #56 (very pale grey) as 100% reflectance. Tuber sugars (sucrose, glucose and fructose concentrations) of freeze-dried sub-samples of tuber tissue were determined by an enzymatic assay adapted from the method of Viola and Davies (1992). Total reducing sugar content was calculated as glucose plus fructose.

### 2.2.4. Statistical design

The customized experimental design followed a replicated split-split plot design for the chambers; the sources formed the first split and the samples (pre-assigned to evaluation dates) formed the second split. A generalized ANOVA analysis using Genstat V statistical software (Genstat Committee 1993) partitioned the sources of variation according to the replication and randomization of the experimental effect. When significant differences ( $P \leq$

0.05) were identified, pairs of data were compared using the least significant difference (LSD). ANOVA analysis was also applied to the 2002 and 2003 data to contrast the factorial combinations of O<sub>2</sub> and CO<sub>2</sub> with the control, ethylene and sealed treatments.

### **2.3. Results and Discussion**

The initial fry colour and sugar content of the tubers at receipt in October and prior to the start of each trial varied among years, among sources within each year and among trial start dates within each year, reflecting differences attributable to production locations, growing seasons, maturity at harvest and the length of time in storage. For example, the mean initial fry colours upon arrival at AFHRC were 74.4, 65.2 and 80.8 Agtron percent reflectance units (ARu) in October 2001, 2002 and 2003, respectively. Mean initial reducing sugar concentrations were 9.0, 7.4 and 5.0 mg g<sup>-1</sup> dry weight (DW) in October 2001, 2002 and 2003, respectively. These were within the normal range of variability of 'Russet Burbank' grown in eastern Canada (Daniels-Lake and Prange, unpublished). Inclusion of multiple sources of potatoes and repetition of the trials within and among years ensured a robust evaluation of the effects of the applied treatments despite the variability. While the treatment responses attributable to year, trial start date or source varied somewhat in magnitude, the nature of responses to the treatments remained consistent among years and among trials within years. In 2002 and 2003 there were no differences between trials within each year. Therefore the data is presented as treatment means of all trials within a year, except for 2004 in which the January and April trial data are presented separately.

Within each trial, there was no statistical interaction between evaluation dates and treatments in either fry colour or sugar concentration. The main effects of treatment and evaluation date were significant in most trials; treatment differences are discussed at length below. Fry colour and sugar concentrations in potato tubers change gradually during storage, reflecting the natural progression of the tubers through maturation, dormancy, dormancy break and sprouting (Burton et al. 1992; Storey and Davies 1992). Although potato cultivars are genetically uniform, sugars and fry colour at harvest, and the rate of progression through these stages, may vary slightly from year to year due to the effects of location, weather and cultural conditions during

growth of the crop (Burton et al. 1992). External factors such as storage temperature can also affect fry colour and sugars, but these were carefully controlled during the trials. Although statistically significant differences between evaluation dates were identified in this work, the differences were small in comparison to treatment differences and were within the natural variability of the material. More importantly, there were no significant interactions between treatment and time (i.e. evaluation dates) in either fry colour or sugars. Therefore, in an effort to be succinct, differences attributable to time will not be discussed further.

In the sealed chambers, O<sub>2</sub> and CO<sub>2</sub> concentrations were slowly modified by the respiratory activity of the tubers. The extreme gas concentrations reached in these chambers, just before to opening at 3-week intervals to remove samples for evaluation, were about 16% O<sub>2</sub> and 4% CO<sub>2</sub>. Therefore the sealed chambers functioned as elevated CO<sub>2</sub>/depleted O<sub>2</sub> treatments.

In all trials conducted in 2002 and 2003, there were no differences in fry colour attributable to the main effects of either reduced O<sub>2</sub> or elevated CO<sub>2</sub> concentrations, or their interaction (Table 2.1). Tuber sugar concentrations (sucrose, glucose, fructose and total reducing sugars) were similarly unaffected (data not presented). In the January 2004 trial only, the mean fry colour of tubers exposed to the 19% O<sub>2</sub> plus 2% CO<sub>2</sub> atmosphere was about 5 ARu lower (i.e. darker colour) and reducing sugar concentration was ca. 1.5 mg g<sup>-1</sup> DW higher than in the control tubers (Tables 2.2, 2.3). In the April 2004 trial, there was no difference in fry colour or reducing sugars attributable to either the main effects or the interaction of reduced O<sub>2</sub> or elevated CO<sub>2</sub> (without ethylene).

In three of the four trials conducted during 2003 and 2004, fry colour was darker in tubers which were exposed to ethylene alone in comparison with control samples (Table 2.2). The change in fry colour attributable to ethylene alone was -8 to -17 ARu (i.e. darker colour) compared with controls in the 2003 and April 2004 trials. In the January 2004 trial, fry colour of tubers from the air plus ethylene check did not differ significantly from the air control. It should be noted, however, that fry colour values varied less than 5 ARu from highest to lowest in the January 2004 trial. This range was much smaller than observed in the 2003 and April 2004 trials, i.e. a range of 16 and 27 ARu,

**Table 2.1.** Fry colour of potatoes stored in atmospheres having modified oxygen and carbon dioxide concentrations. Values for 2002 are means of the 3-week evaluations in four consecutive 3-week trials × 8 potato sources per trial. Values for 2003 are means of 3-, 6- and 9-week evaluations in two consecutive 9-week trials × 4 sources per trial. Fry colour was measured with an Agtron reflectance colourimeter where 0 = black and 100 = very pale grey (almost white).

Treatment	Gas concentrations		Fry colour (Agtron percent reflectance)	
	O <sub>2</sub> (%)	CO <sub>2</sub> (%)	2002	2003
Air	ambient	ambient	70.9	62.8
Sealed	declining <sup>z</sup>	rising <sup>y</sup>	69.4	60.9
Modified atmospheres	21	0	70.7	62.8
		0.5	69.3	-- <sup>x</sup>
		2	69.3	62.7
	20.5	0	71.4	--
		0.5	70.9	--
		2	69.3	--
		19	0	71.6
		0.5	70.5	--
		2	68.8	62.0
	SE (P > 0.05) <sup>w</sup>			1.749 (n=32)

<sup>z</sup> O<sub>2</sub> concentration declined as tubers respired, to a minimum of about 16%

<sup>y</sup> CO<sub>2</sub> accumulated from tuber respiration, to a maximum of about 4%

<sup>x</sup> Treatment combination which was not applied in that year

<sup>w</sup> Differences among means were not significant in either year

respectively (Table 2.2). Such a lack of response to ethylene is somewhat unusual, but is not entirely unknown. During more than 14 years of ethylene research conducted on 'Russet Burbank' at AFHRC, a similar lack of fry colour response in mid-winter following ethylene exposure has been observed in some years (Daniels-Lake and Prange, unpublished data). It is attributable to the growing season and field location, specifically the maturity of the tubers which influences sugar content at harvest and during subsequent storage

(Burton et al. 1992). In some cultivars, fry colour is actually improved by exposure to ethylene during cold storage (Haard 1971).

**Table 2.2.** Fry colour of potatoes stored in atmospheres having modified oxygen and carbon dioxide concentrations, with or without 0.5  $\mu\text{L L}^{-1}$  ethylene. Fry colour measurement as in Table 2.1. Values for 2003 calculated as in Table 2.1. Data for the January and April 2004 trials are presented separately; values are means of the 3-, 6- and 9-week evaluations  $\times$  4 sources per trial.

Treatment		Fry colour (Agtron percent reflectance)		
		2003	2004	
Atmosphere	Ethylene	January and April	January	April
Air	–	62.8 a <sup>z</sup>	76.2 a	82.9 a
0% CO <sub>2</sub> <sup>y</sup>	–	62.0 a	74.8 a,b	85.0 a
2% CO <sub>2</sub> <sup>y</sup>	–	62.4 a	71.5 c	82.7 a
Sealed	–	60.9 a	-- <sup>x</sup>	--
Air	+	55.2 b	73.4 a,b,c	67.0 b
0% CO <sub>2</sub> <sup>y</sup>	+	56.0 b	72.9 b,c	66.5 b,c
2% CO <sub>2</sub> <sup>y</sup>	+	48.5 c	72.4 b,c	61.6 b,c
Sealed	+	46.8 c	71.3 c	57.9 c
SE (P < 0.05)		1.045 (n=24)	0.860 (n=12)	2.598 (n=12)

<sup>z</sup> Means within a column which are followed by the same letter are not significantly different (P < 0.05).

<sup>y</sup> Mean of results from 19 and 21% oxygen atmospheres in 2003; 19% oxygen in 2004.

<sup>x</sup> Treatment combination which was not applied in that year.

Interestingly, in the 2003 and April 2004 trials the tubers which were exposed to both ethylene and elevated CO<sub>2</sub> had fry colour 5 to 8 ARu lower (i.e. fry colour was darker) than with ethylene alone, or 14 to 25 ARu lower than the control tubers stored in air without ethylene (Table 2.2). For example, in the April 2004 trial the fry colour of tubers from the sealed plus ethylene treatment was darker than tubers exposed to the air plus ethylene check, CO<sub>2</sub> or the air control (58, 67, 83 and 83 ARu, respectively). This suggests an

interaction between the two gases which affected potato fry colour. Such an interaction has not been previously described.

**Table 2.3.** Total reducing sugars (glucose + fructose) in potato tubers stored in atmospheres having modified oxygen and carbon dioxide concentrations, with or without 0.5 µL L<sup>-1</sup> ethylene. Values calculated as in Table 2.2

Treatment		Total reducing sugars (mg g <sup>-1</sup> DW)		
		2003	2004	
Atmosphere	Ethylene	January and April	January	April
Air	–	9.0 a <sup>z</sup>	5.7 a	4.0 a
0% CO <sub>2</sub> <sup>y</sup>	–	9.1 a	5.7 a	3.8 a
2% CO <sub>2</sub> <sup>y</sup>	–	8.9 a	7.3 b	3.7 a
Sealed	–	9.6 a	-- <sup>x</sup>	--
Air	+	13.0 b	7.2 b	7.8 b
0% CO <sub>2</sub> <sup>y</sup>	+	12.1 b	7.9 b	8.6 b
2% CO <sub>2</sub> <sup>y</sup>	+	15.4 c	7.6 b	9.3 b,c
Sealed	+	17.0 c	7.9 b	10.6 c
SE (P < 0.05)		0.437 (n = 24)	0.320 (n = 12)	0.670 (n = 12)

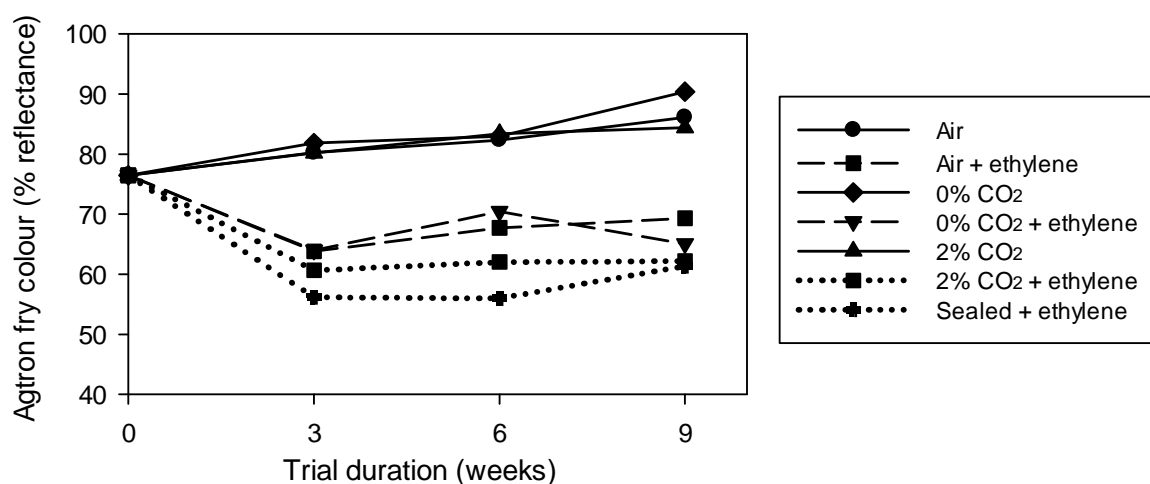
<sup>z</sup> Means within a column which are followed by the same letter are not significantly different (P < 0.05)

<sup>y</sup> Mean of 19 and 21% oxygen atmospheres in 2003; 19% oxygen in 2004

<sup>x</sup> Treatment combination which was not applied in that year

The combined effect of ethylene and CO<sub>2</sub> was particularly evident when the values at each evaluation were considered. Representative fry colour data from the April 2004 trial are provided to illustrate this (Figure 2.1). Separation of the data into three groups is apparent, i.e.: 1) those treatments which did not receive ethylene, with or without elevated CO<sub>2</sub>, which had the lightest fry colour; 2) the ethylene-only treatments, which had darker fry colour than the first group; and 3) those treatments which received both elevated CO<sub>2</sub> and ethylene gas (including the sealed plus ethylene treatment), which had the darkest fry colour within the trial. Although elevated CO<sub>2</sub> alone did not darken

fry colour, the darkening of fry colour in response to ethylene was more severe when CO<sub>2</sub> was also present. Separation of the treatments into these groups was apparent at the first evaluation date (3 weeks after the start of the trial) and remained consistent to the end of the trial (Figure 2.1). The main effects of treatment and time were significant ( $P = 0.001$  and  $0.003$ , respectively). Treatment effects were as previously discussed. Mean fry colour changed slightly during the trial, i.e. 70, 72 and 74 ARu at 3, 6 and 9 weeks, respectively. There was no statistical interaction between these factors, which indicated that the treatment effects were not influenced by the duration of storage, within the time-frame studied.



**Figure 2.1.** Fry colour of potatoes stored from April to June 2004 in atmospheres having modified oxygen and carbon dioxide concentrations, with or without  $0.5 \mu\text{L L}^{-1}$  ethylene. Significant effects: Treatment (SE = 2.598,  $P = 0.001$ ); Time (SE = 0.882,  $P = 0.003$ ); Treatment  $\times$  Time interaction not significant.

Tuber sugars (sucrose, glucose and fructose) in the 2003 and 2004 trials were influenced by ethylene and CO<sub>2</sub> in a manner similar to the effect on fry colour, i.e. sugar values were increased in treatments where fry colour darkened and vice versa (Table 2.3). Since fry colour depends primarily on the reducing sugar content of the tubers and sucrose has little direct effect on colour at the frying temperature used (Burton et al. 1992), further discussion of sugars will focus on total reducing sugars, i.e. glucose plus fructose.

The combined effect of ethylene and CO<sub>2</sub> was also evident in reducing



sugar content in the 2003 and April 2004 trials (Table 2.3). Exposure to CO<sub>2</sub> alone had little or no effect upon reducing sugar content, while exposure to ethylene alone led to increased reducing sugars. Reducing sugar concentrations were still higher in tubers exposed to both ethylene and CO<sub>2</sub>, although in the April 2004 trial only tubers from the sealed plus ethylene treatment had significantly higher reducing sugars than tubers from the ethylene without CO<sub>2</sub> treatment. In the January 2004 trial, reducing sugar concentrations were higher in tubers exposed to CO<sub>2</sub>, ethylene or both, compared with the controls (Table 2.3). As observed in regard to fry colour, the range of reducing sugar concentrations was smaller in the January 2004 trial than in the 2003 or April 2004 trials (2.2, 8.1 and 6.9 mg g<sup>-1</sup> DW, respectively). The minimal response to ethylene is likely attributable to the differences in maturity of the tubers, as discussed previously.

Potato tubers naturally produce ethylene at a low rate, i.e. 0.0008 to 0.015 μL kg<sup>-1</sup> h<sup>-1</sup> from intact tubers (McGlasson 1969; Creech et al. 1973; Korableva and Ladyzhenskaya 1995). The rate of production increases 2 to 25 fold in response to chilling, warming, sprouting, injury, infection by some pathogens and exposure to external ethylene (Poapst et al. 1968; McGlasson 1969; Creech et al. 1973; Korableva and Ladyzhenskaya 1995; Arshad and Frankenberger 2002a). Poapst et al. (1968) found the internal ethylene concentration of potato tubers to be 0.7 μg kg<sup>-1</sup> FW. Many pathogens which infect potato tubers are known to produce ethylene (summarized in Arshad and Frankenberger 2002b). Furthermore, commercial application of the chlorpropham sprout inhibitor by thermal fogging produces ethylene gas which often enters the storage atmosphere with the chlorpropham fog (Duncan 1999; Duncan and Kraish 1999). Stored potatoes may therefore be unintentionally exposed to ethylene gas. In fact, significant concentrations of ethylene (up to 40 μL L<sup>-1</sup>) in commercial potato stores have been recorded (Duncan 1999; A. Briddon, personal communication). Low concentrations of ethylene (≥ 0.4 μL L<sup>-1</sup>) increase reducing sugar concentrations and darken fry colour in a concentration-dependent manner (Prange et al. 1998; Daniels-Lake et al. 2005), which varies among cultivars (Haard 1971; Prange and Daniels-Lake, unpublished data). The ethylene concentration applied in this research (0.5 μL L<sup>-1</sup>) was well within the range of concentrations possible within a commercial storage facility. It was also likely to have had a small but quantifiable influence upon fry colour.

An interaction of ethylene and CO<sub>2</sub> could explain in part the apparently contradictory findings of various published and unpublished research into the effects of CO<sub>2</sub> alone on potato fry colour. It is possible under appropriate conditions, e.g. reduced ventilation and sufficient disease activity, that CO<sub>2</sub> from tuber respiration and ethylene from pathogens and stressed tubers could accumulate in the potato pile to concentrations which would interact to affect fry colour.

The concentration of ethylene within a potato store can be reduced by several means, such as ventilation, scrubbing with absorbents (e.g. activated charcoal) or oxidizers (e.g. potassium permanganate, ozone, *uv* light), or hypobaric conditions to prevent accumulation to physiologically active concentrations (Knee et al. 1985; Sherman 1985; Kader 1992; Reid 1995). Recent work by Prange et al. (2005) using the ethylene-action inhibitor, 1-methylcyclopropene (1-MCP), to prevent darkening of fry colour resulting from ethylene sprout inhibitor leads one to hypothesize that 1-MCP may prevent the darkening described in this paper by blocking the ethylene receptors. Work is currently underway to investigate this hypothesis. CO<sub>2</sub> concentrations in commercial potato storage buildings can be reduced by ventilation or lime scrubbers (Burton et al. 1992; Kader 1992). However, the importance of adequate ventilation in potato storage buildings is re-emphasized, since ventilation is likely the least expensive and most effective method of reducing both CO<sub>2</sub> and ethylene concentrations in potato storage atmospheres.

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## Chapter 3

### **1-Methylcyclopropene Counteracts Fry Colour Darkening Attributable to Carbon Dioxide and Ethylene Interaction \***

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#### **Abstract**

The fry colour of potatoes (*Solanum tuberosum* L.) stored for processing remains an important quality characteristic that can be affected by many factors, including ethylene gas from various sources and the interaction of very low concentrations of ethylene gas ( $< 1\mu\text{L L}^{-1}$ ) and accumulated  $\text{CO}_2$ . Because previous studies show that pre-treatment with 1-methylcyclopropene (1-MCP) can substantially reduce fry colour darkening attributable to applied ethylene, we hypothesized that 1-MCP could also reduce fry colour darkening attributable to the interaction of ethylene and  $\text{CO}_2$ . Trials were conducted over two storage seasons, using 'Russet Burbank' tubers, either untreated or treated with  $0.5\mu\text{L L}^{-1}$  ethylene gas  $\pm 2\%$   $\text{CO}_2$  and  $\pm$  1-MCP. Tubers exposed to ethylene gas had darker fry colour than untreated tubers, whereas the fry colour of tubers exposed to ethylene plus  $\text{CO}_2$  was darker still. However, the fry colour of tubers pre-treated with 1-MCP was as light as that of the untreated tubers. This provides a potential new tool for the potato industry to manage potato fry colour of stored processing potatoes.

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### 3.1. Introduction

Approximately half of the potatoes (*Solanum tuberosum* L.) grown in North America are consumed as French fries or potato chips. For the processors who make these products, fry colour is a vitally important quality characteristic. The preferred light fry colour depends upon low reducing sugar concentrations in the raw tubers (Mazza 1983; Burton et al. 1992). Although researchers and industry experts have long believed that elevated CO<sub>2</sub> in the storage atmosphere results in increased reducing sugars and hence darkening of fry colour, it has recently been shown that this is true only when a trace concentration of ethylene gas is also present (Daniels-Lake et al. 2005b).

Ethylene gas can increase reducing sugar concentrations in potato tubers, leading to darkening of fry colour (Daniels-Lake et al. 2005a; Haard 1971; Prange et al. 1998). The ethylene blocking compound 1-methylcyclopropene (1-MCP) has been shown to prevent darkening of potato fry colour attributable to ethylene (Prange et al. 2005). It was hypothesized that 1-MCP may prevent darkening attributable to the interaction of ethylene and CO<sub>2</sub>, and trials were conducted to test this hypothesis.

### 3.2. Materials and Methods

Trials were conducted during two consecutive years, i.e. January to June 2004 and December 2004 to June 2005, using commercially-grown 'Russet Burbank' potatoes harvested in mid-October of the preceding growing season. Each year, the potato tubers were sourced from four different commercial potato growers located in eastern Canada. After arrival at the lab site, the potatoes were stored for four weeks at 13 °C to permit suberization and wound healing, and then gradually cooled to 9 °C over four weeks and dipped in early December in a 1% a.i. water emulsion of chlorpropham (Sprout-Nip EC, isopropyl n-(3-chlorophenyl) carbamate, 320 g L<sup>-1</sup> a.i., Stanchem Inc., Etobicoke, Ontario, Canada; CIPC) to control sprouting. Two 9-week trial repetitions were conducted consecutively in each year, the first from January to March and the second from April to June. In the 2004 to 2005 storage season, half of the samples were treated and evaluated 3 weeks earlier than the remaining half in each trial.



Samples of 10 tubers (approximately 2 kg) were placed in mesh bags and stored at 9 °C in 0.1 m<sup>3</sup> sealed aluminum chambers during the trials. Each chamber held six samples at the start of each trial and each treatment was applied to two chambers. Samples from two of the potato sources were assigned to one of the pair of chambers receiving the same treatment, according to the statistical design. Relative humidity within the chambers was maintained at 95 to 99% throughout the trials. The chambers were housed within a refrigerated cold-room which maintained the desired temperature  $\pm$  0.3 °C in all chambers throughout the trials.

Storage chamber atmospheres were modified by flushing with compressed gases (Praxair Inc, Dartmouth, Nova Scotia, Canada) to achieve concentrations of 19% O<sub>2</sub>, with or without 2% CO<sub>2</sub> and 0.5  $\mu$ L L<sup>-1</sup> ethylene gas in a factorial arrangement. Chamber atmospheres were refreshed with appropriate compressed gas mixtures four times per day, to maintain the desired gas concentrations. Ambient and respired CO<sub>2</sub> was scrubbed from the 0% CO<sub>2</sub> chamber atmospheres by placing a paper sack containing approximately 0.5 kg of hydrated lime [Ca(OH)<sub>2</sub>; Graymont (QC) Inc., Boucherville, Quebec, Canada] inside the appropriate chambers. To simulate conditions in a poorly-ventilated potato storage building, chambers that were not flushed between evaluation dates were used, with 0.5  $\mu$ L L<sup>-1</sup> ethylene gas added to their atmosphere. The atmosphere of the unventilated chambers was gradually modified by cellular respiration of the tubers (depleted O<sub>2</sub> and increased CO<sub>2</sub>), but returned to ambient conditions at 3-week intervals when the chambers were opened to remove samples for evaluation. Ethylene gas was reintroduced after the chambers were resealed. Control chambers were flushed with medical-grade compressed air. In 2004, lime was used to scrub CO<sub>2</sub> from the control chambers, but in the 2004 to 2005 trials the CO<sub>2</sub> was not scrubbed from the control chambers. The 1-MCP (SmartFresh™, AgroFresh Inc., Springhouse, Pennsylvania, USA), was applied inside the storage chambers just prior to the start of ethylene and CO<sub>2</sub> delivery, at the rate specified on the product label (nominally 0.9  $\mu$ L L<sup>-1</sup>) using the method described in Prange et al. (2005). The 12 treatments applied in all trials are summarized in Table 3.1.

The gas delivery apparatus was as described in Daniels-Lake et al. (2005b). The concentrations of O<sub>2</sub> and CO<sub>2</sub> were measured several times per week with a handheld gas monitor (CheckPoint, PBI Dansensor America, Glen

Rock, New Jersey, USA), and gas delivery rates were adjusted manually as needed to maintain desired gas concentrations. Ethylene concentrations were monitored automatically as described in Daniels-Lake et al. (2005b).

**Table 3.1.** Factors that comprised the treatments.

Treatment name	Composition of chamber atmosphere				pre-treated with 1-MCP <sup>z</sup> ?
	was CO <sub>2</sub> scrubbed?	O <sub>2</sub> (%)	CO <sub>2</sub> (%)	ethylene (μL L <sup>-1</sup> )	
Control	2004: yes 2004-05: no	ambient	2004: 0 2004-05: 0-0.3	0	no
Ethylene	yes	ambient	0	0.5	no
Unventilated <sup>y</sup> + Ethylene	no	declining <sup>x</sup>	rising <sup>w</sup>	0.5	no
Unventilated + Ethylene + 1-MCP	no	declining	rising	0.5	yes
reduced O <sub>2</sub>	yes	19	0	0	no
reduced O <sub>2</sub> + CO <sub>2</sub>	no	19	2	0	no
reduced O <sub>2</sub> + 1-MCP	yes	19	0	0	yes
reduced O <sub>2</sub> + CO <sub>2</sub> + 1-MCP	no	19	2	0	yes
reduced O <sub>2</sub> + Eth <sup>y</sup>	yes	19	0	0.5	no
reduced O <sub>2</sub> + CO <sub>2</sub> + Eth	no	19	2	0.5	no
reduced O <sub>2</sub> + Eth + 1-MCP	yes	19	0	0.5	no
reduced O <sub>2</sub> + CO <sub>2</sub> + Eth + 1-MCP	no	19	2	0.5	yes

<sup>z</sup> 1-methylcyclopropene, an ethylene blocking compound

<sup>y</sup> Atmosphere in the sealed chambers was gradually modified by cellular respiration of the tubers between evaluations. At each evaluation date the chambers were opened briefly, which allowed the chamber atmospheres to return to ambient. Ethylene was reintroduced into the chambers after they were re-sealed.

<sup>x</sup> O<sub>2</sub> declined to a minimum of approximately 16% in these treatments, due to tuber respiration.

<sup>w</sup> CO<sub>2</sub> from tuber respiration accumulated to a maximum of approximately 4% in these treatments.

<sup>v</sup> Ethylene gas

Upon arrival in October of each year and again at the start of each trial, three samples of tubers from each source were evaluated. After 3, 6 and 9 weeks in each trial, one sample from each source × treatment combination was evaluated. Fry colour was evaluated at each date, using the methods described in Daniels-Lake et al. (2005b).

The customized experimental design was a replicated split-split plot. The main plots were the chambers; the sub-plot was tuber source, and sample (pre-assigned to evaluation dates) was the sub-sub-plot. Data were analysed by a generalized analysis of variance using Genstat V statistical software (Genstat Committee 1993), which partitioned the sources of variation according to the replication and randomization of the design. When significant differences ( $P \leq 0.05$ ) were identified, data were compared using the least significant difference.

