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Effects of Elevated CO_2 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-week duration) have shown that the fry colour of stored potatoes (*Solanum tuberosum* L.) can be negatively affected by simultaneous exposure to elevated CO_2 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 kPa CO_2 and 0 or 0.5 μl l^{-1} 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_2+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_2× 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.

Keywords Carbon dioxide · Chip colour · Ethylene · Fry colour · Processing colour

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 (AAFC 2009; Kirkman 2007; USDA 2004). Worldwide production of frozen potato products—primarily frozen French fries—exceeds 2 million metric tonnes annually (USDA 2009). One of the

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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 (Burton et al. 1992; Mazza 1983). During frying, colourless reducing sugars and free amino acids combine in the non-enzymatic 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 concentration of the raw tubers is an important quality aspect of any potatoes offered to the factory for processing. Reducing sugar concentration 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_2 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_2 together with ethylene gas has been found to have an important role (Daniels-Lake et al. 2005a, b, 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_2 on fry colour is less clearly defined. Elevated CO_2 has been reported to darken (Khanbari and Thompson 1994, 1996; Mazza and Siemens 1990; Schouten 1993), 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_2 and ethylene together, no darkening attributable to CO_2 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_2 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_2 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 and Prange 2009; Daniels-Lake et al. 2005a, b, 2008). 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_2, and CO_2 in the potato storage atmosphere. Industry guidelines regarding maximum CO_2 concentration exist in some regions, e.g. Rastovski (1987) and Schaper et al. (1993) recommend a maximum of 1 kPa CO_2 in the storage atmosphere. However, this concentration is easily exceeded and many storage buildings are not equipped with CO_2 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_2 in the same manner as RB. Therefore research trials were initiated to investigate the effect of long-term exposure to elevated CO_2 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 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 (J. R. 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.

Materials and Methods

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 4 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^{-1} 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 ±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.

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 hours, three times per day, to establish and maintain 0 or 2 kPa CO_2 and 0 or 0.5 μl l^{-1} ethylene gas, in a factorial arrangement. Ambient and respired CO_2 was scrubbed from specific chambers by placing a paper sack containing ca. 0.5 kg of hydrated lime ($Ca(OH)_2$; Graymont (QC) Inc., Boucherville, Quebec, Canada) inside the chambers designated for 0 kPa 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 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 the desired CO_2 concentration. The 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).

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 4 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×

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 at ≥3 mm in length (Burton et al. 1992; Reust and Aerny 1985).

Statistics

The customized experimental design was a replicated two-way factorial design with a split plot arrangement. Two levels of CO_2 exposure (0 and 2 kPa) were crossed with two levels of ethylene exposure (0 and 0.5 μl l^{-1}) for four treatments. Treatment was the main plot and evaluation date was the sub-plot. 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 2 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 1. Unless otherwise noted, only results significant at $P \leq 0.05$ are discussed.

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

Table 1 Summary of output from statistical analyses

Source of variation	Contrasts	*df*	Russet Burbank	Shepody	Innovator	Dakota Pearl	
						Hunter L	Hunter a
					P-value		
CO_2		1	<0.001*	<0.001	0.004	0.024	0.029
Ethylene		1	0.049	<0.001	<0.001	<0.001	0.003
CO_2×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_2×evaluation date		6	0.058	0.383	0.018	0.477	0.003
	CO_2×early vs. later	1	0.006	0.211	0.016	0.937	0.241
	CO_2×later linear	1	0.438	0.543	0.012	0.222	0.007
	CO_2×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_2×ethylene×evaluation date		6	0.592	0.974	0.042	0.937	0.790
	CO_2×ethylene×early vs. later	1	0.923	0.902	0.083	0.821	0.999
	CO_2×ethylene×later linear	1	0.742	0.799	0.049	0.785	0.164
	CO_2×ethylene×later quadratic	1	0.517	0.596	0.045	0.253	0.419

