Final Report

The effect of temperature on potato tuber respiration

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Contents

1. Summary

The trial aimed to update and increase understanding of tuber respiration in store. Respiration rate is a key indicator of the physiological activity of tubers and store conditions, particularly temperature, have a significant effect on the rate. Knowledge of the range of respiration rates of current varieties over a temperature range could inform fridge capacity, storage efficiency and running costs.

During the years of the trials improvements in tuber respiration rate methodology were made to increase the accuracy and reproducibility of measurement. These changes included larger sample replication number, measuring larger changes of CO_2 and measuring the same samples throughout the storage period.

The second and third years of the trial were, as far as possible, direct repeats. Tubers of five different varieties were stored at temperatures between 1.0 and 20 C for up to seven months with respiration rate measured at monthly intervals.

There were differences in respiration rate between the varieties with Russet Burbank having the lowest mean respiration rate. King Edward, Maris Piper and Melody had very similar respiration rates and Lady Claire the highest rate. Differences in respiration rate were found between seasons.

Respiration rate varied greatly from intake to end of storage for all varieties. In particular there were large changes from intake to approx. 2 - 3 months' storage at low temperatures (1 and 2.5 C) and at higher temperatures (15 and 20 C). Following this period of adaptation, for each variety there was little difference in the respiration rate at storage temperatures between 1.0 and 9.0 C from two/three months to the end of the storage period.

2. Experimental Section

2.1 Introduction

Respiration rate is a key indicator of the physiological activity of tubers and many factors affect the rate including variety, field growth conditions, maturity level, harvest and handling, damage, disease, sprouting and storage temperature.

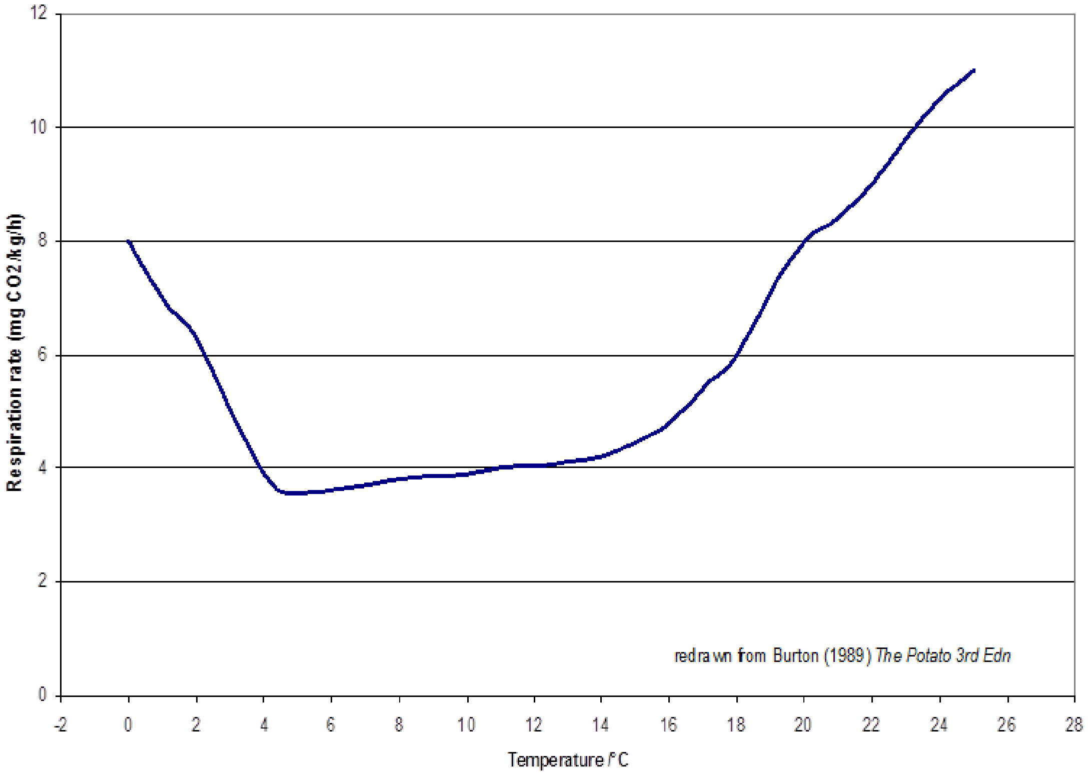
Temperature is the most important store management tool and there are delicate balances to be struck when selecting a store temperature. Higher temperatures accelerate biological deterioration due to disease and sprouting but minimise cold-induced sweetening. Lower temperatures minimise biological deterioration but at increased energy costs for refrigeration, higher levels of cold-induced sweetening which impact on fry colours and acrylamide formation.