### **3.3. Results and Discussion**

‘Russet Burbank’ is recognized as a relatively long dormancy cultivar. Thus tubers stored at 8 to 10 °C without sprout inhibitors normally begin to sprout in late February to mid-March. Observation of the residual tubers held at 9 °C in common storage confirmed this to be true of the material used in these trials (data not presented). In view of the timing of these trials, it is reasonable to assume that in both years the tubers assessed in trials that started in December or January were still dormant (designated the dormant trials), whereas tubers in the trials that started in March were no longer dormant (designated the non-dormant trials).

Although the treatment and storage of half of the samples started three weeks earlier than the second half in 2004 to 2005, statistical comparison indicated that they were not significantly different from each other within the dormant trial; similarly the halves within the non-dormant trial were not different (data not presented). Therefore, the data were treated as replicates within each trial.

In general, fry colour was lighter in 2003 to 2004 than in 2004 to 2005 (75.1 vs. 70.5 Agtron percent reflectance units (ARu), respectively). Fry colour was slightly darker in the dormant trials than in the non-dormant trials (71.7 vs.

73.9 ARu, respectively). In addition, the range of observed fry colours was much wider in the non-dormant trials than in the dormant trials (26.1 vs. 8.7 ARu, respectively). This suggests that dormant and non-dormant tubers responded differently to the applied treatments, particularly in treatments including ethylene (Table 3.2). Since there were no significant treatment  $\times$  year or treatment  $\times$  year  $\times$  evaluation date interactions, only the treatment  $\times$  trial results are discussed.

**Table 3.2.** Fry colour of potatoes stored for nine weeks with or without ethylene gas, elevated CO<sub>2</sub> and/or 1-methylcyclopropene.

Treatment <sup>z</sup>	Fry colour (Agtron percent reflectance)	
	Dormant tubers	Non-dormant tubers
Control	74.7	79.2
Ethylene	70.6	66.1
Unventilated + Ethylene	66.0	56.0
Unventilated + Ethylene + 1-MCP	73.9	78.5
reduced O <sub>2</sub>	73.7	82.1
reduced O <sub>2</sub> + CO <sub>2</sub>	70.2	78.9
reduced O <sub>2</sub> + 1-MCP	73.9	79.7
reduced O <sub>2</sub> + CO <sub>2</sub> + 1-MCP	71.6	79.1
reduced O <sub>2</sub> + Ethylene	70.2	67.8
reduced O <sub>2</sub> + CO <sub>2</sub> + Ethylene	68.5	60.8
reduced O <sub>2</sub> + Ethylene + 1-MCP	74.0	80.8
reduced O <sub>2</sub> + CO <sub>2</sub> + Ethylene + 1-MCP	72.7	77.9
F-probability		< 0.001
estimated standard error		2.099
Least significant difference, 5% confidence level		5.891

<sup>z</sup> Treatments as described in Table 3.1

Previous investigation showed that fry colour was unaffected by reduction of the O<sub>2</sub> concentration in the storage atmosphere to 19% nor by

increasing the CO<sub>2</sub> concentration to 2%, alone or in combination (Daniels-Lake et al. 2005b). Similar results were observed in these trials (Table 3.2). Scrubbing out the CO<sub>2</sub> also had no significant effect on tuber fry colour (data not presented).

In both the dormant and non-dormant trials, potatoes stored with ethylene but without CO<sub>2</sub> had darker fry colour than the controls, although the difference was not significant in the dormant trials (Table 3.2). This is consistent with previous findings (Daniels-Lake et al. 2005a) which demonstrated that even low concentrations of ethylene (< 1 µL L<sup>-1</sup>) can darken fry colour. In contrast, the fry colour of tubers stored with ethylene and CO<sub>2</sub> together was darker than the controls in both trials (Table 3.2). In the non-dormant trials, the fry colour of tubers stored with ethylene and CO<sub>2</sub> together was also darker than with ethylene only, as shown previously (Daniels-Lake et al. 2005b).

When 1-MCP was applied to tubers before exposure to the modified atmosphere treatments, the effects of both ethylene and ethylene plus CO<sub>2</sub> on fry colour were reduced (Table 3.2). In both the dormant and non-dormant trials, the fry colour of tubers exposed to 1-MCP before treatment with ethylene plus CO<sub>2</sub> was as light as the fry colour of control tubers. In the non-dormant trials, and in the unventilated treatment in the dormant trials, fry colour of tubers treated with 1-MCP before exposure to ethylene plus CO<sub>2</sub> was lighter than without 1-MCP pre-treatment (Table 3.2).

These results support the hypothesis that the ethylene-blocking compound 1-MCP can protect stored potato tubers from fry colour darkening attributable to the interaction of ethylene and CO<sub>2</sub>. However, research also suggests some variability among cultivars in the strength and duration of the protective effect of 1-MCP (Daniels-Lake et al. unpublished data). Additional work is warranted to further elucidate the responses of important cultivars. Nonetheless, 1-MCP pre-treatment is a potential new tool to help the potato industry retain good fry colour during long-term storage, if registration for use on this commodity can be obtained.

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## Chapter 4

# The Interaction Effect of Carbon Dioxide and Ethylene in the Storage Atmosphere on Potato Fry Colour is Dose-Related\*

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### Abstract

Previous studies have shown that the fry colour of stored potatoes (*Solanum tuberosum* L.) can be negatively affected by an interaction between elevated CO<sub>2</sub> (2%) and ethylene gas (0.5 µL L<sup>-1</sup>) from various sources. Two consecutive trials were conducted during each of two storage seasons (2006 and 2007), to study the effects of varying concentrations of these two gases. In each year, CO<sub>2</sub> at 0, 0.5, 1.0 or 2.0%, plus 0, 0.25 or 0.5 µL L<sup>-1</sup> ethylene was applied in a factorial design to Russet Burbank tubers for 9 weeks. Trials that began in January 2006 and January 2007 comprised the dormant-tuber experiment; trials that began in April 2006 and April 2007 comprised the non-dormant-tuber experiment. Fry colour of the tubers was evaluated at the start of each trial and thereafter at intervals of 3 weeks. In all trials, when tubers were exposed to different concentrations of CO<sub>2</sub> but without ethylene, fry colour was the same as in untreated controls. When only ethylene was applied, the fry colour was 7 to 22 Agtron percent reflectance units darker than the controls. In the non-dormant-tuber experiment the darkening resulting from ethylene was dose-related, in agreement with previous research. When the tubers were exposed to both CO<sub>2</sub> and ethylene, dose-related responses to both gases were observed in the non-dormant-tuber experiment, i.e. fry colour was darker with an increase in either CO<sub>2</sub> or ethylene when both gases were present. Neither the dose-response to ethylene nor the interaction between ethylene and CO<sub>2</sub> was statistically significant in the dormant-tuber experiment. In both experiments the darkest colour was observed when both gases were present at the highest concentrations. A dose-response of potato fry colour to

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CO<sub>2</sub> in the presence of ethylene has not been reported previously.

#### 4.1. Introduction

The importance of light fry colour to the potato (*Solanum tuberosum* L.) processing industry cannot be overstated. Because most of the North American potato crop must be stored for many months between harvest and processing, it is important to maintain the frying quality of the stored tubers throughout their storage term. Fry colour, which is directly dependent on the concentration of reducing sugars in the tuber tissue (Burton et al. 1992; Mazza 1983), is one of the most important quality attributes of processing tubers. It can be affected by various factors during the storage term.

During long-term storage, the CO<sub>2</sub> concentration may increase considerably in the storage atmosphere. The major sources of CO<sub>2</sub> are tuber respiration and exhaust from internal combustion engines. Reported peak CO<sub>2</sub> concentrations in ventilated potato stores range from 0.6 to 14% (Mazza and Siemens 1990; Schaper et al. 1993). It is recommended that the CO<sub>2</sub> concentration should be maintained below 1% in potato storage atmospheres (Rastovski 1987; Schaper et al. 1993). The reported effects of elevated CO<sub>2</sub> on tuber fry colour vary widely. Some researchers have demonstrated that 2 to 5% CO<sub>2</sub> prevents increases in tuber sugars or does not darken fry colour (Denny and Thornton 1940; Blankson 1988; Daniels-Lake et al. 2005b). Others have shown that 0.5 to 15% CO<sub>2</sub> increases reducing sugar concentrations and/or darkens fry colour compared with tubers stored at ambient concentrations of CO<sub>2</sub> (Mazza and Siemens 1990; Schouten 1993; Khanbari and Thompson 1994, 1996). Season-long monitoring of several commercial stores revealed no correlation between the measured CO<sub>2</sub> concentrations and observed fry colour changes (J Walsh, personal communication).

In contrast, ethylene gas in the storage atmosphere is one of several factors that are known to cause darkening of potato fry colour during storage (Denny and Thornton 1940; Prange et al. 1998; Duncan 1999; Daniels-Lake et al. 2005a). The effect is dose-dependent, i.e. darkening increases as the concentration rises, with saturation of the effect in the range of 1 to 10 µL L<sup>-1</sup> depending on cultivar (ethylene concentrations in µL L<sup>-1</sup> can be approximated



as parts per million, volume per volume) (Daniels-Lake et al. 2005a). Significant sources of ethylene in the storage atmosphere include pathogens, engine exhaust from equipment or vehicles, climacteric fruit stored nearby and as a by-product of chlorpropham sprout inhibitor application (Duncan 1999). Potato tubers naturally produce small quantities of ethylene; sprouting and stresses such as disease and injury increase the production rate (Poapst et al. 1968; McGlasson 1969; Creech et al. 1973; Korableva and Ladyzhenskaya 1995; Suttle 2003). If ventilation is restricted within the pile, or reduced for operational reasons, both ethylene and CO<sub>2</sub> gases can accumulate in the potato storage atmosphere. Apart from instances in which ethylene gas is used as a sprout suppressant or is a contaminant from chlorpropham application, there is little information on actual concentrations of ethylene gas in commercial potato storage atmospheres. Preliminary investigations suggest that ethylene concentrations of 0.1 to 2  $\mu\text{L L}^{-1}$  are not unusual (B Daniels-Lake unpublished data).

Although up to 2% CO<sub>2</sub> has little effect on fry colour by itself, when combined with ethylene the darkening effect resulting from ethylene is increased (Daniels-Lake et al. 2005b, 2008). Storage operators can reduce the risk to their stored potatoes from this potential interaction by ventilating to keep the concentrations of both gases low throughout the storage term. However, there is no published information regarding threshold concentrations, i.e. how low the concentrations of these two gases should be, to prevent their interaction affecting the fry colour of the stored tubers.

Studies were initiated at the potato postharvest physiology facilities at Agriculture and Agri-Food Canada's Atlantic Food and Horticulture Research Centre (AFHRC) in Kentville, Nova Scotia, Canada, to evaluate the effect on potato fry colour of combinations of various concentrations of CO<sub>2</sub> and ethylene gas. One of the goals of this work was to search for threshold concentrations below which the combination of these two gases does not darken potato fry colour.

## **4.2. Materials and Methods**

Trials were conducted from January to June during two consecutive years, 2006 and 2007. In each year, commercially-grown Russet Burbank

potatoes harvested in mid-October were obtained soon after harvest from four different commercial potato growers located in eastern Canada. To permit suberization and wound healing, the tubers were held for four weeks at 13 °C, and then cooled at a rate of 1 °C per week to 9 °C. All tubers used in the trials were dipped in early December in a 1% a.i. water emulsion of chlorpropham (Sprout-Nip EC, isopropyl n-(3-chlorophenyl) carbamate, 320 g L<sup>-1</sup> a.i., Stanchem Inc., Etobicoke, Ontario, Canada; CIPC) sprout inhibitor, and allowed to air-dry. Because previous studies have suggested that the response to the CO<sub>2</sub> and ethylene interaction may be stronger in non-dormant than in dormant tubers (Daniels-Lake et al. 2005b, 2008), the trials were divided into two experiments to separately evaluate tubers in these physiologically distinct states. In each year, two consecutive 9-week trials were conducted, i.e. 10 January to 21 March and 18 April to 20 June in 2006, and 16 January to 19 March and 17 April to 19 June in 2007. The two trials that started in January comprised the dormant experiment, and the two trials that started in April comprised the non-dormant experiment. Only sprout-inhibited tubers were included in the trials, to retain the focus on the effects of CO<sub>2</sub> and ethylene on fry colour. Additional tubers from the same sources but which had not been treated with CIPC were stored in common storage at 9 °C until June of each year, and were monitored for sprouting as an indicator of the dormancy status of the material used in the trials.

Samples weighing approximately 2 kg (10 tubers) were placed in mesh bags and stored during the trials in 0.1 m<sup>3</sup> sealed aluminum chambers (constructed locally). Two sets of 12 chambers were used; each gas treatment was delivered to one chamber in each set. Two of the four source-lots of potatoes were assigned to each set of chambers. At the start of each trial each chamber held six samples (three samples from each of two sources), pre-designated for specific evaluation dates. The chambers were placed in a refrigerated cold-room which maintained the temperature at 9 ± 0.3 °C.

The chamber atmospheres were modified with medical-grade compressed air (Praxair Inc, Dartmouth, Nova Scotia, Canada) plus 0, 0.5, 1 or 2% CO<sub>2</sub> (Praxair Inc) and 0, 0.25 or 0.5 µL L<sup>-1</sup> ethylene gas (Praxair Inc) in a factorial arrangement. Three times per day the chamber atmospheres were flushed for 60 min at approximately 2 L min<sup>-1</sup> with appropriate compressed gas mixtures to maintain the desired gas concentrations and replenish consumed O<sub>2</sub>. The gas delivery apparatus was as described in Daniels-Lake et al.

(2005b). Control chambers (0 CO<sub>2</sub> and 0 ethylene) were flushed with unamended compressed air. A paper sack containing approximately 0.5 kg of hydrated lime [Ca(OH)<sub>2</sub>; Graymont (QC) Inc., Boucherville, Quebec, Canada] was placed inside the 0 CO<sub>2</sub> chambers to scrub ambient and respired CO<sub>2</sub>.

O<sub>2</sub> and CO<sub>2</sub> concentrations were measured several times per week, using a handheld gas monitor (CheckPoint, PBI Dansensor America, Glen Rock, New Jersey, USA). Ethylene concentrations were continuously monitored using an automated system as described in Daniels-Lake et al. (2005b). Gas delivery flow-rates were adjusted manually as needed to maintain the desired gas concentrations in the chambers. Oxygen in the chamber atmospheres was consistently 20% or higher. Carbon dioxide and ethylene were maintained within 10% and 20%, respectively, of the desired treatment concentrations.

An open plastic jar, 6 cm in diameter and containing approximately 300 mL of distilled water, was placed inside each chamber to help maintain high humidity. The relative humidity (RH) inside the chambers was checked several times per week, and remained at 95 to 99% RH.

The fry colour of three samples of 10 tubers from each source was evaluated in early November of each year (shortly after arrival at AFHRC) and at the start of each trial in January or April. The fry colour of one 10-tuber sample from each source × treatment combination (4 sources × 12 treatments) was evaluated at 3, 6 and 9 weeks during each trial, using the methods described in Daniels-Lake et al. (2005b). Fry colour scores in Agtron percent reflectance units (ARu) were based on a scale of 0 to 100, representing the calibration range from black to very pale grey, respectively.

The customized experimental design was a replicated two-way factorial with a split plot arrangement. The main plot was treatment (CO<sub>2</sub> × ethylene) and the sub-plot was evaluation date. Experiments were replicated physically by using potatoes of the same cultivar from four separate growers each year, and replicated in time by conducting the trials in two different years. The data for both years were combined for statistical analysis by analysis of variance, using Genstat statistical software (Genstat Committee 2008). Orthogonal and polynomial contrasts were used to determine differences across treatments, levels of treatments and evaluation times. This provided insight into the

pattern of the responses, in addition to identifying differences between specific treatments. In all analyses, differences were considered significant if  $P \leq 0.05$ .

### 4.3. Results and Discussion

Within each year, all tubers used in both trials had been treated with CIPC sprout inhibitor on the same date; these tubers did not sprout during either trial. In January of each trial year, the extra tubers which had not been treated with CIPC were not yet sprouting and therefore considered to be still dormant. In contrast, in April of each year dormancy had ended and these tubers were sprouting vigorously (data not presented). This reflects the long dormancy of the Russet Burbank cultivar.

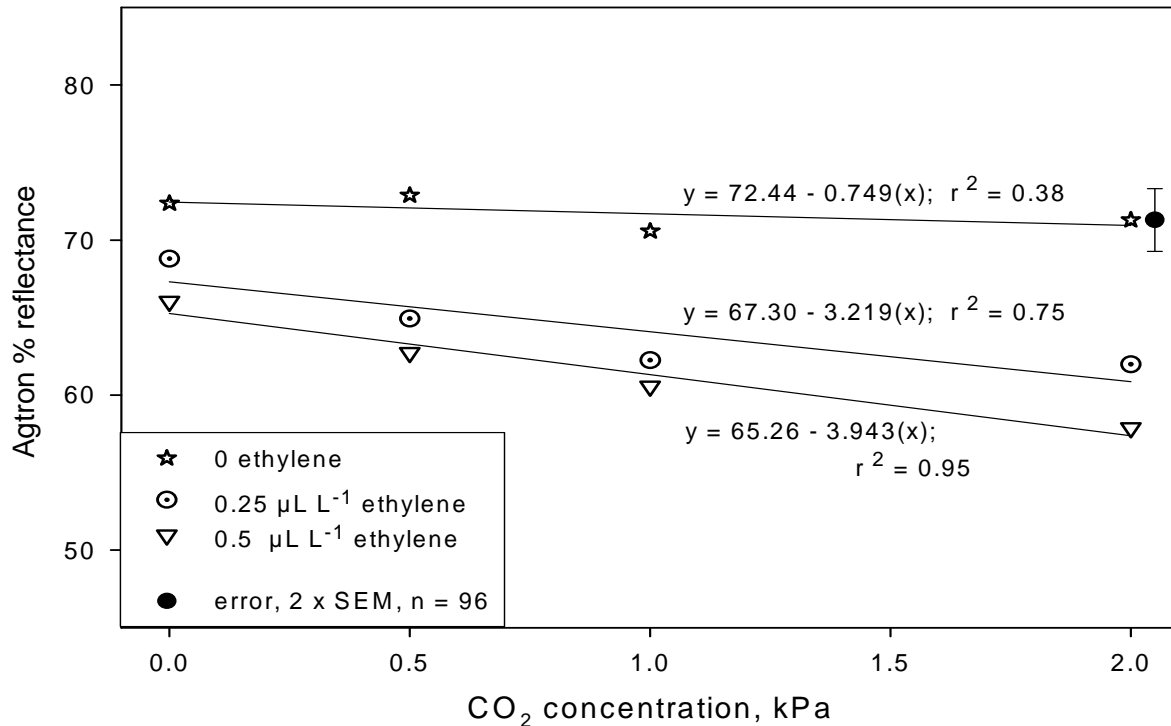
Mean tuber fry colour upon arrival at AFHRC was  $69.5 \pm 5.4$  (mean  $\pm$  SD,  $n = 4$ ) and  $65.5 \pm 6.9$  ARu, in 2006 and 2007, respectively. This reflects normal variation attributable to growing seasons and production factors, including differences in maturity.

In the dormant experiment, the main effects on fry colour of CO<sub>2</sub>, ethylene and evaluation date (time) were significant ( $P = 0.014$ ,  $P < 0.001$  and  $P < 0.001$ , respectively). The interaction of ethylene and evaluation date was also significant (quadratic ethylene  $\times$  quadratic evaluation date,  $P = 0.011$ ), whereas other interactions were not significant.

The statistical main effect of CO<sub>2</sub> on fry colour in the dormant experiment, although significant, appears to be associated with the effect of the ethylene in some of the treatments included in these means, because the fry colour of tubers exposed to CO<sub>2</sub> without ethylene was the same at all levels of CO<sub>2</sub> treatment (Figure 4.1). This is consistent with previous findings regarding fry colour of tubers exposed to 0.5 and 2% CO<sub>2</sub> without ethylene (Daniels-Lake et al. 2005b, 2008).

The fry colour of tubers exposed to ethylene in the dormant experiment was darker than the fry colour of tubers not exposed to ethylene (71.8, 64.5 and 61.8 ARu in 0, 0.25 and 0.5  $\mu\text{L L}^{-1}$  ethylene, respectively; Table 4.1, Figure 4.1). However the response was similar at the two ethylene concentrations. Darkening attributable to ethylene was apparent at all levels

of CO<sub>2</sub> treatment (Figure 4.1), which is consistent with previous findings (Daniels-Lake et al. 2005b). Although the CO<sub>2</sub> × ethylene interaction was not statistically significant (P = 0.691) in the dormant experiment, two trends were suggested by the data: fry colour darkening in response to CO<sub>2</sub> only when ethylene was also present, and a dose-response to CO<sub>2</sub> when the gases were applied together (Figure 4.1).



**Figure 4.1.** Mean fry colour of potato tubers stored for nine weeks beginning in January (dormant experiment, 2006 and 2007 data combined) with various concentrations of CO<sub>2</sub> and ethylene. Significant effects: CO<sub>2</sub> (P = 0.014); ethylene (P < 0.001). Vertical bar represents 2 × standard error of the mean

Fry colour was progressively lighter (i.e., higher colour scores) at successive evaluation dates in the dormant experiment (Table 4.1). Mean fry colour was 65.0, 65.5, and 67.6 ARu at 3, 6 and 9 weeks, respectively. This is mainly attributable to declining hexose concentrations with increasing time, likely as a result of tuber respiration or conversion back to sucrose (Isherwood 1973; Parkin and Schwobe 1990).

In the dormant experiment the fry colour of tubers which were not exposed to ethylene had progressively lighter fry colour from 0 to 9 weeks (Table 4.1). In contrast, the tubers exposed to ethylene had darker fry colour

at 3 weeks than at 0 weeks. Thereafter, the fry colour of the ethylene-treated tubers also improved with increasing time. However, the fry colour of ethylene-treated tubers remained darker than the fry colour of tubers which were not exposed to ethylene throughout the dormant experiment (Table 4.1). The response to ethylene across time was similar at both concentrations. This is consistent with the work of other researchers, who reported progressive recovery of ethylene-darkened fry colour with additional time in storage (Parkin and Schwobe 1990; Prange et al. 1998; Daniels-Lake et al. 2005a, 2007).

**Table 4.1.** Fry colour of potatoes stored with CO<sub>2</sub> and/or ethylene gas for nine weeks, means of 2006 and 2007 data.

a. Dormant experiment

CO <sub>2</sub> (%)	Ethylene (µL L <sup>-1</sup> )	Time after start of trials, weeks			
		0	3	6	9
Agtron percent reflectance units					
0	0	69.5	71.8	71.7	73.7
	0.25		68.1	67.3	71.0
	0.5		64.8	65.8	67.5
0.5	0		71.6	72.1	75.0
	0.25		65.7	63.1	66.0
	0.5		61.7	63.0	63.5
1	0		68.2	70.8	72.7
	0.25		61.7	60.7	64.4
	0.5		59.5	60.7	61.6
2	0		70.1	71.2	72.6
	0.25		60.9	60.9	64.1
	0.5		55.7	58.8	59.1
Significant effects:		CO <sub>2</sub> : P = 0.014, SEM <sup>z</sup> = 1.166			
		Ethylene: P < 0.001, SEM = 1.014			
		Time: P < 0.001, SEM = 0.333			
		Ethylene × Time (quadratic × quadratic): P = 0.011, SEM = 2.288			
		Other interactions not significant			

<sup>z</sup> Standard error of the mean  
(table continued on next page)

**Table 4.1**, continued  
b. Non-dormant experiment

CO <sub>2</sub> (%)	Ethylene (μL L <sup>-1</sup> )	Time after start of trials, weeks			
		0	3	6	9
Agtron percent reflectance units					
0	0	76.7	77.8	81.6	80.4
	0.25		66.5	67.4	65.4
	0.5		56.2	58.9	58.3
0.5	0		80.2	80.5	80.3
	0.25		64.0	63.1	65.4
	0.5		56.2	57.7	56.9
1	0		79.7	78.7	81.1
	0.25		61.9	63.4	64.3
	0.5		55.4	57.8	55.9
2	0		78.0	80.7	78.2
	0.25		57.9	57.0	59.7
	0.5		53.6	53.8	53.5
Significant effects:		CO <sub>2</sub> : P < 0.001, SEM <sup>z</sup> = 0.588			
		Ethylene: P < 0.001, SEM = 0.507			
		Time: P = 0.029, SEM = 0.324			
		CO <sub>2</sub> × Ethylene (linear × quadratic): P = 0.003, SEM = 1.016			
		Other interactions not significant			

<sup>z</sup> Standard error of the mean

In the non-dormant experiment, the main effects on fry colour of CO<sub>2</sub>, ethylene and evaluation date (time) were significant (P < 0.001, P < 0.001 and P = 0.029, respectively), as was the interaction of CO<sub>2</sub> and ethylene (linear CO<sub>2</sub> × quadratic ethylene, P = 0.011). The other interactions were not significant.

Mean fry colour in the non-dormant trials improved with time (Table 4.1). The fry colour of tubers exposed to ethylene darkened sharply from 0 to 3 weeks, and remained much darker at 6 and 9 weeks than the controls (Table 4.1). However the interaction of ethylene with time was not statistically significant (P = 0.495) in the non-dormant experiment. The fry colour

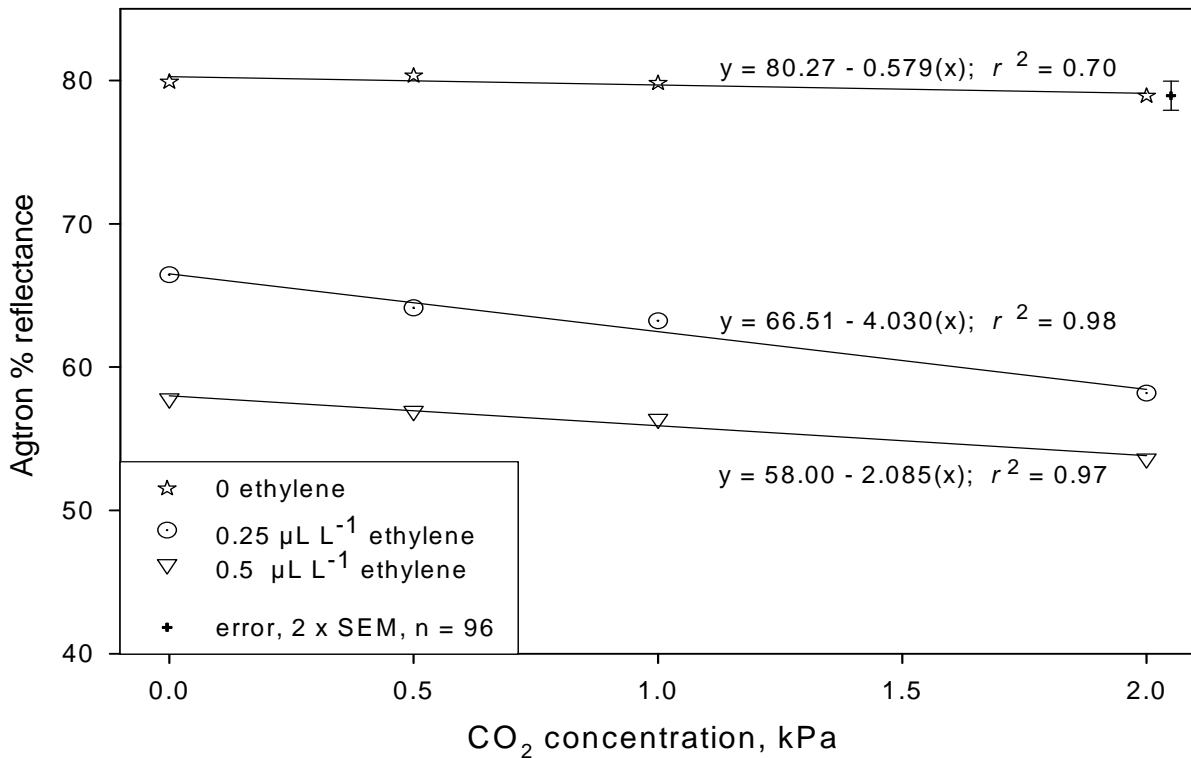
darkening attributable to  $0.5 \mu\text{L L}^{-1}$  ethylene was greater than to  $0.25 \mu\text{L L}^{-1}$  ethylene, reflecting a dose-related response to the ethylene in the non-dormant experiment (Table 4.1). This is consistent with the findings of Daniels-Lake et al. (2005a), who showed a dose-dependent relationship between darkening of fry colour and exposure of tubers to ethylene concentrations of 0.4 and  $4.0 \mu\text{L L}^{-1}$ .

