Effect of Storage Temperature on Potato (*Solanum tuberosum* L.) Tuber Glycoalkaloid Content and the Subsequent Accumulation of Glycoalkaloids and Chlorophyll in Response to Light Exposure

D. Wynne Griffiths,* Henry Bain, and M. Finlay B. Dale

Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, United Kingdom

Tubers from six potato cultivars were placed into either 10 or 4 °C stores immediately postharvest. Replicated tuber samples were analyzed for glycoalkaloid (TGA) content immediately postharvest, after 6 and 14 weeks storage at 10 °C and after 6 weeks storage at 4 °C. Subsamples from the 10 °C store were removed after 1, 2, 3, 4, and 8 weeks, respectively, stored for a further 6 weeks at 4 °C, and again analyzed for TGA content. After each sampling date, tubers were exposed for 96 h to light and analyzed for both chlorophyll and TGA concentrations. The results indicated that the exposure of tubers from some cultivars, such as Brodick and Pentland Crown, to low temperatures within 2 weeks of harvest resulted in a relatively rapid accumulation of glycoalkaloids to levels close to or exceeding the recommended safe maximum level of 200 mg of TGA per kilogram of fresh weight, while other cultivars, such as Eden and Torridon, appeared insensitive to cold stress. Storage for 6 weeks at both 10 and 4 °C resulted in a greater accumulation of glycoalkaloids in response to light exposure relative to that observed immediately postharvest, with the tubers from all six cultivars stored at 4 °C producing over twice the amount of TGA as those stored at 10 °C. Storage at 10 °C prior to 6 weeks storage at 4 °C resulted in smaller photoinduced increases in TGA content but even after 8 weeks at 10 °C followed by 6 weeks at 4 °C, the photoinduced increases in all cultivars were significantly higher than that recorded for tubers stored continually at 10 °C, which had values comparable to those obtained immediately postharvest. In all cultivars photoinduced chlorophyll accumulation was little affected by storage temperature but was slightly, although significantly, reduced as time in storage increased from 6 to 14 weeks. The significance of these results in relation to consumer safety and plant breeding are discussed.

Keywords: *Glycoalkaloids; chlorophyll; storage; light exposure; potato; Solanum tuberosum L.*

INTRODUCTION

Although potato (*Solanum tuberosum* L.) tubers are an excellent source of dietary protein, vitamin C, carbohydrates, and iron for both humans and domesticated livestock (Storey and Davies, 1992), they have the capacity to synthesize the potentially toxic compounds, α-solanine and α-chaconine, in considerable quantities. These two compounds are structurally similar and can be considered as differently glycosylated forms of the steroidal alkaloid solanidine (Kuhn et al., 1955) and, because of their stability to heat (Bushway and Ponnampalam, 1981), neither compound is significantly reduced in concentration by common cooking processes such as boiling, frying, or baking.

At low concentrations, the presence of these glycoalkaloids may enhance the flavor of potatoes, but at levels exceeding 150 mg per kilogram of fresh weight a bitter taste may be perceived (Sinden et al., 1974). The inadvertent consumption by humans of large quantities of glycoalkaloids can lead to illness and, in extreme cases, death (reviewed by Friedman and McDonald, 1997). It has been calculated (Morris and Lee, 1984) that the relative toxicities of α-solanine and α-chaconine are comparable to that of strychnine with the toxic dose being in the order of 2−5 mg per kilogram of bodyweight.

* Author to whom correspondence should be addressed (fax 01382 562426; e-mail wgriff@scri.sari.ac.uk).

In view of this, a level of 200 mg per kilogram of fresh weight has been accepted generally as the upper limit for the glycoalkaloid content of tubers from new cultivars (Sinden and Web, 1972). More recently, the National Institute for Agricultural Botany suggested an upper level of 60 mg per kilogram of fresh weight as a guideline for breeders (Parnell et al., 1984), and this call for a lower recommended maximum value has been supported recently by several research scientists (Slanina, 1990; Potus and Adrian, 1995).