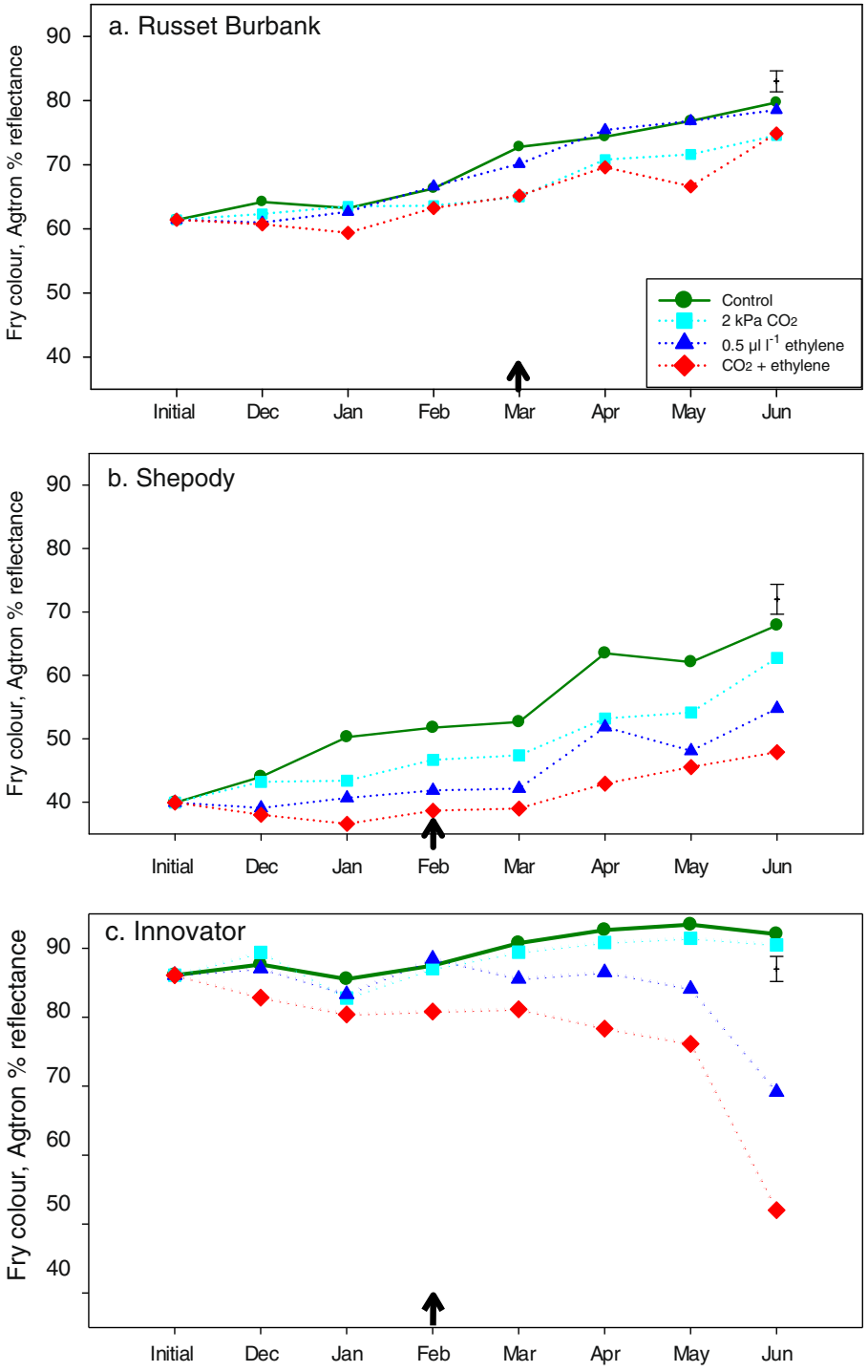
*P values of 0.05 or less were considered significant

second year of trials (data not presented). Despite these differences, the responses to the treatments were very similar across years within cultivars.

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 (Fig. 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 (Fig. 1).