The response of fry colour to  $\text{CO}_2$  in the non-dormant experiment was dependent upon whether ethylene was also present (Table 4.1, Figure 4.2). The tuber fry colour in all treatments with  $\text{CO}_2$  but without ethylene remained equivalent to the colour of the control tubers. In contrast, tubers exposed to ethylene without  $\text{CO}_2$  had darker fry colour than the controls or tubers exposed to  $\text{CO}_2$  only (Figure 4.2). The dose-related response to ethylene concentration was apparent at all  $\text{CO}_2$  concentrations in the non-dormant experiment. Tubers stored with both ethylene and  $\text{CO}_2$  had darker fry colour than either the control tubers or the tubers exposed to  $\text{CO}_2$  only (Table 4.1, Figure 4.2). At the highest  $\text{CO}_2$  concentration, the fry colour of tubers stored with both gases had darker fry colour than with ethylene alone. The darkest fry colour in the non-dormant experiment was observed in tubers exposed to both gases at the highest concentrations. These observations indicate a dose-related response to both  $\text{CO}_2$  and ethylene. The response to  $\text{CO}_2$  increments was greater at  $0.25$  than at  $0.5 \mu\text{L L}^{-1}$  ethylene, as the different slopes for these two lines demonstrate (Figure 4.2). This observation is intriguing, because it suggests that an additional factor may be involved. The gases appear to be interacting at the metabolic level, likely affecting respiration rate, starch-sucrose or sucrose-hexose inter-conversion rates, and perhaps other enzymatic pathways.

The responses to the  $\text{CO}_2$  and ethylene treatments appeared to be somewhat different in the two experiments, which concurs with previous reports (Daniels-Lake et al. 2005b, 2008). The dormant and non-dormant states are recognized as different as a result of progressive physiological ageing of the tubers during long-term storage, even among CIPC-treated tubers when no sprouting is apparent. Physiological aging affects numerous aspects of tuber metabolism, including plant growth regulator concentrations, starch mobilization, respiration rate, sugars, membranes, activity and abundance of various enzymes, and gene activation. From the present work, it is not clear which of these were affected by exposure to the combination of



CO<sub>2</sub> and ethylene, except that the darkened fry colour is evidence of elevated reducing sugars. Additional research is needed to elucidate the influence of the many factors involved, in both dormant and non-dormant tubers.



**Figure 4.2.** Mean fry colour of potato tubers stored for nine weeks beginning in April (non-dormant experiment, 2006 and 2007 data combined) with various concentrations of CO<sub>2</sub> and ethylene. Significant effects: CO<sub>2</sub> × ethylene (linear CO<sub>2</sub> × quadratic ethylene, P = 0.003). Vertical bar represents 2 × standard error of the mean

Neither a threshold concentration (below which there was no effect on fry colour), nor a saturation concentration (above which there was no additional effect on fry colour) was identified for either gas within the concentration ranges applied in these experiments. Additional study is needed to determine these concentrations. Nevertheless, the results have clearly demonstrated that fry colour can be affected by as little as 0.5% CO<sub>2</sub> when a trace concentration of ethylene is also present. Because the dose-response to CO<sub>2</sub> in the presence of ethylene has not been reported previously, these results provide an important new factor for consideration by the potato

processing industry to more effectively manage potato fry colour during long term storage.

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## Chapter 5

# Effects of Elevated CO<sub>2</sub> and Trace Ethylene Present Throughout the Storage Season on the Processing Colour of Stored Potatoes\*

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### **Abstract**

Previous short-term trials (9-weeks duration) have shown that the fry colour of stored potatoes (*Solanum tuberosum* L.) can be negatively affected by simultaneous exposure to elevated CO<sub>2</sub> plus a trace concentration of ethylene gas. In the present study, trials were conducted during each of two storage seasons (2008-2009 and 2009-2010), to examine the effects of long-term exposure to these two gases during the entire November to June storage season. In each year, 0 or 2% CO<sub>2</sub> and 0 or 0.5 µL L<sup>-1</sup> ethylene were applied in a factorial design to tubers of four processing cultivars (Russet Burbank, Shepody, Innovator and Dakota Pearl). Processing colour of the tubers was evaluated at the start of each trial and at intervals of 4 weeks thereafter. In the three French fry cultivars (i.e. Russet Burbank, Shepody and Innovator), the fry colour of tubers exposed to CO<sub>2</sub> plus ethylene together was darker than the controls. In the chipping cultivar Dakota Pearl, the gas treatments had only a small effect on chip colour. Fry colour darkening due to an interaction of CO<sub>2</sub> × ethylene × time was significant only in Innovator. Processing colour of all cultivars was darkened by these gases, but the magnitude and timing of the responses varied widely between gases, among cultivars, and from the start to the end of the season.

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## 5.1. Introduction

Production of processed potato products such as French fries and potato chips (known as chips and crisps, respectively in the UK) uses approximately one-half of the potato crops in North America and western Europe (USDA 2004; Kirkman 2007; AAFC 2009). Worldwide production of frozen potato products - primarily frozen French fries - exceeds 2 million metric tonnes annually (USDA 2009). One of the most important quality aspects of processed potato products is finished colour after the fry processing. Although the precise shade preference varies slightly among markets, a light colour is preferred over a dark colour in both French fries and potato chips. Colour is primarily determined by the quantity of reducing sugars, predominantly glucose and fructose, in the tubers before processing (Mazza 1983; Burton et al. 1992). During frying, colourless reducing sugars and free amino acids combine in the Maillard reaction to produce brown melanoidin compounds. When these compounds are produced in sufficient quantities, the colour of the processed product is darkened. Therefore the reducing sugar content of the raw tubers is an important quality aspect of any potatoes offered to the factory for processing. Reducing sugar content of the tubers is influenced by cultivar, growing season, tuber maturity (i.e. physiological age) and post-harvest conditions (Burton et al. 1992).

To provide a consistent long-term supply of potatoes for processing, much of the crop is stored for significant periods of time after harvest. Retention of good tuber quality during many months of storage depends upon appropriate conditions in store, including suitable temperature, humidity, and ventilation rate (Gottschalk and Ezekiel 2006; Kirkman 2007). Ventilation serves multiple roles in the storage of potatoes, including temperature management, humidity control, replenishment of oxygen consumed by tuber respiration and removal of the carbon dioxide generated by respiration (Burton et al. 1992).

Elevated CO<sub>2</sub> in the storage atmosphere was long thought to directly affect sugars and therefore fry colour, but more recently the combined effect of moderately elevated CO<sub>2</sub> together with ethylene gas has been found to have an important role (Daniels-Lake et al. 2005a, 2005b, 2008; Daniels-Lake and Prange 2009). The effect of ethylene gas on potato fry colour and the underlying tuber reducing sugars is well established (Haard 1971; Parkin and

Schwobe 1990; Prange et al. 1998). The response is dose-dependent, and varies somewhat among cultivars (Daniels-Lake et al. 2005a, 2007). In contrast, the effect of CO<sub>2</sub> on fry colour is less clearly defined. Elevated CO<sub>2</sub> has been reported to darken (Mazza and Siemens 1990; Schouten 1993; Khanbari and Thompson 1994, 1996), to lighten (Denny and Thornton 1940), and to have no effect on colour (Blankson 1988). In recent short-term studies (up to 9 weeks) of the response of Russet Burbank (RB) tubers to CO<sub>2</sub> and ethylene together, no darkening attributable to CO<sub>2</sub> alone was observed (Daniels-Lake et al. 2005b, 2007, 2008; Daniels-Lake and Prange 2009). Darkening of fry colour appears to be largely attributable to ethylene gas, but with an enhanced response when CO<sub>2</sub> is also present, suggesting an interaction (Daniels-Lake et al. 2005b, 2007, 2008; Daniels-Lake and Prange 2009).

Recently, measurable concentrations of acrylamide, a suspected human carcinogen, were identified in some processed potato products and other cooked starchy foods (Tareke et al. 2002). Acrylamide is a Maillard reaction product which is formed when the amino acid asparagine participates in the reaction (Majcher and Jeleń 2007; Serpen and Gökmen 2009). It has been shown that dark colour in processed potato products can be associated with elevated acrylamide content (Li et al. 2006; Majcher and Jeleń 2007; Serpen and Gökmen 2009), which emphasizes the value of a light finished colour in processed potato products. It also reinforces the need to avoid conditions which increase tuber sugar concentrations in potatoes which are destined for processing.

In view of these points, investigations of the effects on potato processing colour of CO<sub>2</sub> and ethylene in combination have continued. The studies reported previously have dealt with short-term exposure (up to 9 weeks) of potatoes to the two gases, using a single cultivar (Daniels-Lake et al. 2005a, 2005b, 2008; Daniels-Lake and Prange 2009). However potato tubers are usually stored for a much longer period, up to 8 months after harvest and frequently much longer. During this time, the tubers continue to age physiologically, with significant changes in tuber biochemistry and responsiveness to stresses (summarized in Burton et al. 1992). Storage operators work throughout the storage term to maintain good storage conditions, including favourable headspace concentrations of O<sub>2</sub>, and CO<sub>2</sub> in the potato storage atmosphere. Industry guidelines regarding maximum CO<sub>2</sub>

concentration exist in some regions, e.g. Rastovski (1987) and Schaper et al. (1993) recommend a maximum of 1% CO<sub>2</sub> in the storage atmosphere. However, this concentration is easily exceeded and many storage buildings are not equipped with CO<sub>2</sub> monitoring equipment. With regards to ethylene, very few storage operators monitor this gas, despite the fact that it is produced by the tubers (particularly if stressed), by pathogens, and by fuel-burning equipment such as vehicle engines and heaters. Although ethylene production rates of tubers are relatively low, ethylene can accumulate to significant concentrations when the ventilation is reduced (e.g., to minimize the refrigeration load) or when pathogens are active.

Since these gases have been shown to affect the colour of stored potatoes during short-term trials, it was considered important to investigate the effects of exposure to these two gases throughout a typical North American storage term, i.e. November to June. Furthermore, many cultivars in addition to RB are utilized for processing. Since colour is equally important when processing these cultivars, it is important to determine whether other cultivars respond to the ethylene and CO<sub>2</sub> in the same manner as RB. Therefore research trials were initiated to investigate the effect of long-term exposure to elevated CO<sub>2</sub> and trace ethylene, alone and in combination, on the processing colour of four important processing cultivars. RB is perhaps the most popular French fry cultivar in North America, with relatively long dormancy and good processing quality following storage. It is frequently processed from storage until June, and often later. Shepody (SH) is another very popular French fry cultivar, but with somewhat shorter dormancy than RB. SH processing is usually completed before the end of March. Innovator (IN) has been gaining popularity in Canada during recent years as a suitable French fry cultivar. Dormancy duration of IN is similar to RB; the industry is still fine-tuning their management practices to optimize its performance (JR Walsh, personal communication). Dakota Pearl (DP) is a popular potato chip cultivar which can be successfully processed from moderately cool (6 °C) storage (CFIA 2011). The dormancy duration of DP at the storage temperature used in these trials was similar to RB.



## **5.2. Materials and Methods**

### **5.2.1. Potatoes**

Trials were conducted at the Agriculture and Agri-Food Canada potato postharvest research lab at the Atlantic Food and Horticulture Research Centre in Kentville, Nova Scotia, Canada, during two consecutive years, i.e. November 2008 to June 2009 and November 2009 to June 2010. Cultivars tested were RB, SH, IN and DP, which were harvested in September or October of the 2008 and 2009 growing seasons.

Each year, tubers of each cultivar were sourced from two different commercial potato growers located in eastern Canada, except DP which was from a single source in each year. Following delivery to the lab, the potatoes were stored for ca. four weeks at 13 °C to permit suberization and wound healing, cooled to 9 °C gradually over four weeks and in early December were dipped in a 1% a.i. water emulsion of chlorpropham (Sprout-Nip EC, isopropyl n-(3-chlorophenyl) carbamate, 320 g L<sup>-1</sup> a.i., Stanchem Inc., Etobicoke, Ontario, Canada; CIPC) to control sprouting during the trials.

Samples of 10 tubers (approximately 2 kg) were placed in mesh bags and the bags placed in PVC baskets within individually ventilated stainless steel chambers. The chambers were stored in a temperature-controlled room which maintained the desired temperature  $\pm 0.3$  °C in all chambers throughout the trials. Each gas treatment was applied to two chambers; each of these two chambers contained a basket of samples from one tuber source of each cultivar. At the start of a storage season each basket held seven samples, each sample was pre-assigned to one of seven evaluation dates.

### **5.2.2. Storage and Treatments**

Exposure to the gas treatments began in late November of each year. The storage chamber atmospheres were flushed with compressed gases (Praxair Inc, Dartmouth, Nova Scotia, Canada) for 1.5 h, three times per day, to establish and maintain 0 or 2% CO<sub>2</sub> and 0 or 0.5  $\mu\text{L L}^{-1}$  ethylene gas, in a factorial arrangement. Ambient and respired CO<sub>2</sub> was scrubbed from specific

chambers by placing a paper sack containing ca. 0.5 kg of hydrated lime ( $\text{Ca}(\text{OH})_2$ ; Graymont (QC) Inc., Boucherville, Quebec, Canada) inside the chambers designated for 0%  $\text{CO}_2$  atmospheres. Relative humidity within the chambers was maintained at ca. 95% throughout the trials, with the help of an open tray of distilled water placed inside each chamber.

The gas delivery equipment and controls were as described previously (Daniels-Lake et al. 2005b). The  $\text{CO}_2$  concentration was checked approximately daily, using a handheld gas monitor (CheckPoint, PBI Dansensor America, Glen Rock, New Jersey, USA); the gas delivery rates were adjusted manually as needed to maintain desired  $\text{CO}_2$  concentration. The  $\text{CO}_2$  concentrations were re-checked approximately bi-weekly, using a Vaisala handheld analyser (Model GMP70, Vaisala, Vantaa, Finland). The ethylene concentrations were automatically monitored around the clock, as previously described (Daniels-Lake et al. 2005b).

### 5.2.3. Evaluations

In this report, French fry colour and chip colour are referred to collectively as processing colour. Each year, the processing colour of three samples of tubers from each source was evaluated soon after their arrival at the lab in Kentville. At intervals of four weeks after the beginning of the gas treatments until June of the following year, the processing colour and weight loss of pre-designated samples from each source  $\times$  treatment combination were evaluated. The fry colour of the three French fry cultivars was evaluated in the manner described in Daniels-Lake et al. (2005b). Chip colour of the chipping cultivar, DP, was assessed on the same schedule, in the following manner: five to ten median slices from each tuber in a sample were fried at 190 °C in 100% canola oil (Capri Oil, Bunge Canada, Oakville, Ontario, Canada) until bubbling had slowed to only 1-2 bubbles per second per slice. The finished chips were cooled to room temperature on absorbent paper and stored in clear plastic bags at -30 °C until measurement of crushed chips using a Hunter Lab colour analyser (LabScan model WE, Lyssack Associates, Toronto, Canada). Only the Hunter L (light to dark, higher numbers indicate a whiter shade) and the Hunter a (red to green, higher numbers indicate a stronger red hue) are reported here, as is common practice in the chipping industry. The preferences are a high Hunter L score and a low Hunter a score.

Although the tubers for the trial were sprout inhibited with chlorpropham, this did not stop physiological ageing within the tuber but only prevented sprout growth. Additional samples of tubers from each source were reserved in identical storage conditions but without sprout inhibitor treatment, to monitor dormancy break and sprouting. Ventilation of these reserved tubers was with air only. The reserved samples were visually inspected on the same dates as the processing colour was evaluated. A cultivar was judged to be sprouting if 80% of the reserved tubers had sprouts greater than 3 mm in length (Reust and Aerny 1985; Burton et al. 1992).

#### 5.2.4. Statistics

The customized experimental design was a replicated two-way factorial design with a split plot arrangement. Two levels of CO<sub>2</sub> exposure (0 and 2%) were crossed with two levels of ethylene exposure (0 and 0.5  $\mu\text{L L}^{-1}$ ) for four treatments. Treatment was the main plot and evaluation date was the subplot. Using potatoes of the same cultivar from two different growers each year provided physical replication, and conducting the trials in two different years provided replication in time. The data from the two years were combined and analysed statistically by ANOVA using Genstat statistical software (VSN International 2010). Differences across treatments, levels of treatments and evaluation dates were further assessed using orthogonal and polynomial contrasts, which provided insight into the pattern of the responses. The orthogonal contrast compared the responses before and after dormancy ended (i.e. Early and Later groupings of evaluation dates, as described below), and the polynomial contrast evaluated the response across multiple evaluation dates in the Later group of evaluation dates. The statistical comparisons are outlined in Table 5.1. Unless otherwise noted, only results significant at  $P \leq 0.05$  are discussed.

### 5.3. Results

Year to year variations within each cultivar in regard to fry colour, sprouting and response to the applied treatments were quite small, except for an unusually dark initial colour in SH and strong darkening in IN at the final evaluation, both during the second year of trials (data not presented). Despite

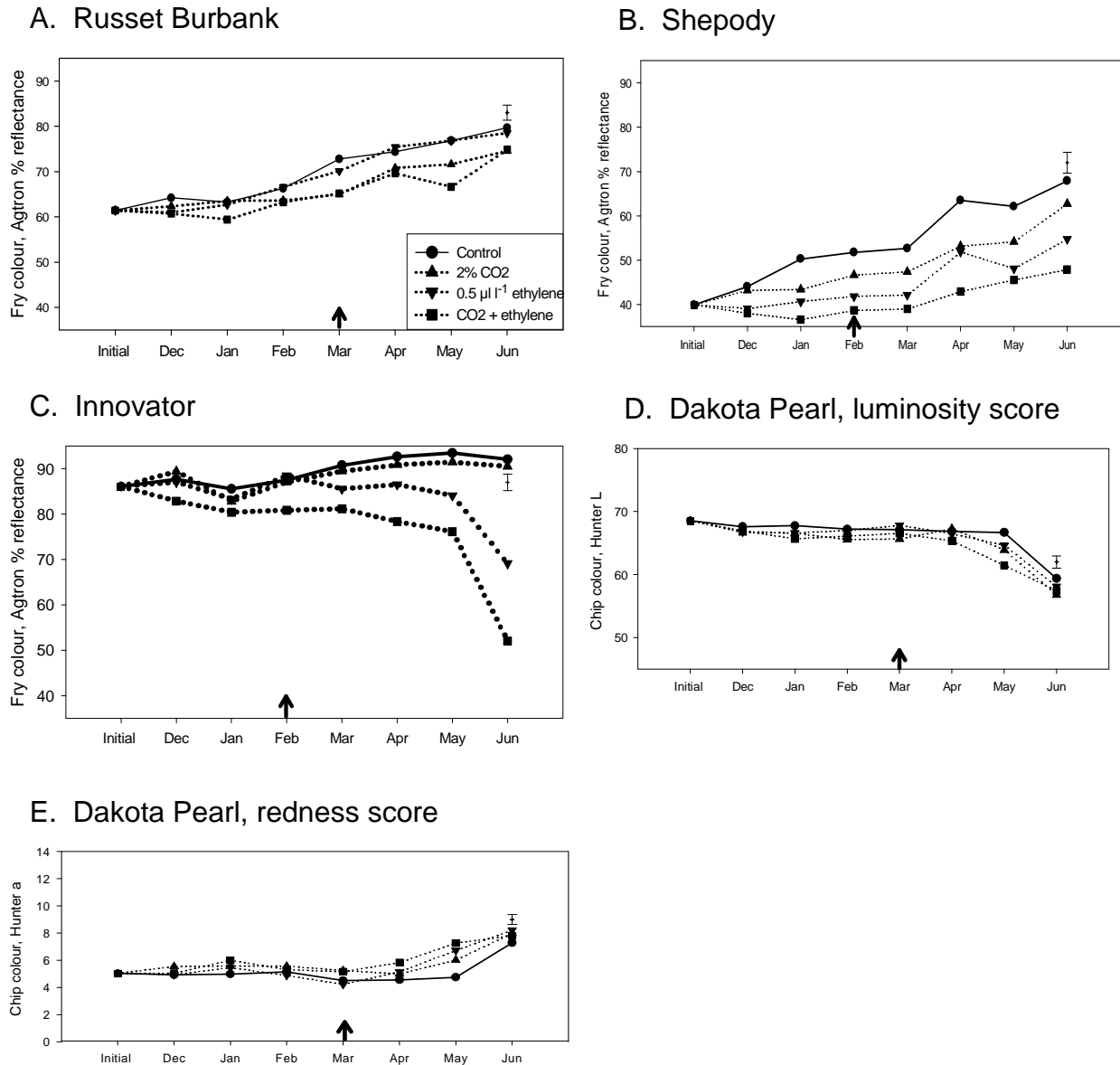
these differences, the responses to the treatments were very similar across years within cultivars.

**Table 5.1.** Summary of output from statistical analyses

source of variation	contrasts	df	Russet			Dakota Pearl		
			Burbank	Shepody	Innovator	Hunter L	Hunter a	
			P-values					
CO <sub>2</sub>		1	<0.001 <sup>z</sup>	<0.001	0.004	0.024	0.029	
ethylene		1	0.049	<0.001	<0.001	<0.001	0.003	
CO <sub>2</sub> · ethylene		1	0.507	0.068	0.019	0.464	0.335	
evaluation date		6	<0.001	<0.001	<0.001	<0.001	<0.001	
	Early vs. Later	1	<0.001	<0.001	0.465	<0.001	<0.001	
	Later - linear	1	<0.001	<0.001	<0.001	<0.001	<0.001	
	Later - quadratic	1	0.408	0.576	<0.001	<0.001	<0.001	
CO <sub>2</sub> · evaluation date		6	0.058	0.383	0.018	0.477	0.003	
	CO <sub>2</sub> · Early vs. Later	1	0.006	0.211	0.016	0.937	0.241	
	CO <sub>2</sub> · Later - linear	1	0.438	0.543	0.012	0.222	0.007	
	CO <sub>2</sub> · Later - quadratic	1	0.171	0.372	0.128	0.365	0.050	
ethylene · evaluation date		6	0.829	0.291	<0.001	0.611	0.751	
	ethylene · Early vs. Later	1	0.272	0.043	<0.001	0.345	0.712	
	ethylene · Later - linear	1	0.682	0.136	<0.001	0.469	0.661	
	ethylene · Later - quadratic	1	0.634	0.732	<0.001	0.854	0.198	
CO <sub>2</sub> · ethylene · evaluation date		6	0.592	0.974	0.042	0.937	0.790	
	CO <sub>2</sub> · ethylene · Early vs. Later	1	0.923	0.902	0.083	0.821	0.999	
	CO <sub>2</sub> · ethylene · Later - linear	1	0.742	0.799	0.049	0.785	0.164	
	CO <sub>2</sub> · ethylene · Later - quadratic	1	0.517	0.596	0.045	0.253	0.419	

<sup>z</sup> P-values of 0.05 or less were considered significant

Sprouting was observed in the reserved tubers of all cultivars, beginning at the February evaluation in SH and IN, and at the March evaluation in RB and DP. In the three French fry cultivars (RB, SH and IN), the fry colour score of tubers in the control treatment increased (lightened) steadily throughout the storage term (Figure 5.1). This is commonly observed, and reflects declining reducing sugars during long-term storage (Burton et al. 1992; Mazza 1983). This change was greatest in SH, and least in IN (Figure 5.1).



**Figure 5.1.** Processing colour of tubers stored with or without CO<sub>2</sub> or ethylene gas; A. Russet Burbank, B. Shepody, C. Innovator, D. Dakota Pearl Hunter L, E. Dakota Pearl Hunter a. Data points are means from two years of trials. A higher score is preferred, except in (E), where a lower score is preferred. Vertical bars indicate ± SEM for the interaction of CO<sub>2</sub> × ethylene × evaluation date. The arrow near the X-axis indicates the evaluation date at which significant sprouting was first observed in similar tubers which were stored under identical conditions but without a sprout inhibitor.

In all three French fry cultivars, colour was darker in the CO<sub>2</sub> + ethylene treatment than in the control (Figure 5.1). These differences were larger at the end of the trials than at the beginning, which concurs with previous observations for RB that the response to CO<sub>2</sub> + ethylene appears to be greater

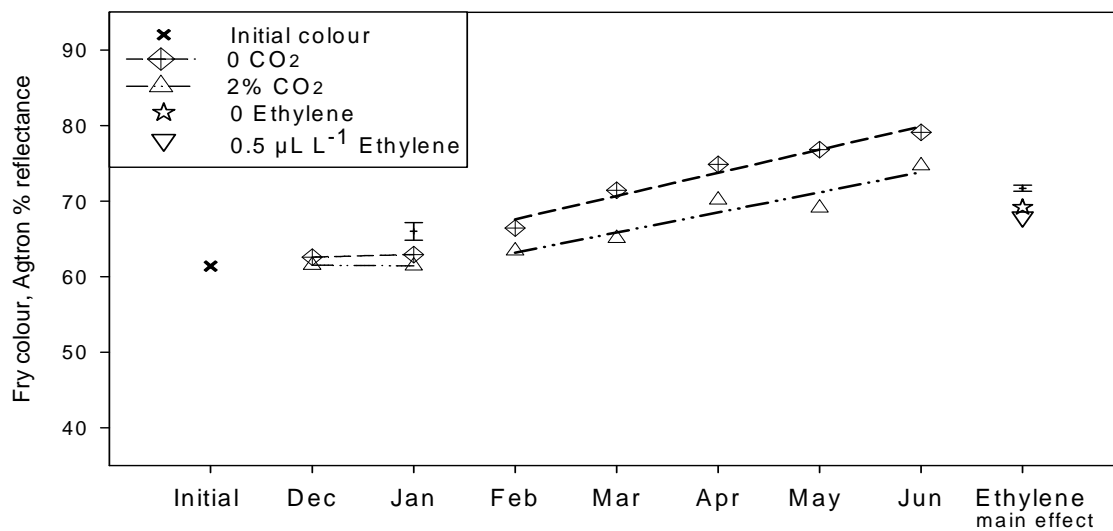
in post-dormant than in dormant tubers (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009).

### 5.3.1. Russet Burbank

In RB, the response of fry colour to the applied treatments at the December and January evaluations was similar to previously published reports (Figure 5.1a; Daniels-Lake et al. 2005a, 2005b, 2007, 2008; Daniels-Lake and Prange 2009), i.e. in both this study and the published reports, the CO<sub>2</sub> had little effect on fry colour when present alone, the ethylene darkened the colour slightly when present alone, and simultaneous exposure to these two gases darkened the colour more than ethylene alone. However, under continued exposure to these gases the fry colour in RB aligned according to the presence or absence of CO<sub>2</sub> (Figure 5.1a). From the February evaluation (i.e. 12 weeks after the start) until the end of the trials, the untreated control tubers and tubers stored with ethylene alone had essentially the same fry colour. In contrast, the fry colour of tubers in the CO<sub>2</sub> and the CO<sub>2</sub> + ethylene treatments were very similar at the February, March, April and June evaluations, but both were darker than the colour of tubers in the control and ethylene only treatments at each evaluation from February to June, inclusive (Figure 5.1a). Interestingly, the onset of this apparent shift in response was slightly later than the duration of the previous short-term trials (i.e. ca. 12 weeks vs. 9 weeks, respectively; Daniels-Lake et al. 2005a, 2005b, 2007, 2008; Daniels-Lake and Prange 2009). It is possible that the earlier work may not have had sufficient duration to capture some of the effects of the CO<sub>2</sub> and ethylene exposures.