Although the total glycoalkaloid content of potato tubers is genetically controlled (Sanford and Sinden, 1972; Sanford et al., 1995), the levels found at harvest are strongly influenced by environmental effects during the growing season (Friedman and McDonald, 1997 and references therein). Additionally, postharvest treatments may significantly increase tuber glycoalkaloid content. In particular, exposure to direct sunlight (Percival et al., 1996) or artificial light (Dale et al., 1993; Percival and Dixon, 1994) increases glycoalkaloid concentration with the magnitude of the observed increase being cultivar-dependent (Griffiths et al., 1994). Bruising and impact damage during harvesting and grading may also increase glycoalkaloid levels in tubers (Olsson, 1986) with significant differences being found between cultivars (Dale et al., 1998).

The effects of storage temperature on tuber glycoalkaloid content have been studied in comparatively few cultivars with somewhat conflicting results. Zitnak

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(1953) reported that after 6 weeks storage at 4−6 °C, potato tubers contained almost twice the glycoalkaloid content of those stored at 12−15 °C (data from Maga, 1980), while Salunke et al. (1972) found only small increases in tubers stored at 0 and at 8 °C and much greater increases in those stored at 15 and 24 °C. Storage at 10 °C has also been shown to increase glycoalkaloid content (Cronk et al., 1974; Love et al., 1994) while subsequent reduction of the storage temperature to 4.4 °C resulted in only a minor increase (<10 mg per kilogram of fresh weight) in glycoalkaloid content (Love et al., 1994). The latter result would appear to be in agreement with that of Griffiths et al. (1997), who also found that the glycoalkaloid content of potatoes stored for 9 weeks at 10 °C then removed to lower temperature stores (2−4 °C) did not differ significantly from those stored continually at 10 °C. However, cultivar-dependent differences were found between samples placed immediately postharvest into stores at 10, 7, and 4 °C, with some cultivars accumulating glycoalkaloids more rapidly at the lower temperatures while others were relatively insensitive to storage temperatures.

Exposure to light also increases the concentration of chlorophyll in potato tubers, resulting in the familiar effect known as "sunburn" or "greening". Although the accumulated chlorophylls are harmless and tasteless to humans, greened potatoes are generally rejected by the consumer due to the perceived linkage between greening and glycoalkaloid content. While a significant correlation between chlorophyll and glycoalkaloid accumulation on an individual cultivar level (Dale et al., 1993) has been reported, in the majority of recent intervarietal comparisons (Spoladore et al., 1983; De Maine et al., 1988; Griffiths et al., 1994) no such correlations have been identified and indeed detailed biochemical investigations (Edwards et al., 1998) concluded that there was no direct metabolic link between chlorophyll and glycoalkaloid biosynthesis. The effect of storage at ambient temperature prior to light exposure has been demonstrated to reduce the rate of chlorophyll synthesis in the majority of the cultivars studied (Griffiths et al., 1994), but little if any information is available regarding the effects of storage temperature on photoinduced chlorophyll accumulation.

Traditionally, in the United Kingdom, potato tubers are stored for approximately 10−14 days at 12−15 °C prior to being moved to prolonged low temperature storage. During this time, commonly referred to as the curing period, both skin set and wound healing occur thus reducing the susceptibility of the stored tubers to both disease and excessive moisture loss. Under certain circumstances such as when the crop has been rained on, waterlogged, or has a high infection with a rotting disease the curing period is commonly dispensed with and only short-term storage recommended (Potato Marketing Board, 1996).

The objective of this study was to determine the effects of different storage times at 10 °C prior to storage at 4 °C on total tuber glycoalkaloid content and to ascertain whether storage conditions modified the subsequent accumulation of both glycoalkaloids and chlorophyll in response to light exposure.

MATERIALS AND METHODS

Plant Material. Tubers from the six cultivars (Table 1) used in this study were harvested from field trials grown using normal agronomic practices in 1996 at a site located at Mylnefield, Dundee. Tuber samples were taken 1 day prior to burn-down of the foliage and 2 weeks later (i.e., normal harvest date). After lifting, the tubers were hand washed and five medium-sized tubers (Table 1) were randomly assigned to each replicate. Four replicates were assigned to each treatment and if not immediately used for further experimentation or analysis were placed into either 10 or 4 °C stores at ambient relative humidity within 24 h of lifting. Four replicates from each cultivar lifted at the normal harvest date were removed from the 10 °C store after 1, 2, 3, 4, and 8 weeks and immediately placed in the 4 °C store for a further 6 weeks prior to analysis and/or experimentation.