In all three French fry cultivars, colour was darker in the CO_2+ethylene treatment than in the control (Fig. 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_2+ethylene appears to be greater in post-dormant than in dormant tubers (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009).

Fig. 1 Processing colour of tubers stored with or without CO_2 or ethylene gas; **a** RB, **b** SH, **c** IN, **d** DP luminosity score and **e** DP redness score. Data points are means of data from 2 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_2× 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


a. Russet Burbank
b. Shepody
c. Innovator
Fry colour, Agtron % reflectance
90
80
70
60
50
40
Initial
Dec
Jan
Feb
Mar
Apr
May
Jun
Control
2 kPa CO2
0.5 µl l-1 ethylene
CO2 + ethylene

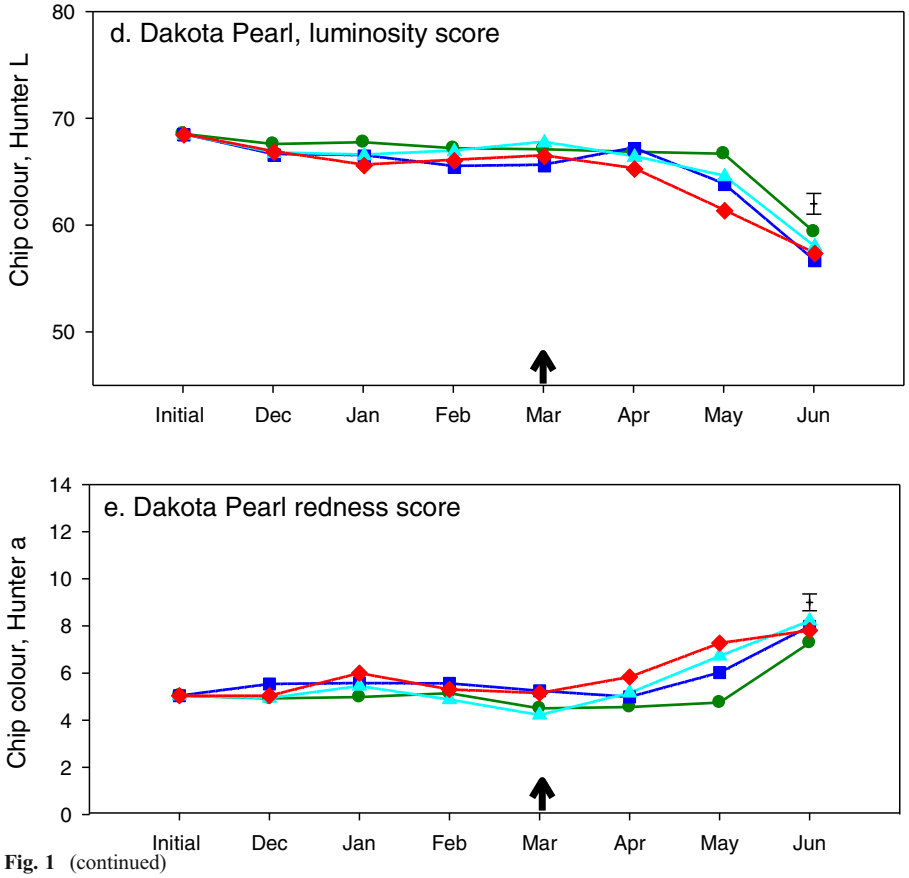


Fig. 1 (continued)

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 (Fig. 1a; Daniels-Lake et al. 2005a, b, 2007, 2008; Daniels-Lake and Prange 2009), i.e. in both this study and the published reports, the CO_2 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_2 (Fig. 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_2 and the CO_2+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 (Fig. 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 vs. 9 weeks, respectively; Daniels-Lake et al. 2005a, b, 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_2 and ethylene exposures.

The general ANOVA analysis of the RB data indicated significant differences attributable to the main effects of CO_2, ethylene and evaluation date ($P<0.001$, $P=0.049$ and $P<0.001$, respectively), but the two- and three-way interactions were not significant ($P>0.05$ for all; Table 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 μl l^{-1} ethylene, respectively (Fig. 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 (Fig. 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).