The general ANOVA analysis of the RB data indicated significant differences attributable to the main effects of CO<sub>2</sub>, ethylene and evaluation date ( $P < 0.001$ ,  $P = 0.049$ ,  $P < 0.001$ , respectively), but the 2-way and 3-way interactions were not significant ( $P > 0.05$  for all; Table 5.1). Although the main effect of ethylene on fry colour of RB was significant ( $P = 0.049$ ) the difference was less than 2 Agtron percent reflectance units (ARu), i.e. 69.2 and 67.9 ARu in 0 and 0.5  $\mu\text{L L}^{-1}$  ethylene, respectively (Figure 5.2). The possible influence of ethylene on RB fry colour at the early evaluation dates was not statistically significant, and with increased storage time this was no longer observed (Figure 5.1a).

In order to better understand the bi-modal nature of the responses as the storage duration increased, the December and January evaluations (before dormancy ended) were designated the Early phase of the trials and the remaining five evaluations were grouped together and designated the Later phase of the trials. Then the data were further analysed using statistical contrasts of the Early and Later phases. Neither the interaction of ethylene × evaluation date nor the contrast of Early vs. Later within this interaction was significant in RB ( $P = 0.829$  and  $P = 0.272$ , respectively).



**Figure 5.2.** Changes in fry colour of RB tubers during storage, in response to CO<sub>2</sub> (mean values across two ethylene levels) and ethylene (mean values across two CO<sub>2</sub> levels). Data points are means of two trials. Vertical bars represent  $\pm$  SEM (from left to right) for the orthogonal contrast between the Early and Later groupings of the evaluations within the interaction of CO<sub>2</sub> × evaluation date (1.158,  $P = 0.006$ ), and for the main effect of ethylene (0.400,  $P = 0.049$ )

Within the interaction of CO<sub>2</sub> × evaluation date for RB tubers, the orthogonal contrast of Early vs. Later was significant ( $P = 0.006$ ; Figure 5.2). The effect of CO<sub>2</sub> in the Later phase of the trial was much greater than during the Early phase, as the wider separation of the regression lines demonstrates. As observed in the previous short-term studies (Daniels-Lake et al. 2005a, 2005b, 2007, 2008; Daniels-Lake and Prange 2009), CO<sub>2</sub> did not darken fry colour during the Early phase of these trials (Figure 5.2). The fry colour scores of tubers exposed to 0 and 2% CO<sub>2</sub> improved (lightened) steadily during the Later phase of the trials, and the rate of improvement was approximately the same, as the similar slopes indicate. However, the fry

colour of RB tubers which were exposed to 2% CO<sub>2</sub> was ca. 5 ARu lower at each evaluation than the fry colour of tubers in the 0 CO<sub>2</sub> treatments (Figure 5.2).

### 5.3.2. Shepody

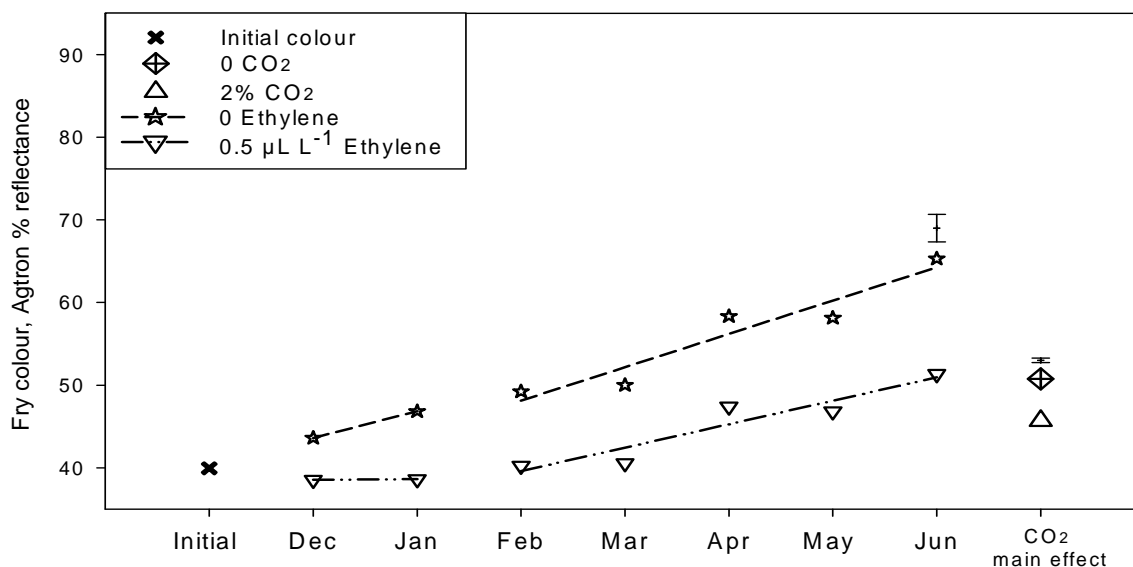
In SH tubers the main effects of CO<sub>2</sub>, ethylene and evaluation date on fry colour were all significant ( $P < 0.001$  for each). Although the 2- and 3-way interactions were not significant, the F-probability for the CO<sub>2</sub> × ethylene interaction in SH was only slightly beyond the 5% threshold for significance ( $P = 0.068$ ; standard error of the mean (SEM) = 0.399), which suggests a trend that may be industrially relevant even though it is not statistically significant at  $P < 0.05$ . The mean fry colour scores were 56.0, 50.1, 45.5 and 41.2 ARu in the control, CO<sub>2</sub>, ethylene and CO<sub>2</sub> + ethylene treatments, respectively, suggesting a consistent, progressively darker fry colour in tubers from these treatments throughout the trials (Figure 5.1b). This trend is similar to the published findings from short-term trials using RB (Daniels-Lake et al. 2005a, 2005b, 2007, 2008; Daniels-Lake and Prange 2009), except for the darkening in the CO<sub>2</sub> treatment which was not observed in the previous work. Fry colour appeared to be darker in the CO<sub>2</sub> treatment than in the Control at the January evaluation, i.e. 8 weeks after the start of the trials. This trending persisted until the end of the trials (Figure 5.1b), and was consistent across both years (data not presented).

Ethylene had a strong effect on the fry colour of SH tubers (Figure 5.3). This is consistent with the findings of Prange et al. (2005) who reported that Shepody tubers are more sensitive to ethylene than Russet Burbank, and Gichohi and Pritchard (1995) who found that fry colour and tuber sugars in Shepody are more sensitive than in Russet Burbank to stresses such as low storage temperature and application of maleic hydrazide sprout inhibitor. The orthogonal contrast under the ethylene × evaluation date interaction revealed that the effect of ethylene on SH in the Early phase of the trial differed from the effect in the Later phase ( $P = 0.043$ ). Fry colour remained dark in response to ethylene exposure at the December and January evaluations, whereas without ethylene the colour became lighter with increased time (Figure 5.3). However, in the Later phase the colour of tubers stored with trace ethylene improved at almost the same rate as without ethylene, as the slopes of the regression lines



indicate. This suggests that the SH tubers were recovering steadily from the effects of the ethylene gas exposure, although not quickly enough to catch up with the untreated control tubers.

CO<sub>2</sub> also darkened fry colour of SH tubers, by approximately 5 ARu over the entire trial (Figure 5.3). This is similar to the effect of CO<sub>2</sub> on the fry colour of RB tubers discussed above, although the interaction with evaluation date was not significant in SH tubers (Table 5.1). The effect of CO<sub>2</sub> on SH fry colour may reflect the greater sensitivity of SH to stresses, compared with RB (Gichohi and Pritchard 1995; Prange et al. 2005).



**Figure 5.3.** Changes in fry colour of SH tubers in response to CO<sub>2</sub> (mean values across two levels of ethylene) and ethylene (mean values across two levels of CO<sub>2</sub>). Data points are means of two trials. Vertical bars represent ± SEM (from left to right) for the orthogonal contrast between Early and Later groupings of evaluation dates within the interaction of ethylene × evaluation date (1.658, P = 0.043), and for the main effect of CO<sub>2</sub> (0.282, P < 0.001)

### 5.3.3. Innovator

In the IN tubers, the 3-way interaction of CO<sub>2</sub>, ethylene and evaluation date was significant (P = 0.042; Table 5.1; Figure 5.1c). Fry colour of IN tubers exposed to elevated CO<sub>2</sub> alone was similar to the controls throughout the entire trial period. However, in the ethylene treatment, fry colour of IN

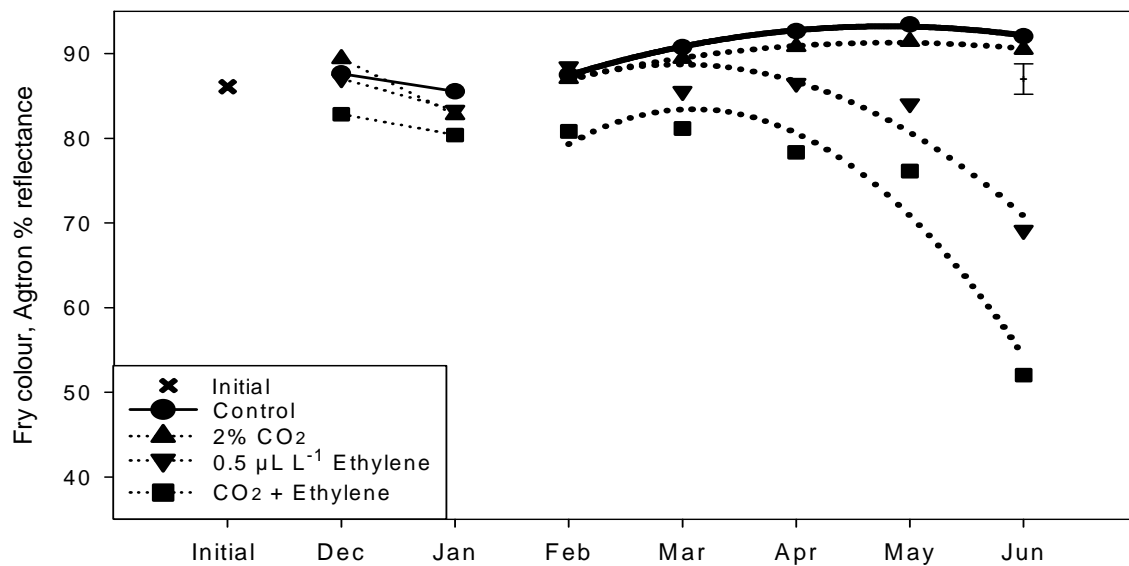
tubers was similar to the control tubers until the February evaluation, inclusive, but was darker than the controls thereafter (Figure 5.1c). In the CO<sub>2</sub> + ethylene treatment, fry colour declined from the start to the end of the trial, and was darker than the controls throughout trial. This is similar to the response of RB tubers to short-term exposure to these two gases (Daniels-Lake et al. 2005a, 2005b, 2007, 2008; Daniels-Lake and Prange 2009), except in these trials with IN the response to ethylene was not observed until March when the tubers were no longer dormant. In the ethylene and CO<sub>2</sub> + ethylene treatments, the fry colour scores were much darker than the control and CO<sub>2</sub> treatments at the June evaluations (Figure 5.1c). Fry colour of IN tubers in the CO<sub>2</sub> + ethylene treatment was by far the darkest of all treatments at the June evaluation, i.e. ca. 40 ARu darker than the control.

The polynomial contrast of Later evaluation dates within the three-way interaction of CO<sub>2</sub> × ethylene × evaluation dates was also significant for IN ( $P = 0.045$ ; Figure 5.4). Fry colour declined slightly in all treatments during the Early phase of the trials, although only the CO<sub>2</sub> + ethylene treatment had darker fry colour than the control. However, during the Later phase of the trials tuber fry colour in the control and CO<sub>2</sub> treatments lightened as storage time increased, but darkened in an exponential manner in the ethylene and CO<sub>2</sub> + ethylene treatments (Figure 5.4). The tubers apparently became more sensitive to the ethylene and CO<sub>2</sub> + ethylene treatments as their physiological age approached senescence. These observations suggest that fry colour of IN tubers is relatively insensitive to CO<sub>2</sub>, is somewhat sensitive to ethylene, but is very sensitive to the presence of the two gases together.

#### 5.3.4. Dakota Pearl

In the potato chip cultivar DP, there was very little difference in colour (both Hunter L and Hunter a; luminosity and redness, respectively) among treatments (Figure 5.1d and 5.1e). This reflects the relatively low tuber reducing sugars in all DP samples (data not presented), which is rather typical of chipping cultivars. At the May and June evaluations, both Hunter L and Hunter a darkened slightly in all treatments (Figure 5.1d and 5.1e). This may be attributable to increasing physiological age and approaching senescence, which often causes tuber sugars to increase (Burton et al. 1992). Nevertheless, there were small but significant differences in Hunter L scores in

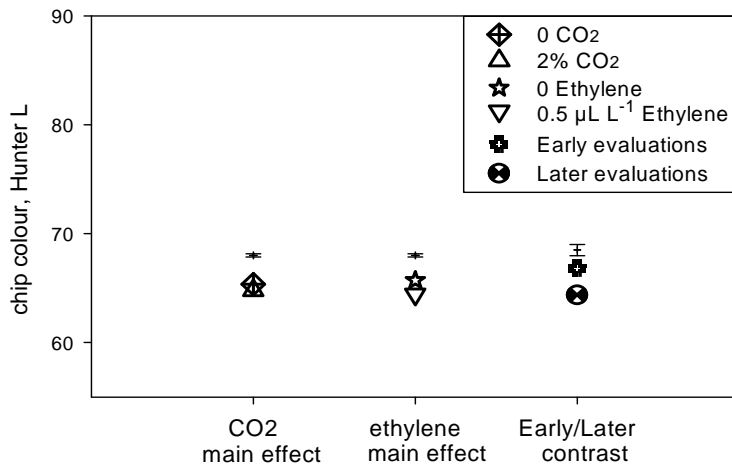
response to the main effect of CO<sub>2</sub>, the main effect of ethylene and the orthogonal contrast of Early vs. Later evaluations ( $P < 0.001$ ,  $P = 0.024$  and  $P < 0.001$ , respectively; Table 5.1; Figure 5.5a). Significant differences were also observed in Hunter a scores in the interaction of CO<sub>2</sub> × evaluation date and the main effect of ethylene ( $P = 0.050$  and  $P = 0.003$ , respectively; Figure 5.5b).



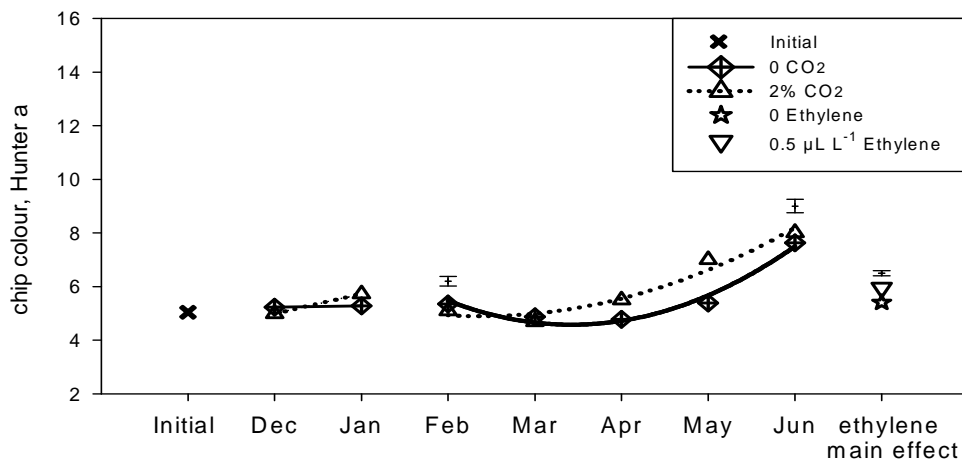
**Figure 5.4.** Changes in fry colour of IN tubers during storage, in response to two levels of CO<sub>2</sub> and two levels of ethylene gas in a factorial design. Data points are means of two trials. Vertical bars represent  $\pm$  SEM (from left to right) for the interaction of CO<sub>2</sub> × ethylene × evaluation date (1.814,  $P = 0.042$ ) and for the polynomial contrast (quadratic relationship) in the Later grouping of evaluation dates within the interaction of CO<sub>2</sub> × ethylene × evaluation date (1.814,  $P = 0.045$ ).

The change in DP Hunter L chip colour attributable to CO<sub>2</sub> was less than 1 unit darker, and ca. 1.5 units darker in response to ethylene ( $P = 0.024$  and  $P < 0.001$ , respectively; Figure 5.5a). Within the interaction of CO<sub>2</sub> × evaluation date, there was no difference in DP Hunter a chip colour attributable to CO<sub>2</sub> in the Early phase. However chip colour was up to 0.9 units redder in response to CO<sub>2</sub> during the Later phase of the trial (quadratic polynomial contrast,  $P = 0.050$ ; Figure 5.5b). The change in Hunter a scores attributable to ethylene was ca. 0.5 units redder ( $P = 0.003$ ; Figure 5.5b). While these changes were small, they were consistent and represent an effect on chip colour which could be avoided by storage management activities.

## A. Luminosity score



## B. Redness score



**Figure 5.5.** Changes in chip colour of DP tubers during storage, in response to CO<sub>2</sub> (mean values across two levels of ethylene gas), ethylene (mean values across two levels of CO<sub>2</sub>) and the orthogonal or polynomial contrasts; A. Hunter luminosity scores and B. Hunter redness scores. Data points are means of two trials. Vertical bars represent  $\pm$  SEM, i.e. in graph A. (from left to right) for the main effect of CO<sub>2</sub> (0.149,  $P = 0.024$ ), for the main effect of ethylene (0.149,  $P < 0.001$ ) and for the orthogonal contrast between the Early and Later groupings of evaluation dates (0.5120,  $P < 0.001$ ); and in B. (from left to right) for the orthogonal contrast between the Early and Later phases of the trials (0.1768,  $P < 0.001$ ), for the polynomial contrast (quadratic relationship) in the Later grouping of evaluation dates within the interaction of CO<sub>2</sub>  $\times$  evaluation date (0.2597,  $P = 0.050$ ) and for the main effect of ethylene (0.0961,  $P = 0.003$ ).

#### **5.4. Discussion and Conclusions**

These data indicate that the processing colour of potato tubers under long-term storage can be influenced by both trace ethylene and elevated CO<sub>2</sub> in the storage atmosphere, although the magnitude and timing of the responses varied somewhat among cultivars. Some cultivars were more sensitive to one gas or the other when applied alone, however, in all three French fry cultivars the colour was darker when CO<sub>2</sub> and ethylene were present together than when both were absent (Figure 5.1).

The data suggest that, during prolonged exposure to these gases, the fry colour of RB tubers was not darkened by exposure to trace ethylene if CO<sub>2</sub> was absent. This is surprising, since previous reports have indicated that darkening attributable to ethylene, with or without CO<sub>2</sub>, appears to be stronger late in the storage term than during the early months of storage (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009). The difference may be attributable to the earlier starting date and longer duration of exposure in the present study, which is consistent with the findings of Prange et al. (1998) who reported that the fry colour of tubers treated with a sprout-inhibiting concentration of ethylene gas quickly darkens and then gradually recovers to a lighter colour with continued exposure time. The small degree of darkening in RB in response to ethylene and the subsequent rapid recovery are attributable to the low concentration used (Daniels-Lake et al. 2005a, 2009). The very long exposure time in the present work likely allowed the tubers to recover from the effects of the ethylene exposure. Therefore the greater darkening reported previously when both gases were applied was not observed in the longer trials reported here. In addition, the long duration of exposure to CO<sub>2</sub> revealed a response to this gas which was not apparent in the shorter trials reported previously (Daniels-Lake et al. 2005b, 2009), but is consistent with the work of Khanbari and Thompson (1994) and Schouten (1993).

A greater sensitivity of SH tubers compared with RB to ethylene and other stressors (Gichohi and Pritchard 1995; Prange et al. 2005) was also apparent in response to elevated CO<sub>2</sub> and CO<sub>2</sub> + ethylene. The IN and DP tubers responded somewhat differently than either SH or RB to these gases. These differences are not surprising, since differences among cultivars are commonly observed in response to factors such as soil fertility, water supply, diseases or storage temperature. However, it reinforces the importance of

assessing cultivars individually and explains the variable effects of CO<sub>2</sub> reported in the literature as noted in the introduction.

After darkening in response to a gas treatment occurred, the difference in colour between control tubers and gas-exposed tubers apparently stabilized to a consistent level in both SH and RB (Figure 5.1a, 5.1b), i.e. the colour scores progressively improved in both the control and the gas-treated tubers, but the control tubers continued to have a lighter colour than the treated tubers at each evaluation date after January. In other words, the rate of improvement was approximately the same in treated and control tubers, but the starting points differed due to the gas treatments. The improvements in colour scores may be attributable to respiration of sugars, reduction in the rate of conversion of sucrose to reducing sugars, or conversion of reducing sugars back to sucrose.

In the IN and DP tubers, processing colour of tubers in the control treatment was relatively stable throughout the trials, except at the final evaluation in DP (Figure 5.1c, 5.1d, 5.1e). The rapid increase in colour scores observed at successive evaluation dates in SH and RB was not observed in IN and DP, nor was the darkening attributable to the gas treatments observed, except in IN in the CO<sub>2</sub> + ethylene treatment and in the ethylene alone treatment from March onward. The relative stability of colour in the control tubers may be attributable, at least in part, to the relatively light initial processing colour of IN and DP in comparison with RB and SH (Figure 5.1). The data seem to suggest that processing colour is less affected by both storage duration and applied treatments when the initial colour is very light than when the colour begins at a darker shade. However, this is likely most attributable to cultivar differences.

The darkening of processing colour observed near the end of the trials in IN and DP is likely attributable to advancing physiological age, which may have increased their sensitivity to the gas treatments. Exposure to CO<sub>2</sub> alone had little to no effect on processing colour of these two cultivars (Figure 5.4, 5.5).

In general, any change in processing colour in response to a stimulus is attributable to either an increase in the concentration of reducing sugars in the tubers, either from accelerated starch breakdown and conversion of sucrose to

reducing sugars, or from a reduction in the sink for those sugars, e.g. slower respiration, or reduced rate of conversion to sucrose and starch, or inhibited sprout growth, or some combination of these factors (Burton et al. 1992; Storey and Davies 1992). When the two gases studied here were present simultaneously, the effect on processing colour observed in these trials may actually be additive, rather than a direct interaction. Each gas likely affects a different metabolic pathway, and the rate and degree of each response is influenced by cultivar and probably also by physiological age. The current data suggest that the responses to the gases follow different time-courses among the cultivars, and that one gas or the other appears to dominate the effect, depending on cultivar. The overlap of these responses made it difficult to distinguish the effects of ethylene from the effects of CO<sub>2</sub>, because both were measured by changes in processing colour. The short duration of the previous trials (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009) may have obscured the effects of each gas. In those trials, exposure to the CO<sub>2</sub> and ethylene began either in December or in March. In contrast with the work reported here, the tubers used in the March trials of the previous work were not exposed to either gas before the trials started, except for the endogenous quantities of both gases and atmospheric concentrations of CO<sub>2</sub> (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009). The treatment concentrations of CO<sub>2</sub> and ethylene applied in this study were well above the endogenous and atmospheric levels, and elicited the reported responses. Nevertheless, the concentrations of CO<sub>2</sub> and ethylene applied here can easily occur in the atmosphere of commercial storage buildings.

The observed response of IN tubers to the two gases was more consistent with effects observed in the short-term trials with RB (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009) than were the observed long-term effects on RB. This may reflect a true interaction occurring in these tubers; alternatively the effects of these gases were more strongly influenced by the physiological age of the tubers in IN than in the other cultivars. Investigation of the effects of the gas treatments on tuber metabolites such as the enzymes involved with carbohydrate storage and breakdown would help to provide insight into these questions. However, such investigations were beyond the scope of the trials reported here.

Despite these complications it is clear that both trace ethylene and elevated CO<sub>2</sub> in the storage atmosphere are important in the maintenance of

fry colour of stored processing potatoes, although sometimes in different time-frames. Furthermore, the dynamic nature of potato storage conditions, in which concentrations of these two gases can vary independently across both short and long time-scales, emphasizes the importance of developing a better understanding of their individual and combined effects on fry colour. This could have significant implications for storage of processing potatoes, for which retention of very pale fry colour is an important processing - and therefore economic - concern. Additional trials over several storage seasons would provide further clarification of these responses. In addition, the selection process for new processing cultivars should include an evaluation of the storage time  $\times$  CO<sub>2</sub>  $\times$  ethylene effects.

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## Chapter 6

### The Combined Effect of CO<sub>2</sub> and Ethylene Sprout Inhibitor on the Fry Colour of Stored Potatoes (*Solanum tuberosum* L.)\*

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#### Abstract

Recently it has been shown that the darkening of potato processing colour attributable to a trace concentration of ethylene gas is more severe when CO<sub>2</sub> is also elevated. In view of the increasing use of ethylene gas for sprout suppression in potato storage facilities, it was considered important to determine whether this effect also occurs at the much higher ethylene concentration used in commercial practice. Sprouting and processing colour of the French fry cultivars Russet Burbank, Shepody and Innovator and the potato crisp cultivar Dakota Pearl were tested during the November to June storage season of two consecutive years. Treatments were 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene in a factorial design, plus a chlorpropham check. The 0 CO<sub>2</sub> + 0 ethylene treatment constituted an untreated control. The ethylene exposure was commenced abruptly to maximize its effect on colour. The main effect of ethylene resulted in darker processing colour in all cultivars, whereas darkening attributable to the main effect of CO<sub>2</sub> was observed only in Innovator and Dakota Pearl. The statistical interaction of the CO<sub>2</sub> and ethylene was not significant except in Dakota Pearl Hunter a (redness) scores, although a tendency to darker colour when both gases were present was seen in Russet Burbank and Innovator at all evaluation dates. The results indicate that both gases can affect processing colour when ethylene is used to control sprouting, although considerable variability in the response exists among cultivars. This variability in combination with management of storage conditions such as temperature and CO<sub>2</sub> can be utilized to minimize the impact of these gases on the processing colour of stored potatoes.

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## 6.1. Introduction

For the potato processing industry, the finished colour of their processed products is one of the most important quality aspects. Although the specific preferred shade of processed potato products varies somewhat among marketplaces, a relatively light colour is generally preferred over a dark colour. The light-coloured products return a high market price, and therefore processors will usually pay a higher price to their suppliers as an incentive to obtain tuber lots which will fry to a light colour.

Darkening of processed potato products is the result of Maillard browning during frying. This is a non-enzymatic reaction which occurs in many foods, whereby colourless reducing sugars (mainly glucose and fructose in potatoes) and free amino acids combine during high-temperature cooking (Mazza 1983; Burton et al. 1992). Since acrylamide has been found to be one of the possible Maillard reaction products (Tareke et al. 2002; Serpen and Gökmen 2009), retaining a pale processing colour has gained even greater importance in recent years. A key factor in producing light-coloured processed potato products is to use raw tubers which have low reducing sugar content. Reducing sugar content has also been shown to be the limiting factor in acrylamide production in processed potato products (Biedermann-Brem et al. 2003; Williams 2005).