Table 1. The Mean Tuber Weight per Replicate of the Six Cultivars Utilized in This Study

cultivar	tuber weight (g)	standard deviation
Brodick	167	11.9
Eden	156	15.0
Pentland Crown (P. Crown)	171	15.9
Pentland Dell (P. Dell)	151	15.0
Record	161	10.0
Torridon	172	15.0

Light Exposure. The method used to evaluate the effect of light on the glycoalkaloid and chlorophyll contents of potato tubers was similar to that described by Dale et al. (1993) and Griffiths et al. (1994). After removal from storage, each tuber was cut in half longitudinally and one-half placed, cut surface down, on a tray lined with moist paper toweling. The trays were then placed in an environmental chamber set at 20 °C and ambient relative humidity and illuminated with high-pressure sodium lights (predominant wavelengths 550−650 nm) with a photon flux density of 140 μmol m^{-2} s^{-1} at tray level. After 96 h of exposure to light, a 2-mm slice was removed from the cut surface of each of the halved tubers, which were then quartered and opposite quarters from the five tubers from each replicate were bulked, diced, and immediately frozen in liquid nitrogen. After freeze-drying the samples were milled through a 0.5 mm sieve and stored at −20 °C prior to analysis.

Previous studies (Dale et al., 1993) have shown that under these conditions the increase in glycoalkaloid content due to wounding at the cut surface was minimal compared to that due to light exposure. This was confirmed utilizing the tubers lifted at burn-down and immediately exposed to light. In this case, the remaining half tubers were quartered and opposite quarters bulked to produce two samples per replicate. One sample was immediately diced and frozen in liquid nitrogen and the other placed into a light-proof bag and placed in the environmental chamber for 96 h along with the trays containing the other half tubers exposed to light. Analysis of the glycoalkaloid content of the tubers stored for 96 h in the dark did not differ significantly from those frozen 96 h earlier. Consequently for all other storage treatments the increase in glycoalkaloid content due to light exposure was taken as the difference between the glycoalkaloid content of the half tubers exposed to light for 96 h and that of the opposite halves sampled 96 h earlier (i.e., at the time of halving the tubers).

Chemical Analysis. The dry matter content of the potato tuber samples was taken to be the loss in weight during freeze-drying and expressed as grams of freeze-dried matter per 100 g of fresh weight (g FDM per 100 g FW).

The α-solanine and α-chaconine content of the freeze-dried samples was determined as outlined by Griffiths et al. (1997) utilizing a high-performance liquid chromatographic method based on that of Hellenäs (1986). Total glycoalkaloid (TGA) content was taken as the sum of the individual values for α-solanine and α-chaconine and utilizing the previously determined dry matter content expressed as milligrams of total glycoalkaloids per kilogram of fresh weight (mg TGA kg^{-1} FW).

Total chlorophyll content was determined as outlined by Harborne (1988). The chlorophyll was extracted from the freeze-dried samples using 80% aqueous acetone, and the absorbance of the resulting supernatant measured at 663 and 646 nm in a 1-cm cuvette placed in a Pye Unicam Model

Table 2. The Total Glycoalkaloid Content of Potato Tubers from Six Cultivars at Harvest and after Storage at 10 °C

	glycoalkaloid content (mg kg^{-1} FW)					
	early lift,[a] weeks storage		main lift, weeks storage			cultivar
cultivar	0	6	0	6	14	mean
Brodick	59	89	61	104	90	80
Eden	51	59	38	51	46	49
P. Crown	42	89	51	71	67	64
P. Dell	150	147	126	135	178	147
Record	52	71	48	55	65	58
Torridon	54	65	54	69	70	62
LSD ($P < 0.05$)[b]			19.3			8.6
mean	68	87	63	81	86	
LSD ($P < 0.05$)[b]			7.9			

[a] Tubers lifted preburn-down, 2 weeks prior to main lift. [b] LSD, least significant difference.

PU8800 UV/vis (Unicam Ltd., Cambridge, UK) spectrophotometer. The concentrations were then calculated (Harborne, 1988) from the formula:

$$\text{total chlorophyll (mg L}^{-1}) = 17.3\,(\text{abs 646 nm}) + 7.18\,(\text{abs 663 nm})$$

From these results and the dry matter data, the chlorophyll content of the tubers was determined and expressed as milligrams per kilogram of fresh weight (mg kg^{-1} FW).