Within the interaction of CO_2×evaluation date for RB tubers, the orthogonal contrast of early vs. later was significant ($P=0.006$; Fig. 2). The effect of CO_2 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, b, 2007, 2008; Daniels-Lake and Prange 2009), CO_2 did not darken fry colour during the early phase of these trials (Fig. 2). The fry colour scores of tubers exposed to 0 and 2 kPa CO_2 improved (lightened)

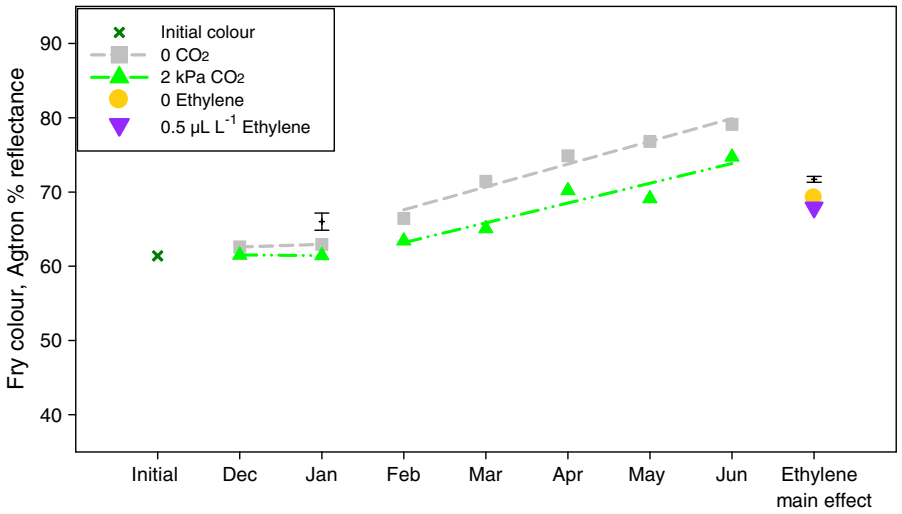


Fig. 2 Changes in fry colour of RB tubers during storage, in response to CO_2 (mean values across two ethylene levels) and ethylene (mean values across two CO_2 levels). Data points are means of two trials. *Vertical bars* represent ±SEM (from *left* to *right*) for the orthogonal contrast between the early and later groupings of the evaluations within the interaction of CO_2×evaluation date (1.158, $P=0.006$) and for the main effect of ethylene (0.400, $P=0.049$)