To ensure that their tubers will have low reducing sugars to meet the processors' requirements, potato producers choose appropriate cultivars and employ careful production and harvest practices. In many production regions, a large portion of the harvested crop must be stored for several months before processing. Although the tubers are usually dormant at harvest, they continue to age physiologically during storage. Tubers which are stored beyond the end of their natural dormancy period will sprout, which increases losses but usually also their reducing sugar content. Sprout inhibitors such as chlorpropham (isopropyl-(N-3-chlorophenyl) carbamate; CIPC) are commonly applied to prevent sprouting and thereby prolong storability. In recent years, consumer concerns about pesticides in foods have spurred development of alternative potato sprout inhibitors, such as 1,4-dimethylnaphthalene, certain plant essential oils and ethylene gas (Buitelaar 1987; Prange et al. 1997, 1998; Kleinkopf et al. 2003).

Ethylene gas at concentrations of ca. 4 to 10  $\mu\text{L L}^{-1}$  in the storage atmosphere throughout the storage period is a safe, clean and effective sprout inhibition method which leaves no residue in the treated tubers (Prange et al. 1998). It has been used extensively in the UK over the past several years, and more recently in several other countries. However, ethylene gas can cause tuber reducing sugars to increase (Prange et al. 1998). Therefore its commercial use to date has been mostly for potatoes destined for the fresh market, where elevated sugars are not usually problematic because home preparation such as boiling is not hot enough to form Maillard products (FAO-CODEX 2009).

The increased sugar content in response to ethylene gas is influenced by cultivar, applied gas concentration, and method of exposure (Gichohi and Pritchard 1995; Prange et al. 2005; Daniels-Lake et al. 2005a, 2007). Careful application methodology greatly reduces or eliminates the effect of ethylene on processing colour (Daniels-Lake et al. 2005a, 2007). This fact, coupled with its efficacy and safety, has generated significant interest in Japan, where ethylene is now used successfully as a sprout inhibitor for tubers processed into potato crisps (H Yamamichi, personal communication).

In recent years, it was discovered that the negative effect of trace amounts of ethylene gas (e.g. 0.5  $\mu\text{L L}^{-1}$ ) on potato fry colour is increased when elevated CO<sub>2</sub> (e.g. 2%) from tuber respiration or other sources is also present (Daniels-Lake et al. 2005b). This response is dose-dependent for both gases (Daniels-Lake and Prange 2009), can be mitigated by pre-treatment of the tubers with the ethylene blocker 1-methylcyclopropene (Daniels-Lake et al. 2008), and varies somewhat among cultivars and duration of storage (Daniels-Lake 2012). It is not known, however, whether the interaction with CO<sub>2</sub> is also an important factor affecting processing colour when ethylene is used as a sprout inhibitor, i.e. at much higher ethylene concentrations than the trace amounts assessed previously. Therefore, trials were initiated to investigate the potential interaction at high levels of ethylene.

## **6.2. Materials and Methods**

The trials were conducted during two consecutive storage seasons, i.e. November 2009 to June 2010 and November 2010 to June 2011, at the

Agriculture and Agri-Food Canada potato postharvest research lab at the Atlantic Food and Horticulture Research Centre in Kentville, Nova Scotia, Canada. During both years, potatoes of cultivars Russet Burbank (RB), Shepody (SH), Innovator (IN) and Dakota Pearl (DP) were each obtained from two different commercial potato growers in eastern Canada, except in 2009-2010 when the DP tubers were from a single source only. Each year the potatoes arrived at the lab in mid-October to early November, where they were stored at 13 °C for a few weeks to encourage suberization and wound healing, and then gradually cooled to 9 °C (1 °C per week over four weeks).

Samples of ten healthy, relatively uniform tubers (approximately 2 kg) from a single cultivar × source were randomly selected and placed in mesh onion sacks. The sacks were placed in PVC baskets, sealed inside stainless steel chambers and stored in a temperature-controlled room which maintained the temperature at  $9 \pm 0.3$  °C. Two chambers, each containing four baskets, were assigned to each treatment. At the start of the storage season, each basket held eight sacks of one cultivar from one source, except SH for which only seven sacks were stored due to the shorter storage suitability of this cultivar. Each sack was pre-assigned to an evaluation date according to the experimental design.

Each chamber had dedicated ventilation and atmospheric controls to provide the gas treatments. Five treatment regimes were applied, i.e. 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene gas in a 2 × 2 factorial design, plus a check which was treated with chlorpropham (CIPC) sprout inhibitor. The 0 CO<sub>2</sub> + 0 ethylene treatment constituted an untreated control. Tuber samples for the CIPC check were dipped in a 1% active ingredient (a.i.) water emulsion of chlorpropham (Sprout-Nip EC, 320 g L<sup>-1</sup> a.i., Stanchem Inc, Etobicoke, Ontario, Canada) in early December after the suberization phase was completed.

Three times each day, the storage chamber atmospheres were flushed for 1.5 h with ambient air amended with appropriate compressed gases (Praxair Inc, Dartmouth, Nova Scotia, Canada) to establish and maintain the desired concentrations of gas needed for the treatments. The untreated control and CIPC check chambers were flushed with unamended ambient air on the same schedule. A paper sack containing ca. 0.5 kg of hydrated lime (Ca(OH)<sub>2</sub>; Graymont (QC) Inc., Boucherville, Quebec, Canada) was placed



inside the chambers designated 0 CO<sub>2</sub>, to scrub ambient and respired CO<sub>2</sub> from the chamber atmospheres. An open tray of distilled water was placed inside each chamber to help maintain relative humidity at ca. 95% throughout the trials.

Gas delivery and control equipment was as described by Daniels-Lake et al. (2005b). The commencement of exposure to ethylene gas was done abruptly, which is known to have a significant darkening effect on the processing colour of treated tubers (Daniels-Lake et al. 2007). The abrupt method of introducing the ethylene was chosen for these trials to ensure that any differences attributable to ethylene would be clearly identifiable. The concentration of ethylene gas in the chambers was monitored automatically, as described in Daniels-Lake et al. (2005b). In 2009-2010, the CO<sub>2</sub> concentrations were monitored approximately daily, using a handheld gas monitor (CheckPoint, PBI Dansensor America, Glen Rock, New Jersey, USA). In addition, the CO<sub>2</sub> concentrations were rechecked approximately bi-weekly using a hand-held Vaisala CO<sub>2</sub> instrument (model GMP70, Vaisala, Vantaa, Finland), to confirm the CO<sub>2</sub> measurements. In 2010-2011, the CO<sub>2</sub> concentrations were monitored daily Monday through Friday using the Vaisala instrument only. During both years, manual adjustment of the gas delivery rates ensured that the desired concentration of each gas was maintained inside each of the chambers.

Each year, the initial processing colour of all four cultivars from each source was evaluated soon after the tubers were received at the lab. The French fry colour of RB, SH and IN was assessed as described in Daniels-Lake et al. (2005b), using an Agtron reflectance spectrophotometer (Agtron Inc, Sparks, Nevada, USA) to measure colour scores. Higher Agtron scores represent lighter fry colour. North American French fry processors generally prefer scores of 70 Agtron reflectance units (ARu) or higher and often pay a premium price for tubers which will fry to Agtron scores above 80 ARu. French fries which score in the range of 90 to 120 ARu appear very white to the naked eye. The potato crisp colour of DP was assessed as described in Daniels-Lake (2012), using a Hunter Lab colour analyser (LabScan model WE, Lyssack Associates, Toronto, Canada). Potato crisp processors prefer a high Hunter L score (light to dark, where a higher number indicates a whiter shade) and a low Hunter a score (green to red, where a higher number indicates a stronger red hue). Very light-coloured potato crisps usually have Hunter L and Hunter a scores from 70 to 90 and 3 to 8, respectively. Hunter b scores (blue

to yellow) are not usually noted. During each year the processing colour, weight loss and sprouting of pre-designated samples from each source × treatment combination were evaluated at intervals of four weeks after the beginning of the trial.

The customized experimental design was a replicated two-way factorial design plus a check, in a split plot arrangement with treatment as the main plot and evaluation date as the sub-plot. In addition to the CIPC check, two levels of CO<sub>2</sub> exposure (0 and 2%) crossed with two levels of ethylene exposure (0 and 10 μL L<sup>-1</sup>) provided the four factorial treatments. Physical replication was accomplished by using potatoes of the same cultivar from two different growers within a year, and replication in time was achieved by repeating the trials during a second year. For each cultivar, the data from the 2 years were combined and analysed statistically by ANOVA using Genstat v.15 statistical software (VSN International 2012). Sprout mass and maximum sprout length data were transformed to log<sub>10</sub> values before statistical analysis, to normalize the data. Means were back-transformed before presentation. Differences were considered significant if  $P \leq 0.05$ .

### 6.3. Results and Discussion

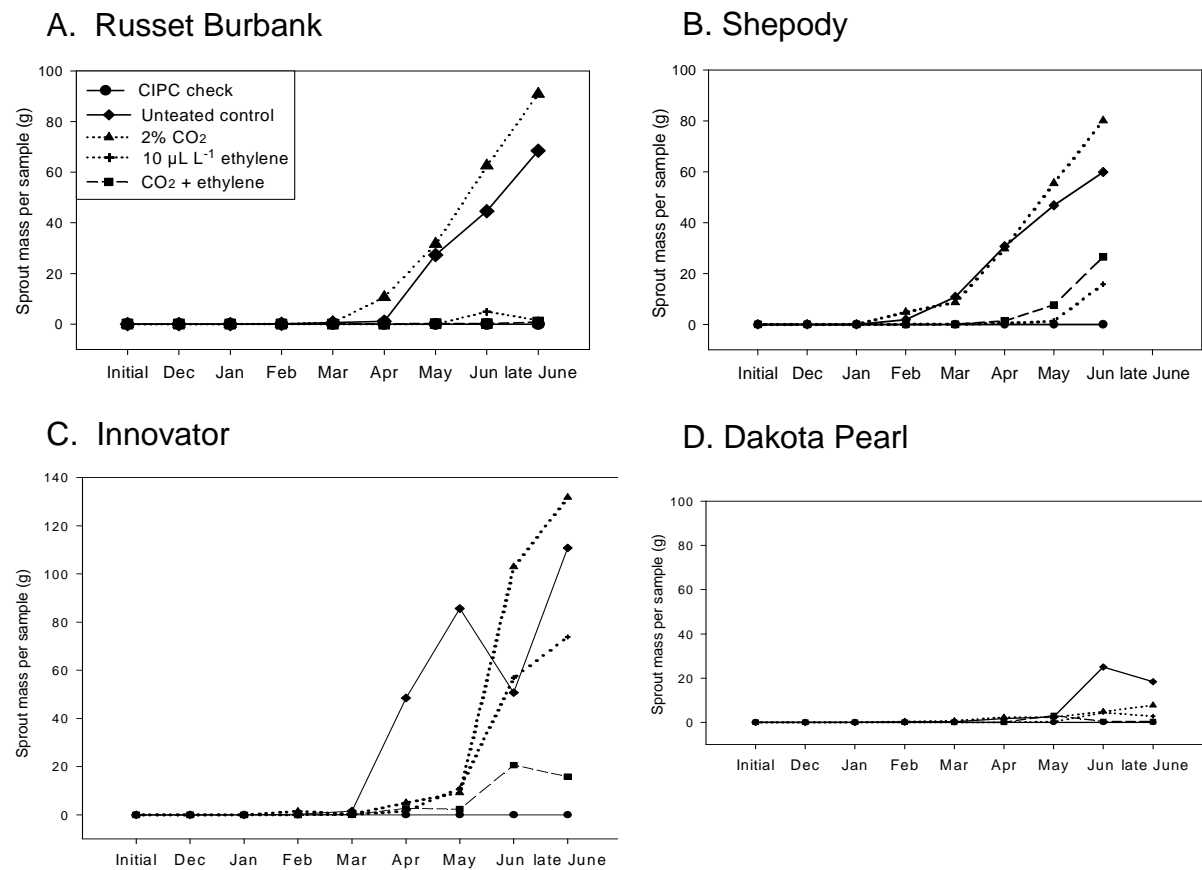
Some variation was observed among cultivars and between years with regard to processing colour and sprouting, which was not surprising. Variability among cultivars in response to ethylene and the combination of CO<sub>2</sub> and ethylene has been reported previously (Prange et al. 2005; Daniels-Lake et al. 2007; Daniels-Lake 2012). The difference between years was not significant within cultivars, except in SH which had much darker initial colour in the first year than in the second year. However, within each cultivar the responses to the treatments were very similar across years.

#### 6.3.1. Sprouting

Sprouting was observed in the untreated control tubers of all cultivars, beginning at the February evaluation in SH, IN, and DP, and at the March evaluation in RB. The overall means in maximum sprout length and sprout mass were greatest in RB and IN, and least in DP (data not presented). SH

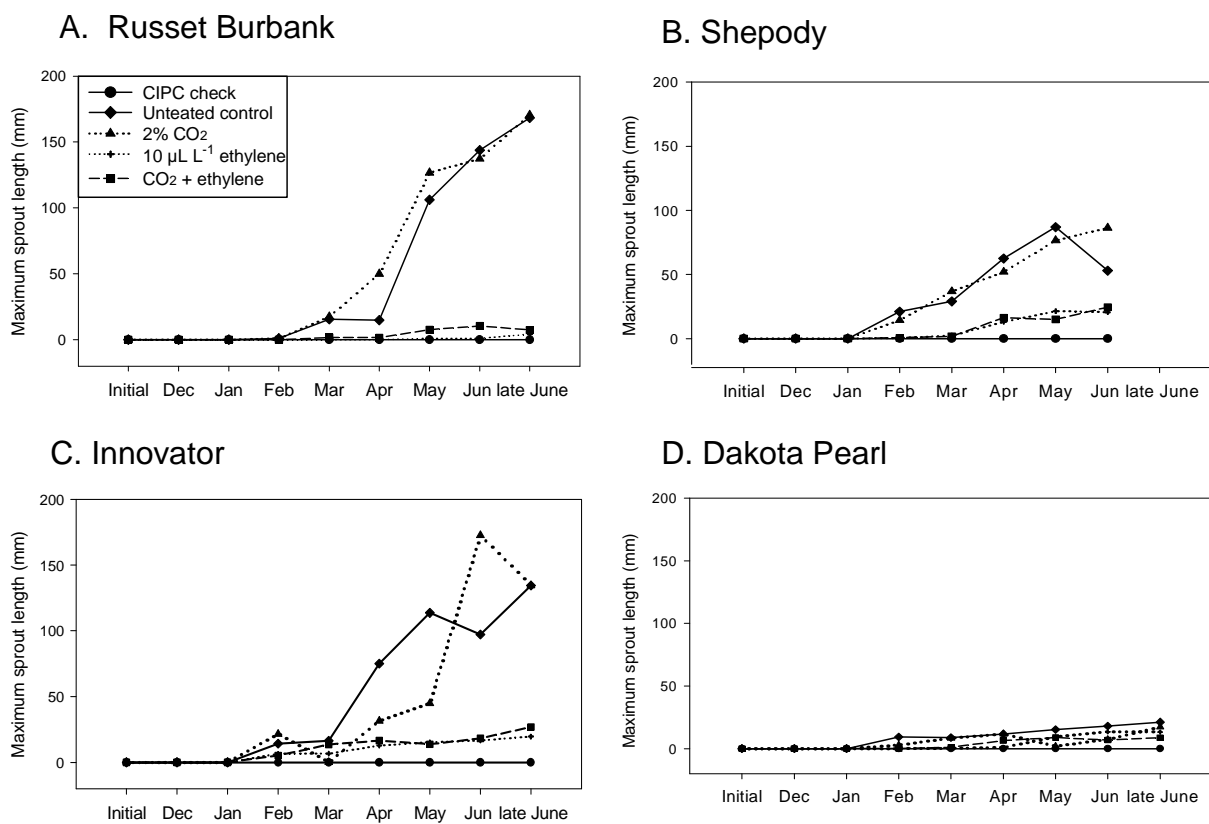
was intermediate between these extremes for both measured sprouting characteristics.

Sprouting was very effectively controlled by the CIPC check treatment in all cultivars for the duration of the trials (Figure 6.1, 6.2). No measurable sprouts were observed in the CIPC treatment in any cultivars at any evaluation dates. In contrast, in both the untreated control and the 2% CO<sub>2</sub> treatments, profuse sprouting was observed in RB, IN and SH. This was expected, since nothing was applied to these tubers to control sprouting. Very little sprouting was observed in DP in any of the treatments, except in the untreated control at the final two evaluation dates (Figure 6.1), suggesting a relatively long natural dormancy for this cultivar despite the appearance of a sufficient number of small sprouts during mid-winter to judge it to be sprouting.



**Figure 6.1.** Mass of sprouts from tubers stored for several months with 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene gas, or chlorpropham (CIPC). Each datum is the mean of four samples of ten tubers, which has been back-transformed from the log<sub>10</sub> value used in the statistical analysis to normalize the data. Standard error values from the statistical analyses apply only to the log<sub>10</sub> means, and therefore are not shown.

Sprouting in the CO<sub>2</sub> treatment was similar to the untreated control ( $P > 0.05$ ) in RB, SH and DP. In IN, sprout mass and maximum length in the CO<sub>2</sub> treatment were lower than in the untreated control at the April and May evaluation dates, but were higher than the control at the June evaluation (Figure 6.1, 6.2). This may suggest a small effect of CO<sub>2</sub> on sprout growth, but more likely it is a reflection of the natural variability within the experimental material. Nevertheless, sprouting of IN tubers in the control and CO<sub>2</sub> treatments was much greater than in the CIPC check or either of the treatments which included ethylene.



**Figure 6.2.** Maximum sprout length among tubers stored for several months with 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene gas, or chlorpropham (CIPC). Each datum is the mean of four samples of ten tubers, which has been back-transformed from the log<sub>10</sub> values used in the statistical analysis to normalize the data. Standard error values from the statistical analyses apply only to the log<sub>10</sub> means, and are therefore not presented

Sprouting was strongly inhibited in the 10 µL L<sup>-1</sup> ethylene and the CO<sub>2</sub> + ethylene treatments, although there was some variability among cultivars in the amount of sprouting observed (Figures 6.1, 6.2). Sprouting in IN and SH

was somewhat greater under ethylene sprout inhibitor than in the CIPC check; however sprouting of ethylene-treated tubers was much less than in the untreated control in both cultivars. Similar variation among cultivars in response to ethylene sprout inhibitor has been reported previously (Prange et al. 2005; Daniels-Lake et al. 2007). The pertinent point is that the concentration of ethylene gas used in these trials was sufficient to significantly inhibit sprouting.

### 6.3.2. Processing Colour

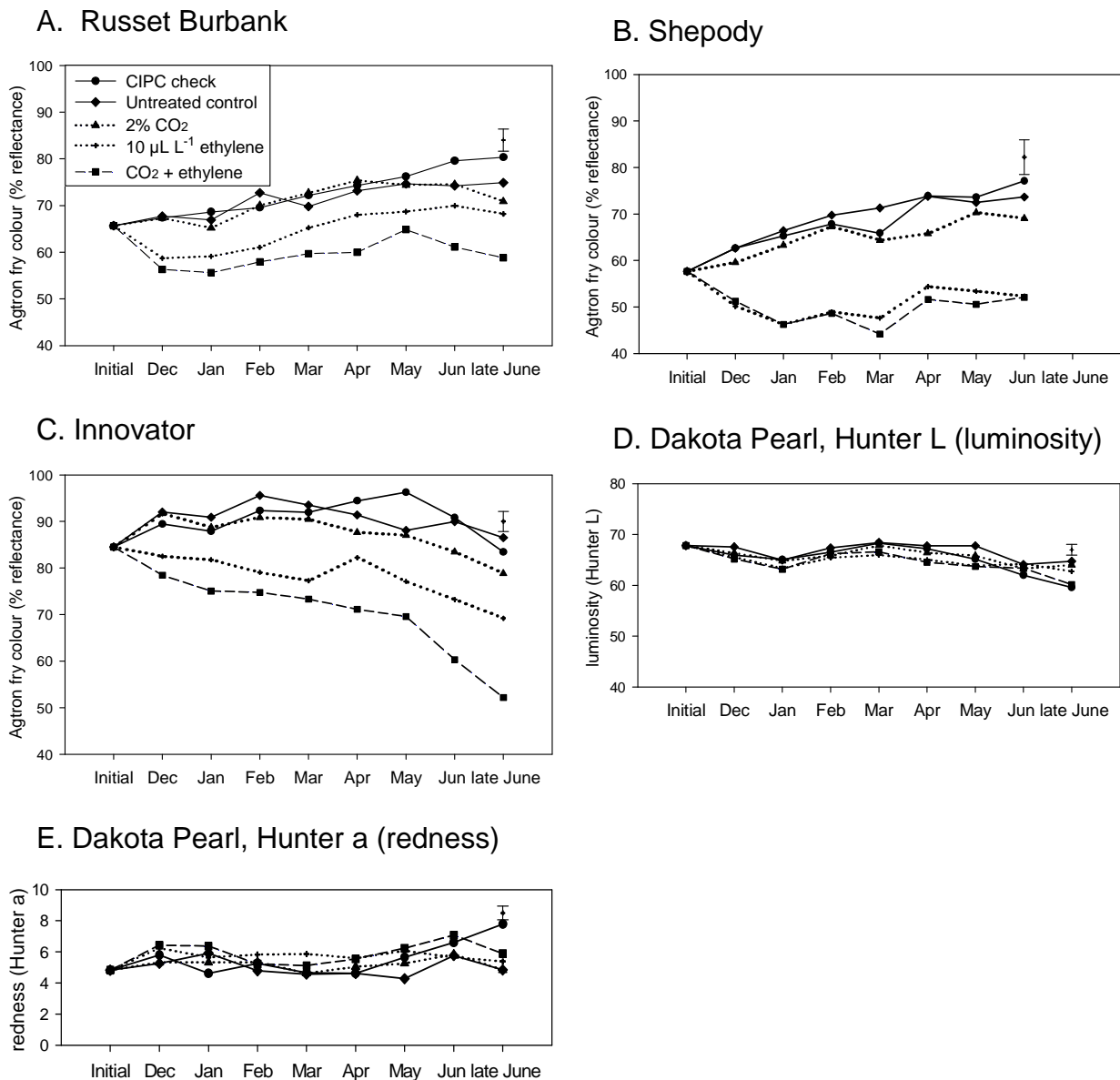
The processing colour of RB and SH tubers in the CIPC check and untreated control treatments lightened progressively as the storage term proceeded (Figure 6.3). This trend was not observed in IN and DP, where processing colour in the check and control tubers changed very little through the April evaluation, inclusive, but darkened slightly at each evaluation thereafter. The main effect of evaluation date on processing colour was significant in RB, SH, IN and DP (Hunter a only;  $P < 0.05$ ), and is likely attributable to cultivar differences and physiological aging.

In all four cultivars, the main effect of ethylene resulted in significantly darker processing colour (Tables 6.1, 6.2;  $P < 0.05$ ). Similar concentrations of ethylene gas introduced abruptly are known to cause darkening of fry colour (Prange et al. 1998; Daniels-Lake et al. 2007). In all cultivars, the darkening attributable to  $10 \mu\text{L L}^{-1}$  ethylene was greater than in the previously-reported work where only a trace level of ethylene ( $0.5 \mu\text{L L}^{-1}$ ) was applied (e.g. 18 vs. 9 ARu, respectively for SH tubers; Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009; Daniels-Lake 2012).

In contrast with the effect of ethylene, the main effect of CO<sub>2</sub> on processing colour was significant only in IN and DP Hunter L scores (Tables 6.1, 6.2). This differs from the recent report of Daniels-Lake (2012), who found that three of these same four cultivars had darker processing colour in response to the same concentration of CO<sub>2</sub>. These differences may be attributable to growing season variations, and emphasize the importance of multi-year trials. They also highlight the need for additional study to further elucidate the effects of elevated CO<sub>2</sub> alone on important processing cultivars.

There were significant two-way interactions in the fry colour of IN tubers,

i.e. evaluation date  $\times$  CO<sub>2</sub>, and evaluation date  $\times$  ethylene, which take precedence over the main effects (Table 6.1;  $P < 0.001$  for both interactions). For CO<sub>2</sub>  $\times$  evaluation date, there was a small but steady trend in the 0 and 2% CO<sub>2</sub> treatments toward darker fry colour as time in storage increased, and this effect was greater in tubers which were treated with 2% CO<sub>2</sub> (Figure 6.4a).



**Figure 6.3.** Processing colour of potato tubers stored for several months with 0 or 2% CO<sub>2</sub> and 0 or 10  $\mu\text{L L}^{-1}$  ethylene gas, or chlorpropham (CIPC). Vertical bars represent  $\pm$  SEM (2.343 at  $P > 0.05$ , 3.734 at  $P > 0.05$ , 2.167 at  $P > 0.05$ , 1.071 at  $P > 0.05$  and 0.434 at  $P < 0.001$ , for Russet Burbank, Shepody, Innovator, Dakota Pearl Hunter L and Dakota Pearl Hunter a, respectively)

**Table 6.1.** French fry colour of tubers stored with 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene gas, or chlorpropham (CIPC). Higher scores indicate a lighter colour and are therefore preferable

Cultivar	CIPC	CO <sub>2</sub> (%)		ethylene (µL L <sup>-1</sup> )		mean	P-value	SEM <sup>z</sup>
		0	2	0	10			
<u>Russet Burbank</u>		Fry colour, Agron percent reflectance						
main effects	CO <sub>2</sub>	73.5	68.3	65.3	- <sup>y</sup>	-	68.1	nsd <sup>x</sup>
	ethylene	73.5	-	-	71.5	62.1		<0.001
	evaluation date <sup>w</sup>							<0.001
interactions							68.1	all nsd
<u>Shepody</u>								
main effects	CO <sub>2</sub>	69.5	60.2	57.4	-	-	61.0	nsd
	ethylene	69.5	-	-	67.8	49.8		<0.001
	evaluation date							0.002
interactions							61.0	all nsd
<u>Innovator</u>								
main effects	CO <sub>2</sub>	90.8	84.4	78.3	-	-	83.3	0.002
	ethylene	90.8	-	-	89.2	73.6		<0.001
	evaluation date							<0.001
CO <sub>2</sub> × evaluation date interaction								
	Dec	89.4	87.2	85.1	-	-		
	Jan	87.9	86.3	81.9	-	-		
	Feb	92.3	87.3	82.8	-	-		
	Mar	92.0	85.4	81.9	-	-		
	Apr	94.4	86.8	79.4	-	-		<0.001
	May	96.2	82.6	78.3	-	-		
	Jun	90.8	81.6	71.9	-	-		
	late Jun	83.4	77.9	65.5	-	-		
ethylene × evaluation date interaction								
	Dec	89.4	-	-	91.9	80.5		
	Jan	87.9	-	-	89.8	78.4		
	Feb	92.3	-	-	93.2	76.9		
	Mar	92.0	-	-	92.0	75.3		
	Apr	94.4	-	-	89.5	76.7		<0.001
	May	96.2	-	-	87.6	73.3		
	Jun	90.8	-	-	86.7	66.8		
	late Jun	83.4	-	-	82.7	60.7		
other interactions							83.3	all nsd

<sup>z</sup> Standard error of the mean<sup>y</sup> Not applicable in this comparison<sup>x</sup> Not significantly different, i.e. P > 0.05<sup>w</sup> To avoid confusion and reduce the size of this table, means data for the 8 evaluation dates are not presented

Similarly in the ethylene  $\times$  evaluation date interaction, the colour darkened steadily as time in storage increased, and this was more severe in tubers treated with  $10 \mu\text{L L}^{-1}$  ethylene (Figure 6.4b). Clearly, both  $\text{CO}_2$  and ethylene darkened fry colour of IN tubers to a greater extent as storage time increased, which is consistent with the suggestion in previously published work (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009; Daniels-Lake 2012) that non-dormant tubers are more sensitive to these gases than are dormant tubers.