Statistical Analysis. Two-way analyses of variance (ANOVA) were calculated as outlined in Snedecor (1955). In all cases the level of significance used was $P < 0.05$.

RESULTS AND DISCUSSION

Constant Storage at 10 °C. *Effect of Harvest Date and Time in Storage.* The total glycoalkaloid (TGA) content of the tubers at harvest (Table 2) were similar in both value and ranking to those previously reported for these six cultivars (Griffiths et al.; 1994; Griffiths et al., 1997). The highest value was found for the cultivar Pentland Dell (126 mg TGA kg^{-1} FW) and the lowest value of 38 mg TGA kg^{-1} FW detected in tubers from Eden. Averaged over all cultivars, there was no significant difference in the TGA content of tubers harvested 2 weeks prior to the main lift, although on an individual cultivar level the values obtained for tubers of Pentland Dell were just significantly higher in those lifted prior to burn down as compared to those harvested 2 weeks later.

For tuber samples from both the early and main lift, storage at 10 °C for a period of 6 weeks resulted (Table 2) in a small, but statistically significant, increase in TGA content when averaged over all cultivars. All six cultivars showed slight increases in tuber TGA content with the greatest increases being found in the cultivars Brodick and Pentland Crown. Storage of the tubers harvested during the main lift for a further 8 weeks at 10 °C did not, when averaged over all cultivars, result in a statistically significant increase in TGA content although on an individual cultivar basis a significant increase was seen in Pentland Dell tubers. The magnitude of the changes in TGA content of the tubers observed in this study was of the same order as that previously reported for a similar range of cultivars cured for 10 days at ambient temperature prior to being placed into a 10 °C store (Griffiths et al., 1997).

Effect of Light Poststorage. Averaged over all cultivars time of harvest had a small, but statistically significant, effect on the accumulation of TGA in tubers exposed to light for 96 h, with the early lifted tubers accumulating slightly less TGA than those lifted 2 weeks later (Table 3). As previously reported (Dale et al., 1993), significant differences were observed between cultivars with the greatest accumulation being found in tubers from Torridon and Brodick. However, in none of the cultivars did the total glycoalkaloid content exceed that of the maximum recommended level of 200 mg TGA kg^{-1} FW. The highest total concentrations were found in Pentland Dell and Brodick tubers from the main lift. In the case of the former the total final concentration (193 mg TGA kg^{-1} FW) was due to an initially high value (126 mg TGA kg^{-1} FW) combined with a relatively low amount accumulated in response to light exposure (67 mg TGA kg^{-1} FW) while in the latter the high tuber concentration (178 mg TGA kg^{-1} FW) was due to a relatively low initial TGA content (61 mg TGA kg^{-1} FW) combined with large accumulations in response to light exposure (117 mg TGA kg^{-1} FW).

Table 3. The Photoinduced Increases in the Glycoalkaloid Content of Potato Tubers from Six Cultivars Exposed to Light for 96 h Immediately Postharvest and after Storage at 10 °C

	glycoalkaloid content (mg kg^{-1} FW)					
	early lift,[a] weeks of storage		main lift, weeks of storage			cultivar
cultivar	0	6	0	6	14	mean
Brodick	40	217	117	253	93	144
Eden	32	59	17	31	21	32
P. Crown	35	195	63	214	109	123
P. Dell	24	191	67	180	46	102
Record	27	166	46	168	104	102
Torridon	99	309	92	231	120	170
LSD ($P < 0.05$)[b]			41.5			18.6
mean	43	190	67	179	82	
LSD ($P < 0.05$)[b]			17.0			

[a] Tubers lifted preburn-down, 2 weeks prior to main lift. [b] LSD, least significant difference.