The increasing cost of energy is a reason for managers to look closely at storage temperatures. Several Potato Council/AHDB projects have investigated aspects of energy use in storage including R458 aiming to provide a cost benefit analysis for the use of warmer temperatures for pre-pack storage whilst R439 and R401 included investigations into methods of reducing energy use in potato storage.

The heat of respiration is important, as it plays a large part in determining fridge capacity because increasingly effective insulation now controls external heat gain in store to a large extent. The effect of storage temperature on respiration rate has been measured in many studies, reviewed by Burton (1989). Burton provided a figure, shown here as Figure 1, which was essentially redrawn from a number of trials carried out by Burton *et al.* (summarised 1989) with additional data points from his own trials. The respiration rate of three older varieties, but which included King Edward, was measured after about one month at the different storage temperatures. This shows the well-known “U” shape curve where respiration rate was at a minimum at about 4 C, very slowly increased as the temperature was raised to 14 C and thereafter rose rapidly with increasing temperature. The respiration rate rose rapidly with decreasing temperatures below 4 C. The temperature range from approx. 2 – 5 C covers the typical range of pre-pack storage temperatures. It can be seen that, according to the figure, an increase in temperature from

2.5 to 4 C would decrease the respiration rate by about 30% and have significance to refrigeration costs.

Figure 1. The relationship between tuber respiration and temperature, redrawn from Burton (1989).



An improved knowledge of respiration will feed into better understanding of potato quality, in particular stresses being experienced and responded to by potatoes in storage.

2.2 Material and methods

2.2.1 Season 2013 - 2014

The varieties King Edward, Lady Claire, Maris Piper, Melody and Russet Burbank were selected for storage at eight unreplicated treatments: 2.5, 9 and 15 C without sprout suppressant and 2.5, 4, 5.5, 6.5 and 9 C with chlorpropham (CIPC) applied. Temperature was maintained within a tolerance of ± 0.5 C**.** Variation was measured by three in-store replicates.

The crops were graded by hand to remove soil, damaged, rotten, green, misshapen and undersize (<45mm) tubers. Approx. 3kg tubers were loaded into loosely tied nets and put into storage at 12 C from 29 to 31 October 2013. Intake respiration was measured before CIPC was applied and samples were pulled down or warmed to holding temperatures at a rate of 1 C per day. Relative humidity control was enabled when holding temperature was reached and maintained at 95 ± 5%.

Application of CIPC (*ProLong*, UPL, Warrington, WA3 6AE, UK) was made using a Swingfog SN 50 (Swingtech GmbH, Germany) fitted with a 1mm nozzle. Treatment was at a rate of 42ml per tonne (21ppm CIPC) on 7th November 2013, and the store ventilated between 6 and 7 hours after application.

Assessments were completed at approximately monthly intervals at the dates shown in Table 1. On each occasion the respiration rate of three replicate samples was measured in store using the SBCSR standard operating procedure, each net sealed in a chamber and the CO_2 produced measured. After the fourth sampling occasion the assessment procedure was modified, the samples were left sealed in chambers for a longer period.