The statistical interaction of  $\text{CO}_2 \times$  ethylene was not significant, except in the three-way interaction for DP Hunter a (redness scores) which also included evaluation date ( $P < 0.001$ ; Table 6.2). The lowest (best) Hunter a score was in the untreated control at the May evaluation date and the highest (worst) score was in the CIPC check at the late June evaluation date (4.28 and 7.78, respectively). Although there were some differences among other observed values, there were no consistent differences or trends across evaluation dates which could be attributed to the applied treatments (Table 6.2). This cultivar is considered to be somewhat resistant to low temperature sweetening, and therefore DP tubers are usually stored at a cooler temperature than was used in these trials. Perhaps a stronger response to the applied treatments would have occurred under cooler storage conditions. Alternatively, DP tubers may be resistant to the effects of  $\text{CO}_2$  and/or ethylene on tuber sugars and crisp colour, regardless of temperature. Elucidation of this response was beyond the scope of the present study. However, ethylene is known to effectively control sprouting over a wide range of storage temperatures, i.e. from  $4^\circ\text{C}$  to  $13^\circ\text{C}$ , with a reduced effect on fry colour at the warmer temperatures (Daniels-Lake et al. 2007; J Barnes, personal communication).

In the three French fry cultivars (RB, SH and IN), the darkest fry colour at every evaluation date was observed in tubers from the  $\text{CO}_2 +$  ethylene treatment (Figure 6.3). The colour of tubers exposed to  $10 \mu\text{L L}^{-1}$  ethylene alone was midway between the  $\text{CO}_2 +$  ethylene treatment and the remaining three treatments in both RB and IN. This suggests an additive or interactive effect as observed previously (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange, 2009; Daniels-Lake 2012), i.e. the response to ethylene was greater when  $\text{CO}_2$  was also present. However, in SH tubers, fry colour in the ethylene and  $\text{CO}_2 +$  ethylene treatments was almost identical (Figure 6.3).



**Table 6.2.** Crisp colour of Dakota Pearl tubers stored with 0 or 2% CO<sub>2</sub> and 0 or 10 µL L<sup>-1</sup> ethylene gas, or chlorpropham (CIPC). A higher (whiter) score is preferred in Hunter L, whereas a lower (less red) score is preferred in Hunter a.

## a. Hunter L (luminosity score)

		CIPC	CO <sub>2</sub> (%)		ethylene (µL L <sup>-1</sup> )		mean	P-value	SEM <sup>z</sup>
			0	2	0	10			
main effects	CO <sub>2</sub>	65.0	65.5	64.8	- <sup>y</sup>	-		0.035	0.2006
	ethylene	65.0	-	-	66.1	64.3		<0.001	0.2006
	evaluation date <sup>x</sup>							<0.001	0.5603
interactions							65.1	all nsd <sup>w</sup>	

## b. Hunter a (redness score), main effects

		CIPC	CO <sub>2</sub> (%)		ethylene (µL L <sup>-1</sup> )		mean	P-value	SEM
			0	2	0	10			
main effects	CO <sub>2</sub>	5.62	5.39	5.59	-	-	5.52	nsd	
	ethylene	5.62	-	-	5.1	5.88		<0.001	0.108
	evaluation date							<0.001	0.2229

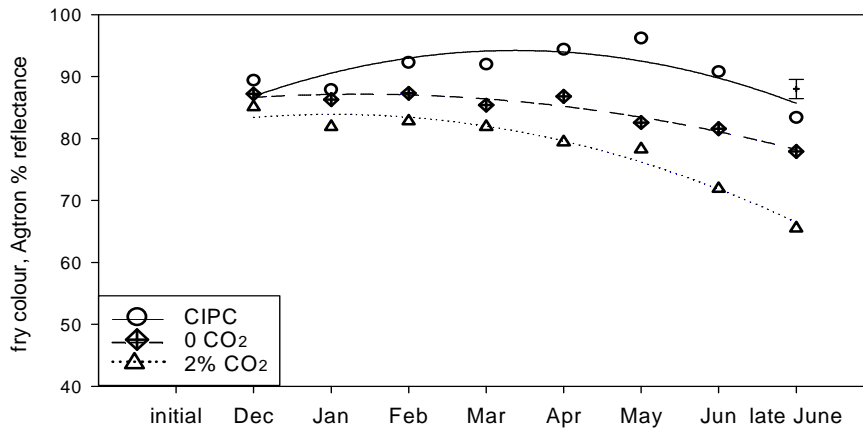
## c. Hunter a, interactions

		CIPC	untreated control <sup>v</sup>	2% CO <sub>2</sub>	10 µL L <sup>-1</sup> ethylene	10 µL L <sup>-1</sup> ethylene + 2% CO <sub>2</sub>	mean	P-value	SEM
CO <sub>2</sub> × ethylene × evaluation date									
		Jan	4.61	5.92	5.32	5.64	6.37		
		Feb	5.27	4.78	5.33	5.82	5.22		
		Mar	4.65	4.56	4.62	5.86	5.12		
		Apr	4.62	4.61	5.04	5.59	5.54	<0.001	0.4434
		May	5.65	4.28	5.26	6.07	6.23		
		Jun	6.60	5.77	5.83	5.64	7.07		
		late Jun	7.78	4.84	4.84	5.39	5.89		
other							5.52	all nsd	

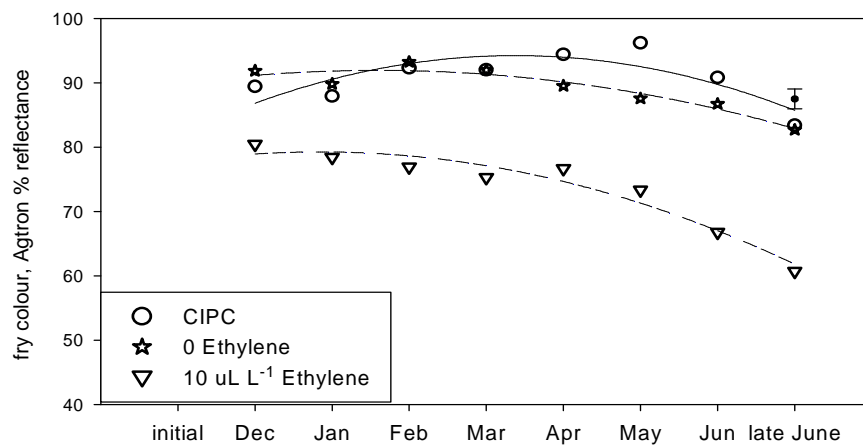
<sup>z</sup> Standard error of the mean<sup>y</sup> Not applicable in this comparison<sup>x</sup> To avoid confusion and reduce the size of this table, means data for the 8 evaluation dates are not presented<sup>w</sup> Not significantly different, i.e. P > 0.05<sup>v</sup> 0 CO<sub>2</sub> + 0 ethylene

This suggests that darkening in response to ethylene overwhelmed any contribution from CO<sub>2</sub>, and reflects the high sensitivity of SH to stresses including ethylene gas noted by other workers (Gichohi and Pritchard 1995; Prange et al. 2005).

A. Carbon dioxide



B. Ethylene



**Figure 6.4.** Effects on the fry colour of Innovator potatoes stored for several months in amended atmospheres. Vertical bars represent  $\pm$  SEM (1.532 at  $P < 0.001$  for both graphs)

In the present study, the tubers which were exposed to the factorial combinations of CO<sub>2</sub> and ethylene were not treated with CIPC sprout inhibitor, although a CIPC check treatment was included for comparison. However, in previously-reported work the tubers in all gas treatments were treated with CIPC sprout inhibitor (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009; Daniels-Lake 2012). Although this represents a difference in the

treatment protocols, CIPC is generally believed to have no effect on the processing colour of the treated tubers (e.g. Blenkinsop et al. 2002). Therefore CIPC treatment is unlikely to have contributed to the observed differences between the present study and previous work.

#### **6.4. Conclusions**

Although the results of the present study suggest that the effect on processing colour was primarily attributable to the presence of ethylene gas sprout inhibitor, there was a tendency in some cultivars to additional darkening when CO<sub>2</sub> was also present (Figure 6.3). This is consistent with published research, in which CO<sub>2</sub> plus a trace concentration of ethylene had a stronger negative effect on the fry colour of some cultivars than did ethylene alone (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009).

It is clear from this work that the presence of elevated CO<sub>2</sub> can contribute to darkening of processing colour in some cultivars when ethylene is used as a sprout inhibitor. However, the results of this study also reinforce assertions by Daniels-Lake et al. (2007) that the effect of ethylene sprout inhibitor on the colour of processed potato products varies among cultivars and can be manipulated by management operations such as choice of storage temperature, CO<sub>2</sub> control and method of ethylene application. Additional study of the effect of these factors on the colour of important processing cultivars will further elucidate these responses. This will provide additional tools to help the potato industry retain high quality during long-term storage of processing potatoes.

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# Chapter 7

## General Discussion

### 7.1 Terminology

Please note the following terminology which will be used in this Chapter, except where otherwise specified:

- The terms “French fries” and “potato chips” will be used in this discussion when referring to the processed potato products which are also known in some regions as “chips” and “crisps”, respectively.
- “Processed” and “processing” refer to commercial-style conversion of raw potatoes into French fries or potato chips, in which deep frying in oil is the significant step.
- “Colour” means the overall light to dark shade of the finished processed products, measured in either Agtron percent reflectance units or Hunter Luminosity (ARu or Hunter L, respectively). Darkening of colour is mainly attributable to Maillard browning during processing; a light colour is considered preferable to a dark colour.
- “Elevated CO<sub>2</sub>” means 2% CO<sub>2</sub> in the storage atmosphere, as applied in the research trials reported in Chapters 2 - 6.
- “Trace ethylene” means 0.5  $\mu\text{L L}^{-1}$  ethylene in the storage atmosphere, as applied in the research trials reported in Chapters 2 - 5.
- “High ethylene” means 10  $\mu\text{L L}^{-1}$  ethylene applied as a sprout inhibitor in the storage atmosphere, as used in the research trials reported in Chapter 6.

### 7.2 Introduction

The finished colour of processed potato products made from tubers which have been stored for several months depends upon the net results during storage of the numerous interconnected metabolic pathways of carbohydrate metabolism and cellular respiration, in combination with maturity

and physiological ageing within the tuber and external environmental factors such as growing conditions in the field, storage conditions after harvest and disease development (Schippers 1977; Marquez and Añon 1986; van Es and Hartmans 1987; Pritchard and Adam 1992; Li 2008). Each of these factors includes several components.

### 7.2.1. Carbohydrate Metabolism

Carbohydrate metabolism is responsible for the interconversion of sucrose, reducing sugars (hexoses) and starch. Among the numerous enzymes involved (for an outline, see Sowokinos 2001 or Li 2008), acid invertase and UDP-glucose pyrophosphorylase are believed to be particularly important in producing the reducing sugars (glucose and fructose in potatoes) which participate in Maillard browning (Sowokinos 1990a, 2001; Sowokinos et al. 1997; McKenzie et al. 2005, 2013). These carbohydrates are also used to build structural molecules for growth of new tissues such as sprouts.

### 7.2.2. Cellular Respiration

Respiration is closely aligned with carbohydrate metabolism because it is the carbohydrates, i.e. glucose and fructose, which are consumed to provide cellular energy. Carbohydrate metabolism and respiration share many enzymes, substrates and products. The respiration rate depends on temperature, cultivar genetics and tuber physiological age (Schippers 1977; Driskill et al. 2007; Bethke and Busse 2010). During the storage period, physiological age reflects whether the tuber is maturing and suberizing after harvest, or dormant, or sprouting, or senescing. The respiration rate is lowest when the tuber is dormant, whereas respiration rates during maturation and sprouting are markedly higher (Schippers 1977; Driskill et al. 2007; Knowles et al. 2009).

Cellular respiration can be broadly divided into cyanide-sensitive and cyanide resistant respiration. Cyanide-sensitive respiration, which requires oxygen to proceed and can be blocked by the addition of cyanide, is the primary method by which cells phosphorylate adenosine diphosphate (ADP) to the higher-energy adenosine triphosphate (ATP) molecules (Salisbury and



Ross, 1978). Cyanide-resistant respiration, also known as the alternative pathway, is much less efficient in producing ATP from carbohydrates, but it does provide some ATP molecules for cellular activities even when conditions are unfavourable for the main respiratory pathways to function. The cyanide resistant pathway does not require oxygen to function, and as the name implies it is not blocked by cyanide. Low oxygen, high CO<sub>2</sub>, and ethylene gas are all believed to induce or accelerate cyanide-resistant respiration in potato tubers (Solomos and Laties 1975; Day et al. 1978; Perez-Trejo et al. 1981; McAvoy and Janes 1990).

The tuber's overall respiration rate is determined by the abundance, activity rates and specific isozymes of the many enzymes involved in the respiratory pathways. These in turn are determined by the particular genetics of the cultivar, the rate of DNA transcription and subsequent translation into proteins/enzymes, the rate of enzyme breakdown, and physiological ageing (Sowokinos 1997, 2001; Pinhero et al. 2007; Li 2008; Stepanova and Alonso 2009; McKenzie et al. 2013). In addition, metabolic activities are controlled by internal signalling molecules, transcription factors, plant growth regulators, promoters, inhibitors, other bioregulators and feedback controls (McAvoy and Janes 1990; Driskill et al. 2007; Pinhero et al. 2007; Suttle 2007; Li 2008; Stepanova and Alonso 2009). Many of the reactions are reversible, with the net direction dependent in part upon substrate and/or product concentrations. The concentration of sugars in a tuber at any point in time therefore depends upon the accumulated effects of the activities and interactions of these many internal metabolic components, with modulation by external factors.

### 7.2.3. External Factors

The important external factors include both preharvest and postharvest components, such as soil fertility, weather and water supply during growth, pesticides, harvest date and handling, temperature at harvest and during storage, storage atmosphere, and stresses from diseases, insects, handling and pile pressure (Sowokinos 1990a, 2001; Kumar et al. 2004; Bethke and Busse 2010). All of these can affect the phenotypic expression of a tuber's genetic makeup and therefore its metabolic responses (Tai and Coleman 1999; Kumar et al. 2004). Of major importance is the temperature during storage, which directly affects the rate of metabolic reactions, but not always in

a simple manner. Since each enzyme has a specific temperature or temperature range for optimum activity, any particular storage temperature will favour some pathways or reactions while others may be hindered. Over time, these differences can lead to either accumulation or depletion of enzyme substrates or products including reducing sugars.

The duration of storage is also important because physiological ageing continues. The length of the storage period may be limited by the natural end of dormancy and growth of sprouts. For tubers which are stored beyond the end of natural dormancy, sprouting and senescence can cause sugar concentrations to increase as a result of the metabolic changes associated with becoming physiologically old tubers (Burton 1992). Sprout inhibitors can significantly extend the duration of storage, but some changes in sugar concentrations may still occur.

#### 7.2.4. Net Effect of Metabolism, Respiration and External Factors

Davies and Viola (1992) remind us that many metabolic pathways co-exist in potato tubers, and compete for common substrates. It is the net effect of all of these pathways and reactions which together determine the tuber reducing sugar content at the time of processing and therefore the processing colour (Burton 1978; Dwelle and Stallknecht 1978; Mazza et al. 1983; Burton et al. 1992; Tai and Coleman 1999; Kumar et al. 2004; Suttle 2007; Li 2008). In simple terms, if cellular respiration and production of reducing sugars during long-term storage are equal, there is no net change and processing colour is unaffected. If production of reducing sugars is greater than consumption by respiration, sugars accumulate and processing colour becomes darker over time. In the opposite scenario, sugars are depleted and colour becomes lighter.

Although many researchers continue working to unravel the fine details of these effects and interactions, the responses are fairly consistent among tubers of the same cultivar. Much knowledge has been accumulated by scientists and the potato industry to help producers and storage managers optimize the quality of the tubers presented to the processors. This, in turn, ensures high quality of the finished processed product which the processors bring to the marketplace.

For successful storage of processing potatoes, one must choose a suitable cultivar, grow it well, harvest it carefully and store it under favourable conditions. For those cultivars which are considered suitable for processing from long-term storage, the net effect of the many factors tends to favour relatively low reducing sugars for some suitable storage period under recognized conditions, to yield acceptably light-coloured products after processing. The preferred cultivars vary among production regions, and storage protocols are adapted for the region and the preferred cultivars to achieve best results. Nevertheless, unexpected increases in the reducing sugar concentrations of stored tubers are frequently observed. This is broadly attributable to a disturbance of the tuber metabolism during storage, but often the specific cause is not apparent. Clearly, further research is warranted.

#### 7.2.5. Project Objectives

The trials undertaken in this research project were focussed on investigating whether two specific external factors in the storage atmosphere, i.e. carbon dioxide and ethylene gas, affect tuber metabolism to cause higher reducing sugar content in the tubers as measured by darker finished colour of the processed potato products. Although understanding the specific activities of the many cellular components is very important from the physiology perspective, they were not studied directly in this project. It was considered useful to step back from that level of detail and investigate the changes in processing colour, including the time-scale of these changes, because this is what matters directly to the potato processing industry. This research was focussed on providing insight into the effects of these gases, in order to generate practical information to help the industry maintain the quality of potato tubers during storage in order to produce high-grade processed potato products which are desirable in the marketplace.

The research trials described in Chapters 2 through 6 addressed several questions regarding the relationships of processing colour and elevated CO<sub>2</sub> with or without ethylene gas, as stated in Section 1.6.3 of the General Introduction, i.e.:

1. Is elevated CO<sub>2</sub> in the storage atmosphere truly a cause of darkening of the processing colour of stored potato tubers?
2. Does ethylene gas play a role in the response to elevated CO<sub>2</sub>?

3. Can the responses to CO<sub>2</sub> and ethylene be prevented or reduced?
4. Are there threshold concentrations of CO<sub>2</sub> and ethylene in potato storage atmospheres, below which darkening does not occur?
5. Do different potato cultivars respond to CO<sub>2</sub> and ethylene in the same manner?
6. Does time in storage, i.e. tuber physiological age, play a role in the responses to CO<sub>2</sub> and ethylene?

This discussion integrates the stepwise information reported in the preceding Chapters into more comprehensive answers to these questions.

### **7.3. Is elevated CO<sub>2</sub> in the storage atmosphere truly a cause of darkening of the processing colour of stored potato tubers?**

In the short-duration trials described in Chapters 2, 3 and 4, elevated CO<sub>2</sub> applied alone did not affect the processing colour of Russet Burbank tubers (Tables 2.2, 3.2, Figure 4.1). However, in the longer duration trials reported in Chapter 5, the main effects of CO<sub>2</sub> and/or the interactions between CO<sub>2</sub> and evaluation date were associated with darker processing colour in all four cultivars (Figures 5.1a-e), and in Chapter 6 the main effect of CO<sub>2</sub> led to darker colour in Innovator tubers (Figure 6.3c).

It is useful to remember that in the 2 × 2 factorial experimental design employed in these trials, the means for the main effect of one factor included the combined results with and without the other factor. In other words, the main effect means for 0 CO<sub>2</sub> included data from both the untreated controls and the ethylene treatment without added CO<sub>2</sub>, while the means for elevated CO<sub>2</sub> included data from the CO<sub>2</sub> alone and the CO<sub>2</sub> plus ethylene treatments. Likewise, the means for the main effect of ethylene included the data from both the untreated controls and the elevated CO<sub>2</sub> treatment without added ethylene, and the means for added ethylene included data from both the ethylene-treated tubers and the CO<sub>2</sub> plus ethylene treatments. Differences among the individual treatments were analysed as interactions between the two main factors, i.e. 0 CO<sub>2</sub> plus 0 ethylene, 0 CO<sub>2</sub> plus ethylene, elevated CO<sub>2</sub> plus 0 ethylene, elevated CO<sub>2</sub> plus ethylene.

While the factorial design is an entirely valid and appropriate scientific

and statistical approach for these trials, the large magnitude of the responses to ethylene may have obscured another important response. When all of the results of all of the trials are considered together, a further observation stands out among the long-duration trials: there was a small but quite consistent trend to darker colour among Russet Burbank, Shepody and Innovator tubers exposed to elevated CO<sub>2</sub> applied alone, which appeared after at least 8 weeks of exposure (Figures 5.1a,b,c and 6.3a,b,c). Although this apparent response of processing colour to CO<sub>2</sub> was consistent within the three French fry cultivars, and was larger in Shepody tubers than in the Russet Burbank and Innovator tubers, its presence seems to have been masked by the much larger effects of the ethylene treatments in these trials.

Unlike plant parts from most other species, exposure of potato tubers to CO<sub>2</sub> increases their respiration rate (Day et al. 1978; Perez-Trejo et al. 1981; Sisler and Wood 1988). The reason for this is unclear, but it may represent a stress response. The elevated CO<sub>2</sub> applied in the trials described in Chapters 2 to 6 may have caused increased respiration in the tubers, although the rates were not measured. An increased respiration rate would have consumed tuber sugars faster and presumably improved (lightened) processing colour, as occurs during reconditioning. However, this is contrary to the observed results. Perhaps the sugar content also increased, to a greater extent than the increased respiration rate could consume.

Alternatively, as shown by Wills et al (1979), perhaps the elevated CO<sub>2</sub> did inhibit tuber respiration. This would at least partly explain the darker colour, i.e. a reduced respiration rate would allow the sugars being produced in the normal course of tuber metabolism to accumulate, darkening processing colour.

High CO<sub>2</sub> (2 to 12%) also increases ethylene production in many plant species including potato tubers, although very high concentrations (20 to 40%) can inhibit ethylene production and actions (Creech et al. 1973; Sisler and Wood 1988). In turn, ethylene increases both respiration rate and production of reducing sugars (Huelin and Barker 1939; Reid and Pratt 1972; Day et al. 1978; Rychter et al. 1979; Prange et al. 1998; cf. Section 7.4.1). Although the resulting increase in ethylene would have been rather small in the trials reported in Chapters 2 to 6, it may have been sufficient to account for the minor darkening which was observed.

Mazza and Siemans (1990) found that accumulated CO<sub>2</sub> in the atmosphere of commercial potato storage buildings during suberization, sprout inhibitor application, and as the tubers approach senescence causes higher sugars and darkens processing colour at these times. However, these observations may instead be attributable to accumulated ethylene from the tubers, from pathogens or from anthropogenic sources such as engine exhaust or burners used in CIPC application, which was likely also present at those times but was not measured. Denny and Thornton (1941) found that storage in 5% CO<sub>2</sub> increases sucrose but not reducing sugars in the tuber. Similarly, Reust et al. (1984) and Workman and Twomey (1970) reported that increased CO<sub>2</sub> in controlled atmosphere storage causes tuber sugars to increase. However, depleted oxygen and possibly an accumulation of ethylene may also account for these observations.

It is interesting to note that the responses to elevated CO<sub>2</sub> in the trials reported here were slightly larger and earlier among tubers which were treated with chlorpropham than without (Chapters 5 and 6, respectively; Figures 5.1a,b,c and 6.3a,b,c). Greater sensitivity of chlorpropham-treated tubers to CO<sub>2</sub> would be surprising, since chlorpropham is not considered to affect the processing colour of stored tubers (Blenkinsop et al. 2002). Furthermore, in the trials reported in Chapter 6, there was no difference in processing colour between the chlorpropham-treated and untreated control tubers in any of these cultivars (Figure 6.3a,b,c). This suggests a possible interaction between CO<sub>2</sub> and chlorpropham, e.g. perhaps the chlorpropham increased the sensitivity of the tubers to CO<sub>2</sub>, or maybe the CO<sub>2</sub> affected the response to chlorpropham. It is more likely, however, that the apparent differences reflect the natural variability of the potato material used in the trials.

In contrast to the observations regarding the three French fry cultivars, the processing colour of tubers of the potato chip cultivar Dakota Pearl was almost unaffected by CO<sub>2</sub> (Figures 5.1d,e, 6.3d,e). There was very little difference in processing colour among all of the treatments at all evaluation dates in all of the trials, in both Hunter L and Hunter a (redness score). Darkening of processing colour associated with the main effect of elevated CO<sub>2</sub> was significant, but the differences were less than 1 Hunter L unit darker than without elevated CO<sub>2</sub> in the trials described in Chapters 5 and 6, i.e. much less than the change in colour from the beginning to the end of storage (Table 6.2, Figure 5.5a). Similarly, the changes in Hunter a, though

statistically significant, were very small and no treatment-related trends were apparent across evaluation dates (Table 6.2, Figure 5.5b).

The minimal response of Dakota Pearl tubers to applied treatments may be attributable, at least in part, to their very low initial reducing sugar content, in comparison with the other three cultivars (0.9 vs. 9.0 to 49.5 mg g<sup>-1</sup> DW, respectively; Table 7.1). Since reducing sugar content is the limiting factor for Maillard browning (Denny and Thornton 1940; Marquez and Añon 1986), when reducing sugar content is very low there is little or no colour development during fry processing. The very small changes in reducing sugars observed in these trials (Table 7.1) may not have been sufficient to affect colour in a perceptible manner for this cultivar.

Storage temperature may have been another important reason for the low response of Dakota Pearl tubers to the applied treatments, since this cultivar is considered partially resistant to low temperature sweetening (CFIA 2013). The relatively warm storage temperature used in these trials (9 °C) may have been sufficient to protect processing colour in Dakota Pearl tubers, by retaining a relatively high respiration rate. Thus any additional sugars resulting from the applied treatments may have been consumed by cellular respiration, leaving little net change in sugars (Tables 7.1, 7.2). Warmer storage (i.e. 13 °C vs. 9 °C) reduces the darkening attributable to ethylene sprout inhibitor in some cultivars (Daniels-Lake et al. 2006), and a similar response may have reduced any effect of CO<sub>2</sub> and CO<sub>2</sub> plus ethylene on the processing colour of Dakota Pearl tubers. Finally, the duration of storage may have influenced the observed results, i.e. perhaps longer storage duration would have revealed a later response in processing colour. This idea is supported by the notably higher sugars and slightly darker colour observed among Dakota Pearl tubers at the end of the trials (Tables 6.2, 7.1, 7.2; Figures 5.5a,b).

#### **7.4. Does ethylene gas play a role in the response to elevated CO<sub>2</sub>?**

##### **7.4.1. Ethylene**

In the short-duration trials described in Chapters 2, 3 and 4, exposure to

trace ethylene gas provoked slight darkening of processing colour in Russet Burbank tubers (Tables 2.2, 3.2, 4.1). This response was also evident in Russet Burbank and Shepody tubers in the longer trials described in Chapters 5 and 6 during the early part of the storage term, but was followed by recovery to a lighter colour as storage continued (Figures 5.1a,b and 6.3a,b). Shepody tubers were more sensitive to trace ethylene than Russet Burbank tubers, as indicated by the greater degree of darkening.