Storage at 10 °C for a period of 6 weeks significantly increased the amount of TGA accumulated by all cultivars in response to their subsequent exposure to light and a broadly similar response was seen in tubers harvested at the early and main lifts. With the exception of Eden, which has previously been shown to accumulate only small amounts of TGA in response to both light exposure and bruising (Dale et al., 1993; 1997), all the other cultivars accumulated at least 120 mg TGA kg^{-1} FW more than the tubers exposed to light immediately postharvest. Consequently, when the TGA content of the tuber prior to light exposure (Table 2) is combined with increases resulting from light exposure (Table 3), it can be calculated that the TGA concentration in the tubers from these five cultivars all exceeded the maximum recommended level of 200 mg TGA kg^{-1} FW with those for Brodick, Pentland Dell, and Torridon exceeding this value by over 50%.

Tubers stored at 10 °C for a period of 14 weeks when exposed to light accumulated significantly less TGA than those stored for only 6 weeks. Averaged over all cultivars the mean value that did not differ significantly from that obtained for tuber samples exposed to light immediately postharvest. Similar results were obtained for duplicate samples of Brodick and Record which although harvested from a different trial had been immediately placed into 10 °C storage postharvest and stored for a period of 26 weeks and subsequently

Table 4. The Photoinduced Increases in the Chlorophyll Content of Potato Tubers from Six Cultivars Exposed to Light for 96 h Immediately Postharvest and after Storage at 10 °C

	chlorophyll content (mg kg^{-1} FW)					
	early lift,[a] weeks storage		main lift, weeks storage			cultivar mean
cultivar	0	6	0	6	14	
Brodick	14	28	23	30	24	24
Eden	5	11	12	12	6	9
P. Crown	11	28	20	24	17	20
P. Dell	8	16	13	14	9	12
Record	18	25	30	30	28	26
Torridon	14	22	20	20	20	19
LSD ($P < 0.05$)[b]			3.2			1.4
mean	12	22	20	22	17	
LSD ($P < 0.05$)[b]			1.3			

[a] Tubers lifted preburn-down, 2 weeks prior to main lift. [b] LSD, least significant difference.

exposed to light for 96 h. The increase in glycoalkaloid contents of 133 and 107 mg TGA kg^{-1} FW resulting from light exposure for Brodick and Record, respectively, were of the same order of magnitude as those found for the tuber samples stored for 14 weeks (Table 3). It would appear therefore that although storage at 10 °C does not significantly affect total glycoalkaloid content of potato tubers their sensitivity to light exposure, particularly immediately postharvest, varies during storage and clearly further studies are required to more precisely assess the time of maximum sensitivity and the extent of genotypic variation for this character.

The effect of harvest date and storage at 10 °C on the subsequent accumulation of chlorophyll in response to light exposure is shown in Table 4. The early lifted tubers from all six cultivars accumulated significantly less chlorophyll than those harvested during the main lift 2 weeks later. However, after 6 weeks storage at 10 °C the amounts of chlorophyll accumulated were almost identical for each cultivar irrespective of time of harvest. Storage for 14 weeks resulted in all cultivars, with the exception of Torridon, exhibiting slight reductions in chlorophyll accumulation in response to light exposure, although as compared to the changes in accumulation noted for the glycoalkaloid contents these changes in chlorophyll content were relatively minor. As previously demonstrated (Griffiths et al., 1993), significant differences were found between cultivars with the greatest amounts of greening being consistently observed in the cultivars Brodick and Record.

Combined Effect of 10 and 4 °C Storage. *Effect of Time of Storage at 4 °C.* Storing tubers immediately postharvest at 4 °C for a period of 6 weeks resulted in significant increase in glycoalkaloid content when averaged over all cultivars (Table 5). On an individual cultivar level the greatest relative increases were seen in Brodick, Pentland Crown, and Record, while both Torridon and Eden increased their glycoalkaloid contents by less than 20 mg TGA kg^{-1} FW, suggesting that both cultivars were relatively insensitive to storage temperature. In the case of Brodick, the concentration of glycoalkaloids exceeded the recommended maximum value by over 10%. These results would suggest that the response of individual cultivars to low-temperature storage cannot be predicted from their response to light exposure, since both this and a previous study (Dale et al., 1993) indicated that Torridon on exposure to light accumulates glycoalkaloids at a similar rate as Brodick.