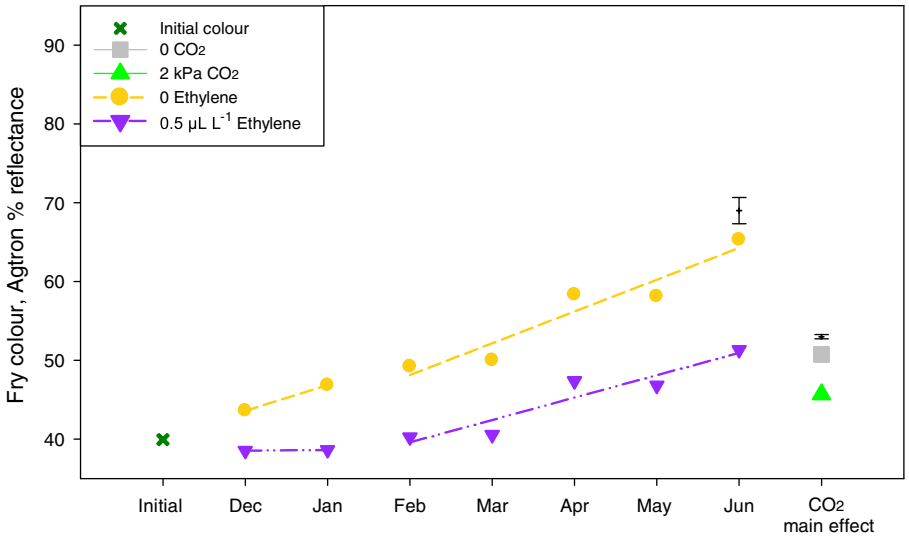


Fig. 3 Changes in fry colour of SH tubers in response to CO_2 (mean values across two levels of ethylene) and ethylene gas (mean values across two levels of CO_2). Data points are means of two trials. *Vertical bars* represent ±SEM (from *left* to *right*) for the orthogonal contrast between early and later groupings of evaluation dates within the interaction of ethylene×evaluation date (1.658, P=0.043), and for the main effect of CO_2 (0.282, P<0.001)

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 kPa CO_2 was ca. 5 ARu lower at each evaluation than the fry colour of tubers in the 0 CO_2 treatments (Fig. 2).

Shepody

In SH tubers the main effects of CO_2, ethylene and evaluation date on fry colour were all significant (P<0.001 for each; Table 1). Although the two- and three-way interactions were not significant, the F probability for the CO_2×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_2, ethylene and CO_2+ethylene treatments, respectively, suggesting a consistent, progressively darker fry colour in tubers from these treatments throughout the trials (Fig. 1b). This trend is similar to the published findings from short-term trials using RB (Daniels-Lake et al. 2005a, b, 2007, 2008; Daniels-Lake and Prange 2009), except for the darkening in the CO_2 treatment which was not observed in the previous work. Fry colour appeared to be darker in the CO_2 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 (Fig. 1b), and was consistent across both years (data not presented).

Ethylene had a strong effect on the fry colour of SH tubers (Fig. 3). This is consistent with the findings of Prange et al. (2005) who reported that SH tubers are

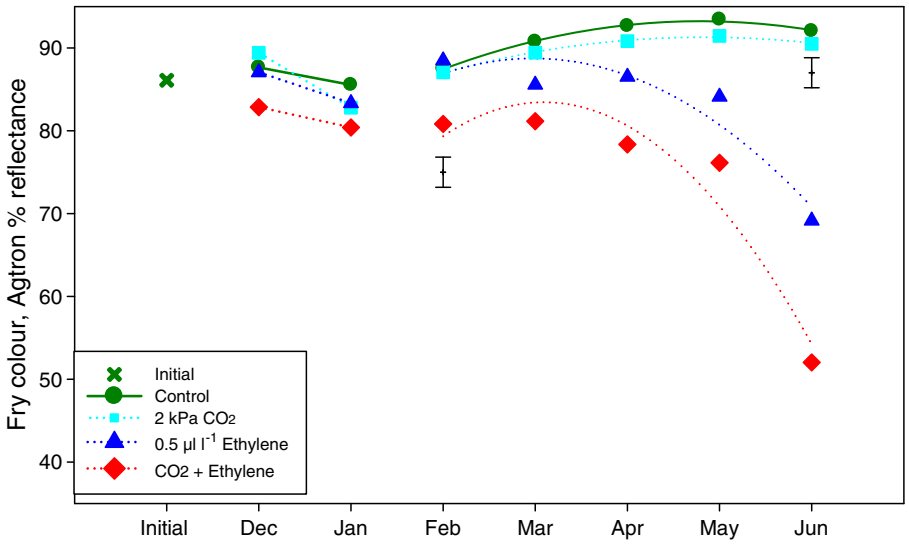


Fig. 4 Changes in fry colour of IN tubers during storage, in response to two levels of CO_2 and two levels of ethylene gas in a factorial design. Data points are means of two trials. *Vertical bars* represents ±SEM (from *left* to *right*) for the interaction of CO_2×ethylene×evaluation date (1.814, P=0.042) and for the polynomial contrast (quadratic relationship) in the later grouping of evaluation dates within the interaction of CO_2×ethylene×evaluation date (1.814, P=0.045)

more sensitive to ethylene than RB, and Gichohi and Pritchard (1995) who found that fry colour and tuber sugars in SH are more sensitive than in RB 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 (Fig. 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_2 also darkened fry colour of SH tubers, by approximately 5 ARu over the entire trial (Fig. 3). This is similar to the effect of CO_2 on the fry colour of RB tubers discussed above, although the interaction with evaluation date was not significant in SH (Table 1). The effect of CO_2 on SH fry colour may reflect the greater sensitivity of SH to stresses, compared with RB (Gichohi and Pritchard 1995; Prange et al. 2005).