**Table 7.1.** Reducing sugar content of four processing cultivars during storage.

a. Tubers stored with 0 or 2% CO<sub>2</sub> with or without 0 or 0.5 µL L<sup>-1</sup> ethylene (Chapter 5)

Cv	Treatment	Evaluation							
		Initial	Dec	Jan	Feb	Mar	Apr	May	Jun
glucose + fructose, mg g <sup>-1</sup> dry weight									
RB	CIPC <sup>y</sup>	14.8	13.7	13.9	11.4	8.7	8.3	7.5	5.7
	+ CO <sub>2</sub>		12.9	12.6	12.3	8.7	8.7	7.4	7.0
	+ ethylene		17.7	14.3	11.9	8.9	8.9	7.2	6.1
	both		16.5	16.7	11.8	10.3	10.3	10.1	7.5
SH	CIPC	49.5	40.0	29.4	29.1	25.4	23.3	20.4	19.0
	+ CO <sub>2</sub>		38.6	33.7	26.1	28.6	24.4	26.2	17.8
	+ ethylene		48.9	37.7	35.4	36.1	29.6	30.3	26.4
	both		43.4	44.1	39.3	36.5	34.7	29.3	33.0
IN	CIPC	9.0	8.5	7.9	6.7	6.2	6.7	5.1	7.5
	+ CO <sub>2</sub>		8.3	9.3	6.9	7.3	7.8	5.8	6.7
	+ ethylene		9.5	9.0	8.5	8.9	9.5	9.5	16.1
	both		11.3	10.3	9.5	9.8	11.7	11.7	19.5
DP	CIPC	0.9	0.8	0.8	0.5	0.6	0.9	1.0	2.6
	+ CO <sub>2</sub>		1.0	0.7	0.6	0.6	0.8	1.5	3.3
	+ ethylene		1.0	1.3	1.1	0.9	0.9	1.0	3.0
	both		1.1	1.0	1.1	0.8	1.1	1.4	3.8

<sup>z</sup> RB, Russet Burbank; SH, Shepody; IN, Innovator; DP, Dakota Pearl

<sup>y</sup> Chlorpropham

(table continued on next page)



**Table 7.1**, continued

b. Tubers stored with 0 or 2% CO<sub>2</sub> with or without 0 or 10 µL L<sup>-1</sup> ethylene (Chapter 6)

Cv	Treatment	Evaluation							
		Initial	Dec	Jan	Feb	Mar	Apr	May	Jun
		glucose + fructose, mg g <sup>-1</sup> dry weight							
RB <sup>z</sup>	CIPC <sup>y</sup>	11.0	10.1	10.7	11.7	9.0	7.5	7.4	6.8
	air control		11.7	9.1	9.3	9.8	7.2	8.2	9.0
	+ CO <sub>2</sub>		11.6	10.6	11.5	9.6	7.5	8.2	8.3
	+ ethylene		16.7	14.9	16.9	14.0	11.0	10.3	10.9
	both		17.3	19.7	18.7	15.0	13.7	11.2	13.8
SH	CIPC	39.9	24.8	21.4	19.7	17.7	17.5	14.7	13.6
	air control		32.5	21.6	21.1	17.2	16.0	14.2	16.2
	+ CO <sub>2</sub>		32.7	25.6	20.9	21.3	20.4	16.0	18.1
	+ ethylene		38.6	33.8	32.2	30.3	26.0	20.1	30.0
	both		30.6	27.5	31.6	31.0	25.6	21.9	29.8
IN	CIPC	9.4	8.8	11.2	10.2	7.3	6.7	5.4	8.9
	air control		8.4	7.9	7.2	7.2	8.3	8.5	9.9
	+ CO <sub>2</sub>		8.4	8.3	8.8	7.7	9.3	8.4	13.9
	+ ethylene		11.6	12.7	14.4	15.8	10.6	13.0	19.5
	both		13.4	11.1	13.8	15.9	15.1	16.0	24.8
DP	CIPC	0.6	0.4	0.4	0.4	0.4	0.4	0.8	1.6
	air control		0.4	0.4	0.5	0.4	0.5	0.4	0.6
	+ CO <sub>2</sub>		0.4	0.3	0.4	0.4	1.0	0.8	2.5
	+ ethylene		0.7	0.8	0.7	0.7	0.7	1.1	1.7
	both		0.7	0.6	0.6	0.7	0.5	1.2	0.6

<sup>z</sup> RB, Russet Burbank; SH, Shepody; IN, Innovator; DP, Dakota Pearl

<sup>y</sup> Chlorpropham

Processing colour in Russet Burbank tubers treated with trace ethylene was equivalent to the colour of control tubers from eight weeks after the start of ethylene exposure until the end of the trials (Figure 5.1a). A response to trace ethylene was not observed in Innovator tubers until 16 weeks after the exposure began (Figure 5.1c). Unlike Russet Burbank and Shepody tubers, the processing colour of Innovator tubers exposed to trace ethylene did not

recover with increasing time in storage, but instead declined (darkened) progressively - precipitously so at the final evaluation in June (Figure 5.1c).

Darkening in response to the higher ethylene concentration used for sprout inhibition was much greater than the response to trace ethylene in all three French fry cultivars (Figures 5.1a,b,c, 6.3a,b,c). In Russet Burbank, Shepody and Innovator tubers, processing colour in the high ethylene treatment was distinctly darker than the controls at the first evaluation, i.e. four weeks after the exposure commenced.

**Table 7.2** Sucrose content of four processing cultivars during storage.

a. Tubers stored with 0 or 2% CO<sub>2</sub> with or without 0 or 0.5 µL L<sup>-1</sup> ethylene (Chapter 5)

Cv	Treatment	Evaluation							
		Initial	Dec	Jan	Feb	Mar	Apr	May	Jun
sucrose, mg g <sup>-1</sup> dry weight									
RB <sup>z</sup>	CIPC <sup>y</sup>	11.4	10.1	10.3	8.9	7.	7.1	6.3	5.1
	+ CO <sub>2</sub>		10.0	9.7	9.5	8.	7.2	6.0	5.7
	+ ethylene		12.7	10.6	9.2	8.	7.6	6.2	5.3
	both		12.1	12.1	9.6	9.	8.4	8.2	6.5
SH	CIPC	38.8	30.3	21.7	21.5	18	15.4	14.4	12.8
	+ CO <sub>2</sub>		28.3	24.5	19.7	20	16.2	17.8	17.8
	+ ethylene		35.7	28.2	26.9	23	20.4	21.7	21.7
	both		32.8	32.8	29.5	26	24.0	21.4	21.4
IN	CIPC	8.2	7.0	6.3	5.7	5.	5.3	4.4	6.0
	+ CO <sub>2</sub>		6.7	7.4	5.5	5.	5.8	4.7	5.5
	+ ethylene		7.6	7.3	7.0	7.	7.6	7.5	12.9
	both		8.6	8.2	7.8	8.	9.0	9.3	16.2
DP	CIPC	1.8	1.7	1.6	1.7	1.	2.0	2.4	4.6
	+ CO <sub>2</sub>		2.1	1.6	2.1	1.	2.6	4.1	7.0
	+ ethylene		1.8	2.1	2.2	1.	1.8	2.8	6.2
	both		2.5	2.2	2.7	1.	2.5	4.4	9.1

<sup>z</sup> RB, Russet Burbank; SH, Shepody; IN, Innovator; DP, Dakota Pearl

<sup>y</sup> Chlorpropham

(table continued on next page)

**Table 7.2**, continued.

b. Tubers stored with 0 or 2% CO<sub>2</sub> with or without 0 or 10 µL L<sup>-1</sup> ethylene (Chapter 6)

Cv	Treatment	Evaluation							
		Initial	Dec	Jan	Feb	Mar	Apr	May	Jun
sucrose, mg/g DW									
RB <sup>z</sup>	CIPC <sup>y</sup>	8.7	8.3	9.0	8.9	7.4	6.6	6.3	6.0
	air control		9.2	8.1	7.1	7.9	6.3	6.3	7.3
	+ CO <sub>2</sub>		9.1	9.0	9.1	7.8	6.2	6.8	6.7
	+ ethylene		13.0	12.1	12.6	11.1	9.0	8.5	8.8
	both		13.8	15.7	13.8	11.7	11.1	9.3	11.2
SH	CIPC	31.1	19.8	16.9	16.0	14.0	12.2	11.6	10.0
	air control		24.0	15.7	14.8	13.1	12.6	11.8	11.8
	+ CO <sub>2</sub>		23.0	17.8	14.9	15.4	15.5	12.6	13.7
	+ ethylene		28.4	23.2	23.3	21.7	20.1	16.6	21.8
	both		21.5	20.2	23.0	22.8	20.2	17.4	21.7
IN	CIPC	8.8	6.9	8.5	7.5	5.3	5.2	4.6	7.1
	air control		6.6	6.2	5.7	5.5	7.4	6.7	7.5
	+ CO <sub>2</sub>		6.7	6.7	6.7	5.6	7.1	6.7	10.0
	+ ethylene		8.8	9.9	10.8	11.2	8.8	10.0	13.6
	both		10.3	8.8	10.6	12.1	11.6	11.9	18.2
DP	CIPC	1.7	1.7	1.5	1.6	1.7	1.6	2.3	3.4
	air control		1.6	1.4	1.5	1.4	1.5	1.0	1.1
	+ CO <sub>2</sub>		1.6	1.6	1.9	1.5	1.0	1.0	4.0
	+ ethylene		2.4	2.2	1.9	1.7	1.8	1.3	3.1
	both		2.7	2.3	2.1	1.7	1.0	1.3	1.7

<sup>z</sup> RB, Russet Burbank; SH, Shepody; IN, Innovator; DP, Dakota Pearl.

<sup>y</sup> Chlorpropham

Gradual recovery to a lighter processing colour was observed in Russet Burbank and Shepody tubers as the storage time increased, despite the continued exposure to ethylene. In Innovator tubers the colour continued to darken throughout the storage term, with no apparent recovery to a lighter colour (Figure 6.3a,b,c). These responses to ethylene alone and the differences among cultivars are consistent with the well-known effects of

ethylene on processing colour of stored potato tubers, i.e. that the response is dose-dependent, temperature-related, usually at least partially recoverable, and with some variation among cultivars (Heulin and Barker 1939; Haard 1971; Prange et al. 1998; Daniels-Lake et al. 2005, 2006).

As an important plant growth regulator, ethylene affects plants and plant tissues in a host of ways which, despite decades of study by legions of researchers, remain incompletely understood. Potato tubers are no exception to this reality. Both endogenous and exogenous sources of ethylene play significant roles.

Potato tubers respond to ethylene gas by increasing their reducing sugar content and their cellular respiration rate, as well as other metabolic responses which are not part of this discussion (Huelin and Barker 1939; Reid and Pratt 1972; Arron et al. 1978; Day et al. 1978; Minato et al. 1979; Rychter et al. 1979; Prange et al. 1998). Although the respiration response may involve both the cyanide-sensitive and cyanide-resistant respiratory pathways (Solomos and Laties 1975; Day et al. 1978), the important point is that ethylene induces increased respiration in potato tubers, thereby consuming reducing sugars.

One can imagine that the respiration and reducing sugar responses may counteract each other in the cells of potato tubers, resulting in no net change in sugars or colour. This could explain why the processing colour of some cultivars does not appear to respond to ethylene. It is also entirely possible that the response of one pathway or the other may dominate in some cultivars, leading to net changes in sugars and processing colour. This would account for the range of changes observed by many other researchers.

Each ethylene response involves a specific set of receptors, with multiple steps between perception and effect (Pierik et al. 2006; Stepanova and Alonso 2009). In addition to the metabolic pathways which are affected, these receptors and their respective signal transduction pathways are also likely to vary among cultivars in their sensitivity to an ethylene stimulus, due to allelic polymorphism in the gene families coding for these enzymes and receptors (Sowokinos et al. 1997; Pierik et al. 2006; McKenzie et al. 2013). The reported variations among cultivars in response to ethylene exposure may be attributable to these variations in sensitivity and magnitude of response.

For example, Haard (1971) found that tubers of the cultivar Monona stored at 4.4 °C have relatively light colour but darken sharply when exposed to ethylene, whereas tubers of the cultivar Kennebec stored at the same temperature have rather dark colour which quickly becomes lighter following ethylene exposure. It is likely that the production of reducing sugars is stimulated more than the respiration rate in Monona tubers, whereas the opposite occurs in Kennebec tubers.

The increase in tuber respiration in response to ethylene reaches a peak within 24 to 30 h at 25 °C but rises more slowly and peaks after a few days at lower temperatures (Reid and Pratt 1972; Arron et al. 1978; Day et al. 1978; Daniels-Lake and Prange, unpublished data). With or without continued ethylene exposure, a few days later the respiration rate falls to a new steady state which is higher than the original rate.

Due to the many receptors and associated regulators which affect tuber metabolic pathways, the responses do not all occur in identical time-frames (Sowokinos 1990b; Li 2008; Stepanova and Alonso 2009). The stimulation of sugar production in response to ethylene seems to be initiated more rapidly than the increase in respiration. Although there is little published research regarding just how quickly the sugar response is initiated, Haard (1971) found that the colour of Monona tubers is much darker within four days after ethylene treatment of tubers stored at 4.4 °C, but the colour does not darken further. This suggests that the peak sugar production is reached by the time of the evaluation at four days. In contrast, the rise in respiration at 4 or 5 °C barely begins by this time (Reid and Pratt 1972; Daniels-Lake and Prange, unpublished data). This suggests that respiration sometimes lags behind sugar production. It is reasonable to believe that in such cases the sugars would accumulate until the rising respiration rate catches up to the rate of sugar production, or until the rate of sugar production declines below the rate of consumption by respiration. As time in storage continues, the increasing respiration rate could eventually overtake the rate of sugar production, which would gradually diminish the pool of reducing sugars and improve (lighten) the processing colour.

After the increased respiration rate in response to ethylene reaches its peak, it declines to a new steady state which is usually higher than the original rate in untreated tubers (Reid and Pratt 1972; Arron et al. 1978; Day et al.

1978; Daniels-Lake and Prange, unpublished data). This new respiration rate is likely a response to the increased pool of sugars, but it may not be sufficient to overcome the increase. Progressive depletion of the sugars can be expected to result in lighter processing colour, which may or may not catch up with the colour of the untreated tubers. Alternatively, if the new respiration rate cannot keep pace with the increased rate of sugar production, processing colour will continue to darken. Observations from the reported work support both of these possibilities, i.e. recovery of processing colour after darkening due to ethylene exposure was observed in Russet Burbank and Shepody tubers, but in Innovator the colour darkened steadily as storage time increased (Figures 5.1a,b,c, 6.3a,b,c).

Differences in the speed at which these two responses to ethylene occur would explain the observed transient darkening of colour in many cultivars, i.e. a rapid increase in production of reducing sugars followed by stimulation of respiration which consumes these additional sugars. Among cultivars which appear to be very sensitive to ethylene, either the effect on the rate of production of sugars is greater than in other cultivars, or the increase in cellular respiration is not sufficient to metabolize the additional reducing sugars, or both. Variability in responses among cultivars may explain the differences observed in regards to the ethylene concentrations at which these responses are saturated, as discussed in Chapter 5.

Some or all of these effects are likely to have contributed to the observed responses of tuber processing colour to ethylene gas. Although the variability in each individual response may have been small by itself, the net result was apparently sufficient to cause the observed differences. Similar variability in the metabolic responses to CO<sub>2</sub> exposure are also likely, and may explain the conflicting reports regarding the effect of CO<sub>2</sub> on processing colour noted in Section 1.3.2.

#### 7.4.2. Ethylene and CO<sub>2</sub> Applied Together

Simultaneous exposure of tubers to elevated CO<sub>2</sub> and ethylene superimposed a further layer of complexity upon the backdrop of the effects of the individual gases. Surprisingly, the observed effects on processing colour were rather straightforward.

When stored tubers were exposed to elevated CO<sub>2</sub> and ethylene together, the processing colour of Russet Burbank, Shepody and Innovator tubers was darker than the controls in all trials including the short-duration trials (Tables 3.2, 4.1; Figures 2.1, 5.1a,b,c, 6.3a,b,c). This was true whether or not processing colour was affected by either CO<sub>2</sub> alone or ethylene alone. The processing colour of tubers exposed to the two gases together was also darker than the processing colour of tubers exposed to ethylene alone, except in Shepody treated with high ethylene where the colour was the same in both treatments (Tables 3.2, 4.1; Figures 2.1, 5.1a,b,c, 6.3a,b,c).

In contrast to the three French fry cultivars, in the potato chip cultivar Dakota Pearl very little difference in processing colour in response to trace ethylene or high ethylene or either of these in combination with CO<sub>2</sub> was observed throughout the storage term in any of the trials (Figures 5.1d,e and 6.3d,e). However the sugar content of the Dakota Pearl tubers appears to suggest trends similar to those observed in the three French fry cultivars, albeit at a much lower range of sugar concentrations (Tables 7.1, 7.2).

The observed effects of CO<sub>2</sub> and ethylene together may reflect a delayed recovery from darkening due to ethylene exposure when elevated CO<sub>2</sub> was also present, or they may be attributable to the sum of the effects of each gas alone, or they may represent a true interaction of the two gases in the tuber metabolic pathways. However, unravelling the physiological mechanism of these responses is beyond the scope and aims of this project.

Nevertheless, for all four cultivars, the changes in sugar content over time reflect the observed changes in processing colour, i.e. that often there was a small response to elevated CO<sub>2</sub>, but there were larger responses to ethylene and to CO<sub>2</sub> plus ethylene (Tables 7.1, 7.2). This supports the idea that the CO<sub>2</sub> may have impaired respiration somewhat, as suggested by Wills et al. (1979). Initial sugar concentrations likely also influenced the responses to the applied treatments, i.e. if the sugars at the beginning of storage were very low then a considerable change in sugar concentration would be necessary to affect processing colour. This is consistent with the observations of Dakota Pearl tubers, which had very low initial reducing sugars and little change in colour throughout the trials (Table 7.1, 7.2; Figures 5.1d,e, 6.3d,e).

### 7.5. Can the responses to CO<sub>2</sub> and ethylene be prevented or reduced?

The most important method to prevent the processing colour responses among tubers exposed to elevated CO<sub>2</sub> and/or ethylene gas is to reduce or eliminate these gases from the storage atmosphere. Although stored tubers produce both gases, ventilation of the stored potatoes with fresh air from outside the building is widely known to be an effective method to reduce CO<sub>2</sub>. Ventilation simultaneously reduces the concentration of any ethylene gas that may also be present. However, this approach is not always an acceptable choice for economic reasons.

In the refrigerated storage facilities used in moderate and warm climatic regions, cooling the storage atmosphere is a major component of the cost of storing potatoes. Venting that cooled air outside and replacing it with warm fresh air which then must be cooled increases that storage cost. For this reason, the ventilation of many potato storage facilities in such areas is restricted to circulation of the cooled air within the building or room, and there is little or no replenishment with outside air. In contrast, in colder climates where outside air is used to cool the storage facility in winter, ventilation is sometimes restricted because the exterior air temperature is too cold to safely introduce into the storage atmosphere unless it is pre-heated to avoid chilling the tubers. This also represents an additional cost, and therefore the addition of fresh air is often restricted during very cold weather. Accumulation of CO<sub>2</sub> and ethylene are likely in both situations. One method which could address these issues is to install heat-exchange equipment in the ventilation system, which uses the exhaust airstream to pre-warm or pre-cool the incoming fresh air as appropriate. This would facilitate refreshment of the storage atmosphere while reducing the ongoing additional expense of doing so.

Another approach which has been used successfully in commercial facilities recently is to scrub CO<sub>2</sub> from the recirculating storage atmosphere with banks of hydrated lime (Ca(OH)<sub>2</sub>), similar to the method used in controlled atmosphere fruit storage. Lime scrubbing was used in the lab-scale research trials described in Chapters 2 to 6, to eliminate CO<sub>2</sub> in the 0 CO<sub>2</sub> treatment chambers. This technology has also been found to be effective in commercial practice to reduce tuber sugar accumulation attributable to CO<sub>2</sub> and ethylene, as demonstrated by better processing colour and reduced acrylamide formation in comparison with equivalent tubers from un-scrubbed storage (A Sardo, Xeda Corp., personal communication).



Use of the ethylene-blocking compound 1-methylcyclopropene (1-MCP) was effective in preventing darkening of the processing colour of stored potatoes in response to the combined effects of CO<sub>2</sub> and ethylene in the storage atmosphere (Table 3.2). Pre-treatment with 1-MCP not only prevented darkening attributable to trace ethylene, but also the combined exposure to CO<sub>2</sub> plus trace ethylene. The processing colour of Russet Burbank tubers pretreated with 1-MCP before exposure to the CO<sub>2</sub> plus ethylene treatment was equivalent to the controls. Although only Russet Burbank tubers were tested in the short-duration CO<sub>2</sub> plus trace ethylene trials in Chapter 3, Prange et al. (2005) found that pre-treatment with 1-MCP prevents darkening of fry colour due to 4 µL L<sup>-1</sup> ethylene sprout inhibitor in season-long trials of Russet Burbank and Shepody tubers. Furthermore, the application of 1-MCP does not reduce the sprout inhibition activity of ethylene, although multiple applications of 1-MCP are needed for effective colour retention during long-term storage (Prange et al. 2005; Daniels-Lake et al. 2006). Recent research by Foukaraki et al. (2012) found similar benefits from 1-MCP pre-treatment of the cultivar Marfona, using 10 µL L<sup>-1</sup> ethylene.

1-MCP is relatively non-toxic and easy to apply as a vapour. It is approved for use on cut flowers and several fruit crops in Canada, the USA and several other nations, but it is not yet registered for use on potatoes in any country. However, recent renewed interest by the international patent holders for 1-MCP suggests that it may become available to the potato industry in several countries in the not-too-distant future (T Eddington, Dow Agrochemicals, personal communication).

#### **7.6. Are there "safe" concentrations of CO<sub>2</sub> and ethylene in potato storage atmospheres, below which darkening does not occur?**

It is clear from the findings in Chapter 4 that the responses to CO<sub>2</sub> and ethylene are dose-dependent, with the magnitude of the response to each gas diminishing proportionately with progressively lower exposure (Table 4.2). However, the dose-related response to CO<sub>2</sub> was observed only when ethylene was also present. Darkening of processing colour in response to 0.5 to 2.0% CO<sub>2</sub> applied without ethylene was not observed in Russet Burbank in any of the short duration trials (Tables 2.2, 3.2, 4.1). Importantly, within the range of gas concentrations applied together (i.e. 0.5, 1.0 and 2.0% CO<sub>2</sub> combined with

0.25 and 0.5  $\mu\text{L L}^{-1}$  ethylene), no threshold concentrations were identified for either gas.

This is not surprising for ethylene. Although the many effects of ethylene gas in various species are known to be dose-dependent, no minimum concentrations or thresholds are recognized. The responses just continue to diminish in magnitude with the decline in concentration, to the limits of study or measurement. A functional threshold could be arbitrarily chosen at the point where the response is insufficient to be problematic in the commercial milieu, e.g. slightly below the concentration which consistently causes noticeable darkening. However, such a definition is somewhat subjective and may vary among processed products and intended markets. Also, extensive testing of cultivars and consumer panels would be needed to establish such values. This task is best left to the potato industry to address.

With regard to  $\text{CO}_2$ , it is a normal constituent of the ambient atmosphere, present at ca. 0.04%. Although the  $\text{CO}_2$  content of the storage atmosphere may be reduced nearer to zero by the use of lime scrubbing, the effect of 2%  $\text{CO}_2$  applied in the trials described in Chapters 2 to 6, i.e. 50-fold higher than ambient, was relatively small as long as ethylene was not present simultaneously. For practical purposes it seems reasonable to propose exposure to ambient  $\text{CO}_2$  as the no-effect level. However, in commercial facilities it is very difficult to maintain such a low level. Currently, many commercial storage managers aim to keep  $\text{CO}_2$  concentrations in the atmosphere of their potato storage rooms below 0.2 to 0.5% (J Walsh, McCain Foods Limited, R Andrews, Crop Systems Ltd, personal communications). This range can serve as an achievable target for storage managers in the real world.

### **7.7. Do different potato cultivars respond to $\text{CO}_2$ and ethylene in the same manner?**

As noted in sections 7.3 and 7.4, there are some general similarities among cultivars in the response of processing colour to  $\text{CO}_2$  and ethylene, but with some variability among cultivars. The three French fry cultivars (Russet Burbank, Shepody and Innovator) responded to the two gases in a broadly similar manner, whereas the chipping cultivar Dakota Pearl hardly responded

at all.

It may seem appropriate to propose that cultivars with very low sugars at harvest, such as found in the Dakota Pearl tubers (Tables 7.1, 7.2) will have little or no darkening of processing colour in response to elevated CO<sub>2</sub> and trace ethylene. However, in studies of several different chipping cultivars which all had similar very low sugars at harvest, some darkened severely in response to 4 µL L<sup>-1</sup> ethylene during storage, while others were essentially unaffected (Daniels-Lake and Prange, unpublished data). Therefore, while it may be reasonable to attribute a minimal response to low initial sugars, it is unwise to suppose that low initial sugar content can be used to predict the response of an untested cultivar to CO<sub>2</sub> and/or ethylene exposure.

On the other end of the scale, there is no evidence from the trials in this project that high initial sugars reduced the magnitude of the processing colour response. Even tubers which had quite dark processing colour at the start could be made to fry darker still (Figures 5.1b, 6.3b). At least until more details of the metabolic changes are uncovered, each important cultivar ought to be evaluated regarding its response to these two gases during storage at the usual temperatures for that cultivar.

#### **7.8. Does time in storage, i.e. tuber physiological age, play a role in the responses to CO<sub>2</sub> and ethylene?**

Time, i.e. the duration of storage, is a very important issue in the commercial storage of processing potatoes. The passing of time contributes to physiological ageing and therefore determines the metabolic status of the tubers at the point when they are processed. In addition, since tubers for processing are often stored for many months, the various metabolic pathways and interactions involved can have long-term cumulative consequences in terms of tuber sugars and therefore processing colour. This may include both positive and negative effects.

The responses to CO<sub>2</sub> and ethylene applied in the trials reported here were greater in magnitude as the tubers aged physiologically with the passage of time. This was apparent in the short term trials (Chapters 2, 3, 4), in which the physiologically older Russet Burbank tubers in the trials conducted late in

the storage season responded to a greater degree than did their counterparts which received the same treatments earlier in the year (Tables 2.2, 3.2, 4.1).

Although the observed effects in the long-duration trials over the full storage season (Chapters 5 and 6) probably reflected cumulative effects from multiple metabolic pathways, as discussed in the preceding sections, the responses to CO<sub>2</sub> plus ethylene were also greater during the late part of the storage season than at earlier evaluation dates (Figures 5.1 and 6.3). This was especially apparent in Innovator at the very end of the trials, in the combinations of CO<sub>2</sub> with both trace ethylene and high ethylene concentrations (Figures 5.1c, 6.3c). At those times, the untreated control tubers were sprouting profusely (Figures 6.1, 6.2c), which is indicative of advanced physiological ageing and approaching senescence among the tubers in all treatments.

Tubers from both the high ethylene and CO<sub>2</sub> plus high ethylene treatments had impaired sprout elongation attributable to exposure to this concentration of ethylene gas (Figures 6.1, 6.2), which is consistent with the findings of others (Rylski et al. 1974; Prange et al. 1998). However, physiological ageing of these tubers was probably not impeded. In fact, the capacity of ethylene to induce sprouting of dormant tubers (Rosa 1925; Rylski et al. 1974; Alam et al. 1994; Coleman 1998) suggests that ethylene accelerates physiological ageing. Therefore the sharply darkened processing colour at the end of the storage term among Innovator tubers exposed to high ethylene may also reflect premature senescence in these tubers.

## 7.9. Main Conclusions

The hypotheses which were tested in this project, as stated in section 1.6.2, were the following:

- H<sub>0</sub>: Accumulated carbon dioxide and ethylene gases, present alone or together in the atmosphere surrounding stored potato tubers, have no effect on the processing colour of those tubers.
- H<sub>1</sub>: Accumulated carbon dioxide in the storage atmosphere affects the processing colour of stored potatoes.
- H<sub>2</sub>: Accumulated ethylene in the storage atmosphere affects the processing colour of stored potatoes.

H<sub>3</sub>: Carbon dioxide and ethylene in the storage atmosphere interact in some way to affect the processing colour of stored potatoes more than either gas alone.

H<sub>0</sub> is rejected. The results of this project indicate that CO<sub>2</sub> and ethylene, either alone or together and depending on the cultivar and physiological age of the tubers, can have a measurable and important effect on the processing colour of stored potato tubers. Thus H<sub>1</sub>, H<sub>2</sub> and H<sub>3</sub> are all accepted.