Table 5. The Total Glycoalkaloid Content of Potato Tubers Stored at 10 °C Followed by 6 Weeks at 4 °C

	total glycoalkaloid content (mg kg^{-1} FW)							
		weeks of storage at 10 °C prior to 6 weeks at 4 °C						
cultivar	at harvest	0	1	2	3	4	8	mean
Brodick	61	229	227	164	136	81	75	139
Eden	38	57	52	48	46	37	43	46
P. Crown	51	156	123	84	77	53	78	89
P. Dell	126	196	165	140	154	141	132	150
Record	48	93	81	53	63	41	56	62
Torridon	54	64	79	54	63	45	54	59
LSD				5.3				9.6
($P < 0.05$)[a]								
mean	63	133	121	90	90	66	73	
LSD				10.3				
($P < 0.05$)[a]								

[a] LSD, least significant difference.

Table 6. The Photoinduced Increases in the Total Glycoalkaloid Content of Potato Tubers Stored at 10 °C Followed by 6 Weeks Storage at 4 °C and Subsequently Exposed to Light for 96 h

	total glycoalkaloid content (mg kg^{-1} FW)							
		weeks of storage at 10 °C prior to 6 weeks at 4 °C						
cultivar	at harvest	0	1	2	3	4	8	mean
Brodick	117	396	502	302	281	283	240	303
Eden	17	199	179	112	101	118	96	117
P. Crown	63	425	302	277	303	293	230	270
P. Dell	67	396	348	269	303	298	261	277
Record	46	309	268	216	233	229	189	213
Torridon	92	427	427	336	387	338	291	336
LSD				59.3				22.4
($P < 0.05$)[a]								
mean	67	359	345	252	268	260	218	
LSD				24.2				
($P < 0.05$)[a]								

[a] LSD, least significant difference.

Storage for a period of 1 week at 10 °C prior to 6 weeks at 4 °C when averaged over all cultivars, resulted in a slight but statistically significant decrease in glycoalkaloid content as compared to those placed immediately at 4 °C, but the concentration in Brodick remained above the maximum recommended value. Increasing the period of storage at 10 °C prior to storage at 4 °C reduced the glycoalkaloid concentration in all cultivars and after 4 weeks at 10 °C all the cultivars had become relatively insensitive to low temperature with the values found being comparable to those obtained at harvest. This would suggest that to maximize consumer safety, the recommended curing period at 10 °C (Potato Marketing Board, 1996) should be increased from 3 to 4 weeks. Further detailed studies are also required to reevaluate the recommended "curing" periods at higher temperatures.

It is clear that if cultivars are to be bred specifically for low-temperature storage, as is currently being sought by the processing industry, breeders should evaluate the response of their potential cultivars not only with respect to sugar accumulation but also to TGA accumulation if they are to avoid inadvertently producing potentially toxic products with no visual cues such as greening normally associated with high glycoalkaloid tubers.

Effect of Light Poststorage. The exposure of tubers stored immediately postharvest at 4 °C for a period of 6 weeks to light resulted in all cultivars exhibiting a