Innovator

In the IN tubers, the three-way interaction of CO_2, ethylene and evaluation date was significant (P=0.042; Table 1; Fig. 1c). Fry colour of IN tubers exposed to elevated CO_2 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 (Fig. 1c). In the CO_2+ethylene treatment, fry colour declined from the start to the end of the trial, and was darker than the controls throughout the trial. This is similar to the response of RB tubers to short-term exposure to these two gases (Daniels-Lake et al. 2005a, b, 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_2+ethylene treatments, the fry colour scores were much darker than the control and CO_2 treatments at the June evaluations (Fig. 1c). Fry colour of IN tubers in the CO_2+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_2×ethylene×evaluation dates was also significant for IN (P=0.045; Fig. 4). Fry colour declined slightly in all treatments during the early phase of the trials, although only the CO_2+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_2 treatments lightened as storage time increased, but darkened in an exponential manner in the ethylene and CO_2+ethylene treatments (Fig. 4). The tubers apparently became more sensitive to the ethylene and CO_2+ethylene treatments as their physiological age approached senescence. These observations suggest that fry colour of IN tubers is relatively insensitive to CO_2, is somewhat sensitive to ethylene, but is very sensitive to the presence of the two gases together.

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 (Fig. 1d, e). 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 evaluation, both Hunter L and Hunter a darkened slightly in all treatments (Fig. 1d, e). 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_2, 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 1; Fig. 5a). Significant differences were also observed in Hunter a scores in the interaction of CO_2×evaluation date and the main effect of ethylene (P=0.050 and P=0.003, respectively; Fig. 5b).

The change in DP Hunter L chip colour attributable to CO_2 was less than 1 unit darker, and ca. 1.5 units darker in response to ethylene (P=0.024 and P<0.001, respectively; Fig. 5a). Within the interaction of CO_2×evaluation date, there was no difference in DP Hunter a chip colour attributable to CO_2 in the early phase. However chip colour was up to 0.9 units redder in response to CO_2 during the later phase of the trial (quadratic polynomial contrast, P=0.050; Fig. 5b). The change in Hunter a scores attributable to ethylene was ca. 0.5 units redder (P=0.003; Fig. 5b). While these changes were small, they were consistent and represent an effect on chip colour which could be avoided by storage management activities.