The long duration of these trials, with repetitions in multiple years and consistent methodologies among various trials, enabled an in-depth evaluation of the processing colour responses to these two gases. These trials captured not only the responses which occurred soon after the treatments commenced, but also the cumulative effects which were not apparent until several months of storage had passed. Since the actual duration of commercial potato storage ranges from a few weeks to many months after harvest, the improved understanding of the responses within both short and long time-frames which results from this research is likely to be useful to the industry. In addition, the inclusion of four cultivars in several of the trials contributes to the understanding of variability among genotypes.

The main conclusions regarding processing colour of stored potatoes which can be drawn from this research include:

1. The processing colour of some cultivars was darkened in response to elevated CO<sub>2</sub>, but the response was usually relatively small (i.e. less than the response to ethylene). Among those cultivars which did respond to the CO<sub>2</sub> alone, the response was not apparent until 8 weeks or more after the exposure began.
2. If processing colour was darkened in response to ethylene at either the trace or high concentration, elevated CO<sub>2</sub> usually made the colour darker still.
3. If processing colour was darkened in response to elevated CO<sub>2</sub>, combination with even the trace concentration of ethylene usually darkened the colour much more.
4. There was usually a response to CO<sub>2</sub> and ethylene applied together, whether or not there was a response to either gas applied alone. This response was apparent at the first evaluation after exposure began, i.e. within three or four weeks.

5. Older physiological age tended to increase the magnitude of these responses. This did not appear to be associated with dormancy break and the start of sprouting, but occurred somewhat later - apparently as senescence approached.
6. Darkening varied in direct relationship with the concentration of both gases. Darkening could be prevented by pre-treatment with 1-MCP, as well as by scrubbing or ventilation to remove CO<sub>2</sub> and ethylene.

Interest in the use of ethylene sprout inhibitor for processing potatoes is increasing (A Briddon, Sutton Bridge Crop Storage Research, R Wustman, Wageningen University Research Centre, personal communications). It is important for those potential new users to understand that the processing colour of important processing cultivars which are moderately sensitive to ethylene exposure (e.g. Russet Burbank and Innovator), may be darkened much more when elevated CO<sub>2</sub> is also present. The research reported here has emphasized the importance of monitoring CO<sub>2</sub> concentrations when processing tubers are stored with ethylene sprout inhibitor and of ensuring that CO<sub>2</sub> levels are kept very low, to minimize the effects on processing colour.

While it is likely that other important processing cultivars will be tested to determine their susceptibility to darkening attributable to ethylene sprout inhibitor, it would also be wise to determine their sensitivity to the combined effect of CO<sub>2</sub> and ethylene together. The findings of this project suggest that, for practical purposes, processing cultivars can be divided into three general groups in terms of their response to exposure to elevated CO<sub>2</sub> together with ethylene sprout inhibitor, i.e. some have little or no response (e.g. Dakota Pearl), some are darker with CO<sub>2</sub> plus ethylene than with ethylene alone (e.g. Russet Burbank and Innovator), and some are already as dark with ethylene alone as they would be with CO<sub>2</sub> plus ethylene (e.g. Shepody). Assigning important cultivars to these categories would be helpful in choosing appropriate storage management protocols, and for decision making regarding which cultivars should or should not be stored together.

In the trials reported in Chapters 5 and 6, the tubers were exposed to the gas treatments continuously for many months, from fall through winter to spring. However, in commercial practice it is more likely that increased concentrations of CO<sub>2</sub> and/or ethylene may not occur continuously for the

entire storage period, or may increase gradually over days or weeks. Gas exposures in the real world may be intermittent, or may only occur during a portion of the storage term. These variations may make the response smaller or later than those observed in this project. Nevertheless, it is important for the processing industry to be aware of the potential for negative effects on the processing colour of stored tubers, to contribute to appropriate storage management decisions.

The treatments applied in this project were started abruptly at the full concentration of the two gases and after the suberization and cooling were completed. In contrast, the application protocols for commercial use of ethylene sprout inhibitor recommend starting at a very low concentration soon after harvest, with progressive increments to the full concentration over several weeks, in order to minimize the negative effects of ethylene upon tuber sugars (J Barnes, Biofresh Ltd, D Garos, Restrain Company, personal communications). Use of these treatment methodologies is likely to also be beneficial in minimizing the effects of CO<sub>2</sub> plus ethylene in commercial practice, by reducing the effects of ethylene.

While all of these methods to avoid additional tuber sugars may increase the cost of successful long-term storage of processing potatoes, these increments must be weighed against the financial and marketing benefits of maintaining tuber quality during long-term storage. Storage managers must choose a method or combination of methods which best suits their particular operational and economic situation, to achieve maximum overall benefits.

## 7.10. Opportunities for Further Research

The findings in this project have contributed to our understanding of the relationships among CO<sub>2</sub>, ethylene gas and processing colour of stored potato tubers. However, this work also suggests several areas in which additional research would be useful. These fall into two broad categories, i.e.:

### Tuber Physiology

- Comparison of the time-lines of the responses to ethylene and CO<sub>2</sub> in terms of processing colour and sugar content.
- Further investigation of the effect of CO<sub>2</sub> on tuber sugar

production, and how this relates to respiration rate.

- Investigation of the variability among different metabolic responses to CO<sub>2</sub> and how these contribute to changes in potato processing colour.

#### Storage Management

- Evaluation of the response of other important processing cultivars to CO<sub>2</sub> plus ethylene.
- Evaluation of the effect of CO<sub>2</sub> plus ethylene sprout inhibitor on processing colour when the ethylene exposure is commenced gradually during the warm suberization period.
- Study of the response of important processing cultivars to CO<sub>2</sub> and ethylene at both higher and lower storage temperatures.
- Testing of low-sugar cultivars such as Dakota Pearl for a longer duration and/or at a lower storage temperature to determine if there is a response to CO<sub>2</sub> plus ethylene.

These questions and many others will continue to drive potato postharvest research in my lab and elsewhere, onward into the future. Each new project contributes another small piece as we endeavour to complete the multi-dimensional puzzle of potato storage. It is very challenging, but always very interesting.

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## Summary

The finished colour of processed potato (*Solanum tuberosum* L.) products is arguably their most important quality attribute. It is directly dependent upon the reducing sugar content of the fresh tubers from which the products are made. Despite variability among regional preferences and specific products, relatively light-coloured products consistently return a higher price in the marketplace than do the same products which are relatively darker in colour. Therefore the potential of stored potatoes to yield light-coloured products when processed, and the retention of that potential during long-term storage, have significant economic importance within the potato industry. The recent discovery of acrylamide, a probable human carcinogen, in many processed products made from starchy foodstuffs such as potatoes further emphasizes the importance of light processing colour, because dark processing colour is associated with increased acrylamide content. For all of these reasons, potato growers strive to produce potatoes which will fry to a light colour when processed, and storage managers work to retain that important quality during the long periods of storage necessary to serve the year-round needs of potato processors in areas with only one growing season per year.

Internal metabolic activities, which are influenced by intrinsic characteristics as well as external factors, can alter the reducing sugar content of stored potatoes, which affects their processing colour. For decades the potato processing industry believed that accumulation in the potato storage atmosphere of moderately elevated concentrations of CO<sub>2</sub> from tuber respiration or other sources caused darkening of the processing colour of these stored potatoes. However, the results of research studies on this topic were sometimes contradictory or inconclusive. Furthermore, it was unclear whether the observed responses were due to the accumulation of CO<sub>2</sub> or were attributable to the accompanying depletion of O<sub>2</sub>.

In contrast, research on the plant growth regulator ethylene, which is naturally produced at very low rates by all plants including potato tubers, has clearly established that exposure to exogenous ethylene can darken the processing colour of stored potatoes. Trace concentrations of ethylene gas, e.g. 0.05 to 1 µL L<sup>-1</sup>, have been observed in potato storage atmospheres. In addition to the tubers, many pathogens produce ethylene, as do heaters and

engines used inside or near potato storage rooms. Historically, little attention was paid to ethylene gas in the potato storage atmosphere until just over a decade ago when it was found to be a contaminant in the treatment airstream when applying chlorpropham sprout inhibitor. In addition, the recent development of ethylene as a sprout inhibitor has also increased interest in the quantity of ethylene in potato storage rooms. Conditions which tend to increase the production and accumulation of CO<sub>2</sub> in the storage atmosphere, e.g. stress, disease, elevated respiration rate and restricted ventilation, also tend to increase the production and accumulation of ethylene gas.

In order to investigate the effect of CO<sub>2</sub> on processing colour, a series of research studies was undertaken beginning with short-term trials using the important French fry cultivar Russet Burbank. In year 1, four consecutive three-week trials were conducted during the November to June storage season, using chlorpropham-treated potatoes from eight commercial growers in New Brunswick, Canada. Suberized and cooled tubers were stored at 9 °C in modified atmosphere chambers which had 21, 20.5 or 19% O<sub>2</sub> and 0, 0.5 or 2% CO<sub>2</sub> in a 3 × 3 factorial design, plus an air-only control and an unventilated treatment in which tuber respiration depleted the O<sub>2</sub> and caused CO<sub>2</sub> to accumulate in the chamber atmosphere. Hydrated lime was placed in the 0% CO<sub>2</sub> chambers to absorb ambient and respired CO<sub>2</sub>. Processing colour was assessed at the beginning and end of each trial. No differences among the treatments were observed.

In year 2, ethylene gas was added to the design, the duration of the trials was increased to 9 weeks and the number of repetitions was reduced to two trials per year beginning in December or January and in March or April. Hydrated lime was used as in year 1. Suberized and cooled Russet Burbank tubers from two or four commercial growers in New Brunswick and Prince Edward Island, Canada, were treated with chlorpropham and stored at 9 °C each year. Because no effects attributable to the depleted O<sub>2</sub> treatments were observed, only the 19% O<sub>2</sub> concentration was continued in years 2, 3 and 4. This was discontinued after year 4. Processing colour was evaluated at the start of each trial and after 3, 6 and 9 weeks in the treatment atmospheres.

The treatments applied in trials during years 2 through 6 addressed three areas of study, i.e. A) whether CO<sub>2</sub> or trace ethylene or the combination



was actually responsible for the darkening of processing colour which had long been attributed to CO<sub>2</sub> alone; B) whether 1-methylcyclopropene (1-MCP) could prevent this darkening; and C) whether the concentration of either CO<sub>2</sub> or ethylene modified the response to the other gas when they were applied together. Applied concentrations of CO<sub>2</sub> and ethylene in all trials included 0 or 2% and 0 or 0.5 μL L<sup>-1</sup>, respectively, in a factorial design. In studies A and B, an unventilated treatment was also included, with or without ethylene. In study B, pre-treatment with 1-MCP was included, for a 2 × 2 × 2 design. The 1-MCP was applied inside the chambers as a vapour, for 48 h prior to beginning the modified atmosphere treatments. In study C, several additional CO<sub>2</sub> and ethylene concentrations were used, i.e. 0, 0.5, 1 and 2% and 0, 0.25 and 0.5 μL L<sup>-1</sup>, respectively, for a 4 × 3 design. For each of these studies, trials were carried out during two consecutive years, providing four repetitions of each treatment regime. In year 3, studies A and B were undertaken simultaneously, using separate storage chambers.

In years 7, 8 and 9, the trials were extended to include the entire fall to spring storage season, and three other cultivars were included in addition to Russet Burbank, i.e. the French-fry cultivars Shepody and Innovator and the potato chip cultivar Dakota Pearl. These long-term trials comprised two studies, i.e. D) to assess the effects of exposure to CO<sub>2</sub> and ethylene over the entire storage term and determine whether other cultivars responded in the same manner as Russet Burbank; and E) to determine whether the results were similar when ethylene was applied at the higher concentration used for sprout inhibition.

Two replicates of each cultivar were obtained from commercial growers in eastern Canada, in October or November of each year, except that only one source of Dakota Pearl was used in years 7 and 8. After suberization and cooling, the tubers were held at 9 °C in modified atmosphere storage chambers which contained 0 or 2% CO<sub>2</sub> with or without ethylene gas, in a 2 × 2 factorial design. The applied concentration of ethylene was either 0.5 μL L<sup>-1</sup> (trace ethylene, study D, years 7 and 8), or 10 μL L<sup>-1</sup> (high ethylene, study E, years 8 and 9). All tubers in study D were treated with chlorpropham, whereas in study E the tubers in the four factorial treatments were not treated with chlorpropham, but a separate chlorpropham check treatment was included each year. Hydrated lime was used as in year 1. Processing colour was

evaluated at the start of the trials in November or December of each year, and at intervals of four weeks until the following June.

The main conclusions from these studies include (as listed in the thesis):

1. The processing colour of some cultivars was darkened in response to elevated CO<sub>2</sub>, but the response was usually relatively small (i.e. less than the response to ethylene). Among those cultivars which did respond to the CO<sub>2</sub> alone, the response was not apparent until 8 weeks or more after the exposure began.
2. If processing colour was darkened in response to ethylene at either the trace or high concentration, elevated CO<sub>2</sub> usually made the colour darker still.
3. If processing colour was darkened in response to elevated CO<sub>2</sub>, combination with even the trace concentration of ethylene usually darkened the colour much more.
4. There was usually a response to CO<sub>2</sub> and ethylene applied together, whether or not there was a response to either gas applied alone. This response was apparent at the first evaluation after exposure began, i.e. within three or four weeks.
5. Older physiological age tended to increase the magnitude of these responses. This did not appear to be associated with dormancy break and the start of sprouting, but occurred somewhat later - apparently as senescence approached.
6. Darkening varied in direct relationship with the concentration of both gases. Darkening could be prevented by pre-treatment with 1-MCP, as well as by scrubbing or ventilation to remove CO<sub>2</sub> and ethylene.

The results of these trials provide useful information which can help the potato industry in general and storage managers in particular to retain light processing colour in stored potatoes. However, more study is needed to further elucidate these responses in other cultivars and under the specific storage conditions utilized in various production regions.

## Samenvatting

De uiteindelijke kleur van het eindproduct van verwerkte aardappelen (*Solanum tuberosum* L.) is misschien wel de belangrijkste kwaliteitseigenschap. Deze kleur, de bakkleur, is direct afhankelijk van het gehalte aan reducerende suikers in de verse knollen waarvan de eindproducten zijn gemaakt. Ondanks variatie in voorkeur tussen regio's en specifieke producten, vertegenwoordigen relatief lichte producten systematisch een hogere marktwaarde dan dezelfde producten die relatief donker van kleur zijn. Daarom vertegenwoordigen het vermogen van opgeslagen aardappelen om lichtgekleurde producten op te leveren bij de verwerking, evenals het behoud van dit vermogen tijdens langdurige opslag, een aanzienlijk economisch belang in de aardappelindustrie. De recente ontdekking van acrylamide, een stof die vermoedelijk kankerverwekkend is voor de mens, in veel bewerkte producten die zijn gemaakt van zetmeelrijke voedingsmiddelen zoals aardappelen, benadrukt verder het belang van een lichte bakkleur. Immers, een donkere bakkleur wordt geassocieerd met een verhoogd gehalte aan acrylamide. Om al deze redenen streven aardappeltelers ernaar om aardappelen te produceren die na frituren een lichte kleur geven. Evenzeer streven beheerders van aardappel-bewaarplaatsen er naar deze belangrijke kwaliteitseigenschap te behouden tijdens de lange bewaarperioden, die nodig zijn om jaarrond aan de behoeften van aardappelverwerkers te voldoen in gebieden met slechts één teeltseizoen per jaar.

Interne metabolische processen, die worden beïnvloed door intrinsieke eigenschappen en externe factoren, kunnen het gehalte aan reducerende suikers in bewaarde aardappelen veranderen en daardoor de bakkleur beïnvloeden. Al decennia lang werd binnen de aardappel-verwerkende industrie aangenomen dat gematigd verhoogde concentraties van CO<sub>2</sub>, afkomstig uit knolademhaling en andere bronnen, in de atmosfeer van de aardappelbewaarplaats de oorzaak waren van de donkere bakkleur van bewaarde aardappelen. Echter, de resultaten van onderzoek op dit gebied waren soms tegenstrijdig of niet eenduidig. Bovendien was het onduidelijk of de waargenomen effecten veroorzaakt werden door ophoping van CO<sub>2</sub> of waren toe te schrijven aan de daarmee gepaard gaande uitputting van O<sub>2</sub>.

Daarentegen heeft onderzoek naar de groeiregulator etheen die van nature in zeer geringe hoeveelheden door alle planten, inclusief

aardappelknollen, wordt geproduceerd, duidelijk aangetoond dat blootstelling aan exogeen etheen er toe leidt dat bewaarde aardappelen na verwerking donkerder van kleur worden. In de atmosfeer van aardappelbewaarplaatsen worden zeer lage concentraties etheengas aangetroffen, in de orde grootte van 0,05 tot 1  $\mu\text{l L}^{-1}$ . Niet alleen de knollen, maar ook veel pathogenen produceren etheen, evenals verwarmingsinstallaties en motoren in of nabij aardappelbewaarruimten. In het verleden werd weinig aandacht besteed aan etheengas in de atmosfeer van aardappelbewaarplaatsen. Iets meer dan 10 jaar geleden werd echter gevonden dat etheen een verontreiniging was in de luchtstroom wanneer chloorprofam als kiemremmingsmiddel werd toegediend. Bovendien heeft de recente ontwikkeling van etheen als kiemremmingsmiddel geleid tot een toegenomen belangstelling voor de hoeveelheid etheen in aardappelopslagruimten. Omstandigheden die kunnen leiden tot een hogere productie en ophoping van  $\text{CO}_2$  in de bewaaratmosfeer, bijv. stress, ziekte, verhoogde ademhaling en beperkte ventilatie, leiden wellicht ook tot verhoging van de productie en ophoping van etheengas.

Om het effect van  $\text{CO}_2$  op de bakkleur te onderzoeken, werd een reeks experimenten uitgevoerd. Allereerst werden de korte-termijn effecten onderzocht op het ras Russet Burbank, een belangrijk fritesras. In het eerste jaar werden vier opeenvolgende proeven van elk drie weken uitgevoerd gedurende het bewaarseizoen dat liep van november tot juni. Voor dit onderzoek werden met chloorprofam behandelde aardappelen van acht commerciële telers in New Brunswick, Canada gebruikt. Gesuberiseerde, koel bewaarde knollen werden bij 9 °C bewaard in kamers waarin de luchtsamenstelling kon worden aangepast. Deze kamers werden ingesteld op 21, 20,5 of 19%  $\text{O}_2$  en 0, 0,5 of 2%  $\text{CO}_2$  in een 3 × 3 factorieel proefschema. Er was bovendien een controle-behandeling waarin geventileerd werd met ongemodificeerde lucht en een ongeventileerde behandeling waarbij de knolademhaling er voor zorgde dat de  $\text{O}_2$  werd uitgeput en de  $\text{CO}_2$  zich ophoopte in de atmosfeer. Aan de kamers met 0%  $\text{CO}_2$  werd gehydrateerde kalk toegevoegd om de  $\text{CO}_2$ , afkomstig uit de omgeving of geproduceerd door knolademhaling, te absorberen. De bakkleur werd bepaald aan het begin en aan het einde van elke proef. Er werden geen verschillen tussen de behandelingen waargenomen.

Vanaf het tweede jaar werden ook behandelingen met etheengas meegenomen in het onderzoek. Bovendien werd de duur van de testen

verlengd tot 9 weken en werd het aantal testperioden teruggebracht tot twee per jaar, beginnend in december of januari en in maart of april. Net als in het eerste jaar werd er gehydrateerde kalk gebruikt. Het materiaal bestond uit knollen van het ras Russet Burbank afkomstig van twee of vier commerciële telers in New Brunswick en Prince Edward Island, Canada. Het materiaal was voor de proeven eerst gesuberiseerd en vervolgens koel bewaard. De knollen werden vervolgens behandeld met chloorprofam en bewaard bij 9 °C. Omdat er geen effecten werden gevonden die toe te schrijven waren aan de behandeling waarin de O<sub>2</sub> werd uitgeput, werden alleen de behandelingen voortgezet waarin de O<sub>2</sub> concentratie 19% was in de jaren 2, 3 en 4. Dit werd na jaar 4 niet langer voortgezet. De bakkleur werd geëvalueerd aan het begin van elke testperiode en na 3, 6 en 9 weken in de behandelde atmosfeer.

De experimenten tijdens de jaren 2 tot en met 6 richtten zich op drie onderzoeksvragen, te weten Studie A) of CO<sub>2</sub> of sporen etheen of de combinatie van beide verantwoordelijk was voor het donkerder worden van de bakkleur, een effect dat lange tijd alleen aan CO<sub>2</sub> toegeschreven werd, Studie B) of 1-methyl-cyclopropeen (1-MCP, een gas dat de werking van etheen belemmert) het donker kleuren kon verhinderen, en Studie C) of de concentratie van of wel de CO<sub>2</sub> of wel het etheen de respons op het andere gas veranderde wanneer zij in combinatie werden toegepast. In alle studies waren de concentraties van de beide gassen 0 of 2% CO<sub>2</sub> en 0 of 0,5 µl L<sup>-1</sup> etheen in een factoriële proefopzet. Studies A en B bevatten ook een ongeventileerde behandeling, met of zonder etheen. In Studie B werd een voor-behandeling met 1-MCP opgenomen, resulterend in een 2 x 2 x 2 proefopzet. De 1-MCP werd toegediend in de kamers als een damp gedurende de 48 uur voor het begin van bewaaratmosfeer-behandelingen. In Studie C werden verschillende extra CO<sub>2</sub>- en etheenconcentraties gebruikt, namelijk 0, 0,5, 1 en 2% CO<sub>2</sub> en 0, 0,25 en 0,5 µl L<sup>-1</sup> etheen resulterend in een 4 x 3 proefopzet. Voor elk van deze studies werden experimenten uitgevoerd gedurende twee opeenvolgende jaren, resulterend in vier testperioden van elk behandelings-regime. In het derde jaar werden Studies A en B tegelijk uitgevoerd, met behulp van aparte bewaarkamers.

In de jaren 7, 8 en 9 werden de proeven uitgebreid tot het gehele bewaarseizoen (van herfst tot en met voorjaar) en werden drie andere rassen opgenomen naast Russet Burbank, te weten de fritesrassen Shepody en Innovator en het chipsras Dakota Pearl. Deze lange-termijn experimenten

omvatten twee studies, namelijk Studie D) het beoordelen van de effecten van blootstelling aan CO<sub>2</sub> en etheen over de gehele bewaarperiode en het vaststellen of andere rassen op dezelfde wijze reageerden als Russet Burbank, en Studie E) het vaststellen of de resultaten vergelijkbaar waren met resultaten die werden verkregen wanneer etheen werd toegediend in de hogere concentratie die gebruikelijk is om spruitremming te bewerkstelligen.

Twee herhalingen van elk ras werden verkregen van commerciële telers in het oosten van Canada, in oktober of november van elk jaar, met dien verstande dat slechts één bron van Dakota Pearl werd gebruikt in de jaren 7 en 8. Na suberisatie en koelen werden de knollen bij 9 °C bewaard in kamers met gemodificeerde atmosfeer met 0 of 2% CO<sub>2</sub> met of zonder etheengas, in een 2 x 2 factoriële proefopzet. De toegepaste concentratie etheen was ofwel 0,5 µl L<sup>-1</sup> (sporen van etheen, Studie D, jaren 7 en 8) of 10 µl L<sup>-1</sup> (hoog etheengehalte, studie E, jaren 8 en 9). Alle knollen van Studie D werden behandeld met chloorprofam, terwijl in Studie E de knollen in de vier factoriële behandelingen niet werden behandeld met chloorprofam. In elk jaar werd echter een aparte controle met een chloorprofam-behandeling opgenomen. Net als in jaar 1 werd gehydrateerde kalk gebruikt. De bakkleur werd geëvalueerd bij het begin van de proeven in november of december van elk jaar, en met tussenpozen van vier weken tot de volgende junimaand.

De belangrijkste conclusies uit deze studies zijn (zoals vermeld in dit proefschrift):

1. De bakkleur van sommige rassen werd donkerder in reactie op een verhoogde CO<sub>2</sub> concentratie, maar de reactie was gewoonlijk relatief klein (dat wil zeggen minder dan de respons op etheen). In de rassen die wel reageren op alleen CO<sub>2</sub>, was de reactie pas 8 of meer weken na begin van de blootstelling aantoonbaar/merkbaar.
2. Indien de bakkleur donkerder werd in reactie op etheen (ofwel in zeer lage dan wel in hoge concentratie), versterkte CO<sub>2</sub> meestal de verkleuring nog verder.
3. Indien de bakkleur donkerder werd in reactie op verhoogde CO<sub>2</sub>, leidde een combinatie met etheen (zelfs in een zeer lage concentratie) meestal tot een nog veel sterkere verkleuring.

4. Meestal was er een reactie op gezamenlijke toediening van CO<sub>2</sub> en etheen (een donkere bakkleur), ongeacht of er een reactie was op één van beide gasen afzonderlijk. Deze reactie was duidelijk bij de eerste evaluatie nadat de blootstelling begonnen was, dat wil zeggen binnen drie of vier weken.
5. Fysiologisch oudere knollen hadden de neiging om sterker te reageren. Dit bleek geen verband te houden met het breken van de kiemrust en het begin van het kiemen, maar kwam iets later - blijkbaar als veroudering naderbij kwam.
6. Het donker kleuren was rechtstreeks afhankelijk van de concentratie van beide gasen maar dit verband vertoonde variatie. Het donker kleuren kon worden voorkomen door een voorbehandeling met 1-MCP, alsmede door het wassen van de lucht of ventilatie om CO<sub>2</sub> en etheen te verwijderen.

De resultaten van deze proeven leveren nuttige informatie op die de aardappelindustrie in het algemeen en bewaarplaatsmanagers in het bijzonder kan helpen een lichte kleur te behouden van aardappel-producten die zijn gemaakt van bewaarde aardappelknollen. Er is echter meer onderzoek nodig om de respons van andere rassen nader te onderzoeken alsmede de respons onder de specifieke bewaar-condities zoals die gangbaar zijn in de verschillende productiegebieden.





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## Curriculum Vitae

Barbara Jean Daniels-Lake was born in the small Canadian town of Windsor, Nova Scotia, on March 18, 1954, near the ancestral farm where she still resides. Her early education was in rural elementary schools, and later at the regional high school in Windsor. After some false starts at a University education, interspersed with periods of private-sector employment, in 1985 she completed her Bachelor of Science degree with High Honours, majoring in Plant Science at the Nova Scotia Agricultural College in Truro, Canada.

Barb has worked in the agricultural industry since completing that first degree, mainly in research at the Agriculture and Agri-Food Canada (AAFC) Atlantic Food and Horticulture Research Centre in Kentville, Nova Scotia. Since 1991, her work has centred on postharvest potatoes, including storage biology, sprout inhibitors and processing traits. This included the identification and development (with Dr R Prange) of ethylene gas as a potato sprout inhibitor. In 2001, she completed a Master of Science degree from Nova Scotia Agricultural College/Dalhousie University, where her thesis topic was ethylene and potato sprouting. She has continued to study the effects of ethylene on stored potatoes up to the present time.

From 1997 to the present, Barb has been employed as a Research Biologist with AAFC. During this time she has led or participated in numerous collaborative research projects, with partners within AAFC as well as external partners from government, industry and academia. She has published many papers in peer-reviewed scientific journals, and made oral presentations at dozens of conferences in several countries. She has also been invited to speak at regional, national and international venues on various aspects of potato postharvest biology.

In 2009 Barb began her pursuit of a Doctoral degree at Wageningen University in the Netherlands. Her research has focused on the effect upon processing colour of CO<sub>2</sub> and ethylene gas together in the atmosphere surrounding potatoes during long-term storage. This thesis and its defence are the culmination of that research.