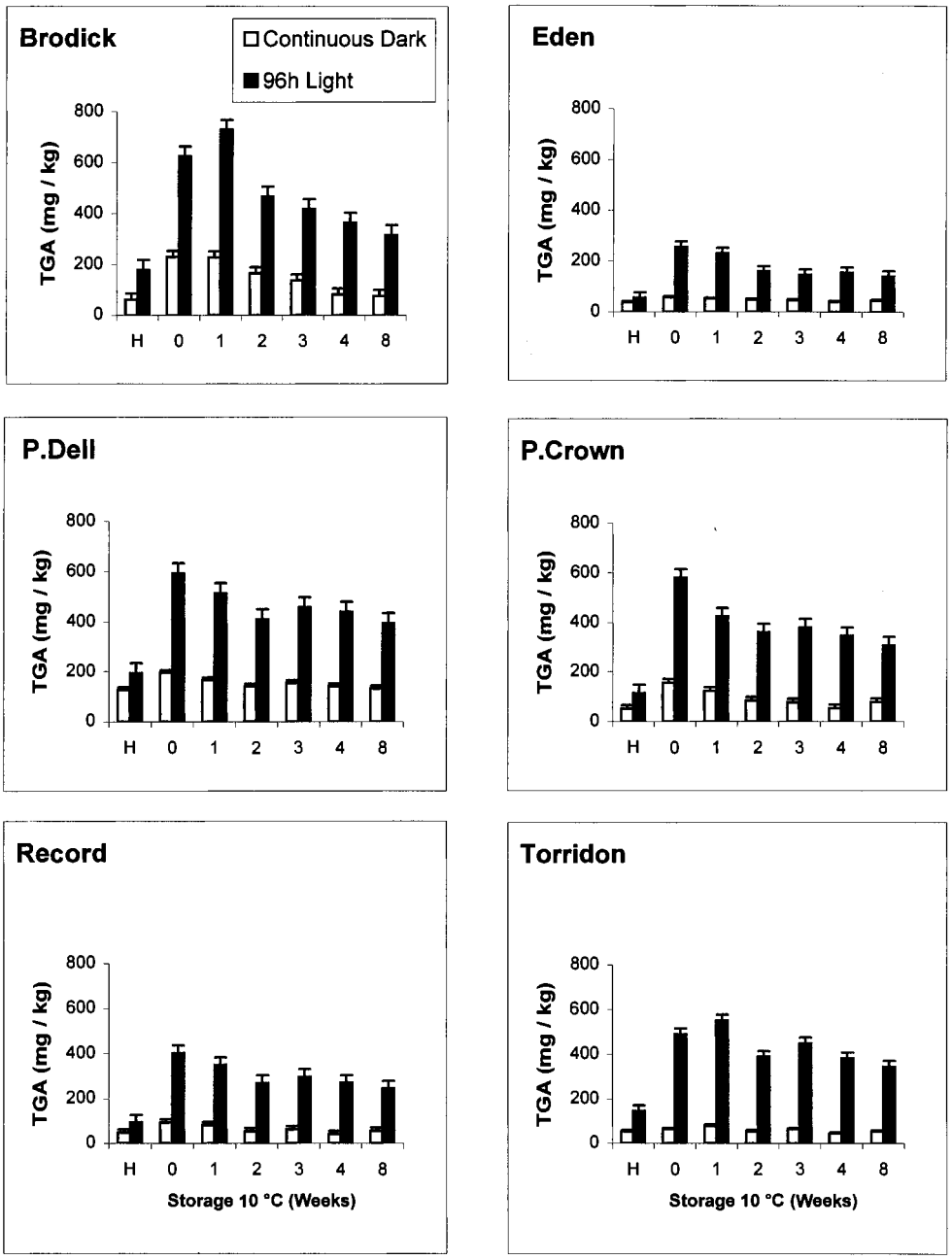

Figure 1. The total glycoalkaloid content (mg kg^{-1} FW) of potato tubers stored at 10 °C followed by 6 weeks storage at 4 °C and subsequently exposed to light for 96 h. (H = at harvest; bars indicate standard errors.)

significant increase in glycoalkaloid content (Table 6). The magnitude of the observed increases were at least twice that seen in the cultivars similarly stored at 10 °C (Table 3), but the relative ranking of the cultivars remained broadly the same. The greatest increases were seen in Brodick, Torridon, Pentland Dell, and Pentland Crown, which all increased by almost 400 mg TGA kg^{-1} FW, while in Eden the increase resulting from light exposure was less than half this value but was four times greater than that observed in the samples stored at 10 °C.

Storage for one week at 10 °C prior to the 6 weeks at 4 °C reduced the observed increase in response to light exposure in all cultivars with the exception of Brodick and Torridon both of which have previously been shown to be particularly sensitive to light exposure (Dale et al., 1993). Thereafter, extending the period at which the tubers were held at 10 °C prior to their movement to a 4 °C store resulted in a decrease in their response to light. However, even after 8 weeks at 10 °C followed by 6 weeks at 4 °C the increases resulting from their subsequent exposure to light was on average at least twice that seen in tubers stored for 14 weeks continually at 10 °C.