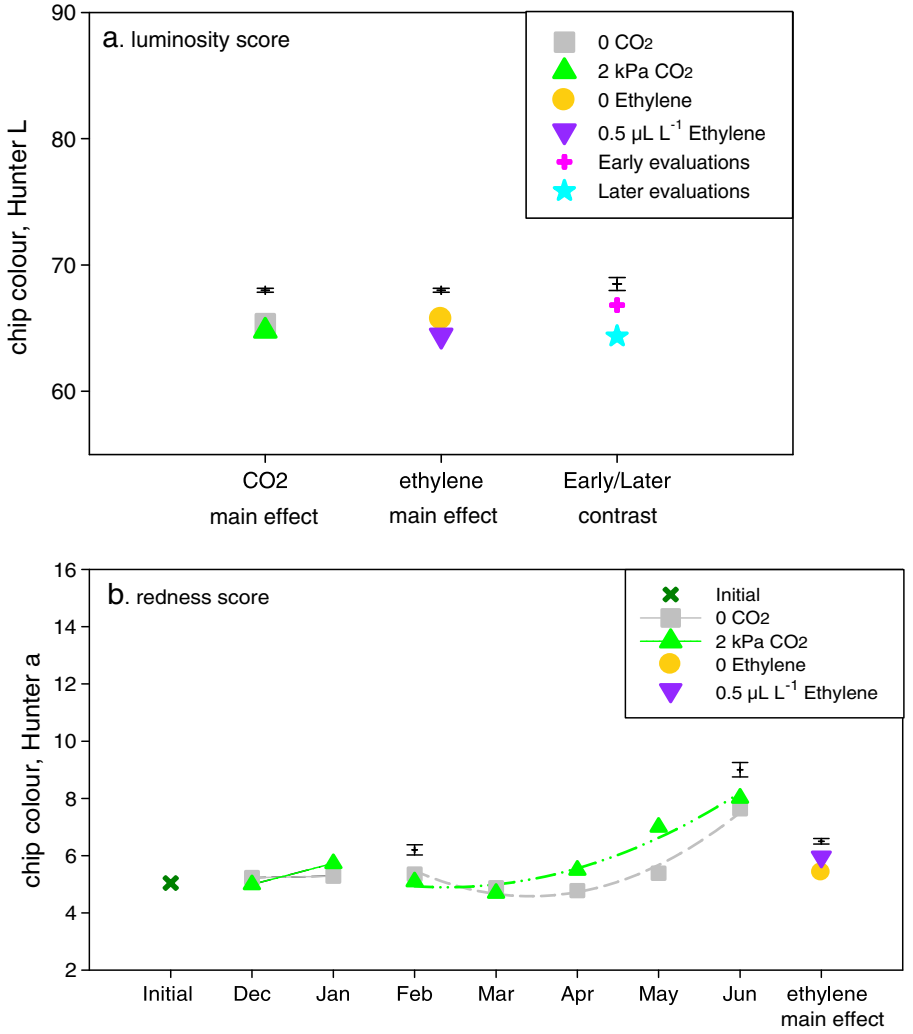


Fig. 5 Changes in chip colour of DP tubers during storage, in response to CO_2 (mean values across two levels of ethylene gas), ethylene (mean values across two levels of CO_2) and the orthogonal or polynomial contrasts; **a** Hunter luminosity scores and **b** Hunter redness scores. Data points are means of two trials. *Vertical bars* represent ±SEM, i.e. in graph a (from *left* to *right*) for the main effect of CO_2 (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_2×evaluation date (0.2597, P=0.050) and for the main effect of ethylene (0.0961, P=0.003)

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_2 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_2 and ethylene were present together than when both were absent (Fig. 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_2 was absent. This is surprising, since previous reports have indicated that darkening attributable to ethylene, with or without CO_2, 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; Daniels-Lake and Prange 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_2 revealed a response to this gas which was not apparent in the shorter trials reported previously (Daniels-Lake et al. 2005b; Daniels-Lake and Prange 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_2 and CO_2+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_2 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 (Fig. 1a, b), 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 (Fig. 1c–e). The rapid increase in colour scores observed at successive evaluation dates in SH and RB was not observed in IN and DP, nor was darkening attributable to the gas treatments observed, except in IN in the CO_2+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 (Fig. 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_2 alone had little to no effect on processing colour of these two cultivars (Figs. 4 and 5).

In general, any change in processing colour in response to a stimulus is attributable to 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 the sugars, e.g. slower respiration, reduced rate of conversion to sucrose and starch, 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_2, 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_2 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_2 (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009). The treatment concentrations of CO_2 and ethylene applied in this study were well above the endogenous and atmospheric levels, and elicited the reported responses. Nevertheless, the concentrations of CO_2 and ethylene applied here can easily occur in the atmosphere of commercial potato storage buildings.

The observed response of IN tubers to the two gases was more consistent with effects observed in the previous short-term trials with RB (Daniels-Lake et al. 2005b, 2008; Daniels-Lake and Prange 2009) than were the long-term effects on RB observed in this study. 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_2 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 × CO_2 × ethylene effects.

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