The combined effects of the increases due to low temperature storage and those in response to light exposure (Figure 1) resulted in tubers containing glycoalkaloid levels well above the recommended maximum value in all cultivars except Eden. In contrast to the light-induced increases in glycoalkaloid content, storage temperature appeared to have little effect on chlorophyll accumulation in all cultivars except Brodick, which appeared to have an increased rate of chlorophyll synthesis in tubers stored immediately at 4 °C or

Table 7. The Photoinduced Increases in the Chlorophyll Content of Potato Tubers Stored at 10 °C Followed by 6 Weeks Storage at 4 °C and Subsequently Exposed to Light for 96 h

	chlorophyll content (mg kg^{-1} FW)							
		weeks of storage at 10 °C prior to 6 weeks at 4 °C						
cultivar	at harvest	0	1	2	3	4	8	mean
Brodick	23	34	49	25	26	24	25	31
Eden	12	14	13	9	8	8	9	10
P. Crown	20	24	22	20	20	21	18	21
P. Dell	13	16	14	13	16	12	9	13
Record	30	28	26	21	25	23	25	25
Torridon	20	20	20	19	22	16	19	19
LSD ($P < 0.05$)[a]				3.9				1.4
mean	21	23	24	18	19	17	18	
LSD ($P < 0.05$)				1.5				

[a] LSD, least significant difference.

prestored for 1 week at 10 °C (Table 7). With this exception, the increase in chlorophyll was almost identical in light-exposed tubers for all other cultivars stored immediately postharvest for 6 weeks at either 10 (Table 4) or 4 °C (Table 7). All cultivars stored continually for 14 weeks at 10 °C exhibited similar accumulations of chlorophyll after exposure to light as those tubers exposed to light after storage for 8 weeks at 10 °C followed by 6 weeks at 4 °C. Averaged over all cultivars, less chlorophyll was accumulated in tubers stored for 14 weeks than in those analyzed immediately postharvest which is in agreement with a previous study utilizing a range of cultivars stored at 6−8 °C sampled within 2 weeks of harvest and again 14 weeks later (Griffiths et al., 1993).

CONCLUSIONS

The exposure of tubers to low temperature appears to have two distinct effects on glycoalkaloid biosynthesis, the magnitude of the effects being dependent on the cultivar, time of exposure relative to harvest, and the actual temperature of the store. Tubers placed immediately into 4 °C storage can, as in the case of Brodick, Pentland Crown, and Pentland Dell, accumulate glycoalkaloids rapidly, while others such as Torridon and Eden are relatively insensitive to this treatment. The observed response could not be predicted from their known response to light exposure. Prior storage at 10 °C reduces the magnitude of this effect with no response to exposure to low temperatures being observed after 3−4 weeks at 10 °C. Storage at 10 °C does not appear to trigger a rapid synthesis of glycoalkaloids in any of the six cultivars studied.

Storage temperature also affected the rate of glycoalkaloid synthesis in response to light exposure. The placing of tubers immediately into either 10 or 4 °C stores for a period of 6 weeks resulted in an increased rate of glycoalkaloid synthesis on exposure to light relative to that found immediately postharvest. After 14 weeks at 10 °C this effect appeared to disappear. The largest increase relative to that observed directly postharvest was in tubers stored at 4 °C. Storage at 10 °C prior to 6 weeks storage at 4 °C reduced the sensitivity of the tubers to subsequent light exposure but even after 8 weeks at 10 °C the placing of tubers for 6 weeks at 4 °C resulted in a greater response to light than those stored continually at 10 °C.

In contrast, the magnitude of the photoinduced increases in chlorophyll content, although cultivar dependent, was little affected by storage temperature. The photoinduced increases were almost identical in tubers stored for 6 weeks at either 4 or 10 °C and in those stored either continually at 10 °C for 14 weeks or at 10 °C for 8 weeks followed by 6 weeks at 4 °C. However increasing storage time from 6 to 14 weeks irrespective of the storage conditions resulted in small but statistically significant decreases in chlorophyll accumulation.

The results presented clearly indicate that increasing storage times at 10 °C prior to transfer to storage at 4 °C result in lower photoinduced increases in glycoalkaloids, which are known to be potentially toxic to the consumer. The application of such regimes would be of benefit in terms of consumer safety especially in view of the increasingly popular trend, particularly in United Kingdom supermarkets, of displaying potato tubers with little if any protection from artificial light sources. However, such benefits would in part be counter-balanced by the possible increased requirements for sprout suppressants. Clearly in the long-term, the consumer would be best served by the production of cultivars with inherently low levels of glycoalkaloids and with low rates of glycoalkaloid accumulation in response to both low temperatures and light exposure.

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