Table 1. Sampling dates for respiration assessment in 2013-14

occasion	date
Intake	01 Nov 2013
1	25 Nov 2013
2	20 Dec 2013
3	21 Jan 2014
4	20 Feb 2014
5	28 Mar 2014
6	25 Apr 2014
7	21 May 2014

2.2.2 Season 2014 - 2015

The varieties King Edward, Lady Claire, Maris Piper, Melody and Russet Burbank were selected for storage at seven unreplicated treatments: 1, 2.5, 15 and 20 C without sprout suppressant, 5, 7.5 and 9 C with chlorpropham (CIPC) applied. Temperature was maintained within a tolerance of ± 0.5 C**.** Variation was measured by five in-store replicates.

The crops were graded by hand to remove soil, damaged, rotten, green, misshapen and undersize (<45mm) tubers and approx. 3kg loaded into loosely tied nets. King Edward, Lady Claire, Maris Piper and Melody were loaded and put into storage at 9 C from 13th October 2014. Intake respiration was measured during storage at 9 C, before CIPC was applied and samples were pulled down or warmed to holding temperatures at a rate of 1 C per day. Relative humidity control was enabled when holding temperature was reached and maintained at 95 $\pm$ 5%.

Russet Burbank was delivered later on 27th October 2014 when it was loaded and intake respiration assessed, with the tubers at an ambient temperature of 14 C. Samples were then transferred to their holding temperatures, warming or pulling down as close to 1 C per day as possible.

Application of CIPC (*ProLong*, UPL, Warrington, WA3 6AE, UK) was made using a Swingfog SN 50 (Swingtech GmbH, Germany) fitted with a 1mm nozzle. Treatments were at a rate of 28 ml per tonne (14 ppm CIPC), and the stores ventilated between 6 and 7 hours after application. Initial applications were made on 16th October 2014 (except for Russet Burbank, 6th November 2014), with a second on 12th February 2015.

Assessments were completed after approximately two, four, six, and eight weeks and then at monthly intervals (Table 2). On each occasion, the respiration rate of five replicate samples was measured in store using the SBCSR standard operating procedure, each net sealed in a chamber and the CO_2 produced measured.

Statistical analysis

The experimental design was a randomised, repeated measures design with 2 factors 'between' subjects (variety and temperature) and one factor 'within' subjects (storage duration). The statistical significance threshold was set at 5% or less and a parametric Analysis of Variance (ANOVA) was used. All statistical analyses were compiled on SPSS software, version 22.0. Graphs were additionally compiled in MS Excel from resulting Descriptive Statistics and Pivot Tables.

Table 2. Sampling dates for respiration assessment 2014-15

occasion	Sampling date
Intake	15 Oct & 27 Oct 2014
1	Two weeks after intake
2	Four weeks after intake
3	Six weeks after intake
4	Eight weeks after intake
5	13-15 Jan 2015 (3 months)
6	9-11 Feb (4 months)
7	12, 13 Mar (5 months)
8	14, 15 Apr (6 months)
9	12, 13 May (7 months)

2.2.3 Season 2015 - 2016

As previously, the varieties King Edward, Lady Claire, Maris Piper, Melody and Russet Burbank were stored this time under eight unreplicated treatments: 1, 2.5, 15 and 20 C without sprout suppressant and 5, 7.5, 9 and 15 C with chlorpropham (CIPC) applied. Temperature was maintained within a tolerance of ± 0.5 C**.** Variation was again measured by five in-store replicates.

The crops were graded by hand to remove soil, damaged, rotten, green, misshapen and undersize (<45mm) tubers and approximately 3kg loaded into loosely tied nets. King Edward and Maris Piper were loaded and put into storage at 13.5 C on 22^th^ September 2015 followed by Melody on 24^th^ September 2015. Intake respiration was measured during storage at this stage, before CIPC was applied and samples were pulled down or warmed to holding temperatures at a rate of 1 C per day. Relative humidity control was enabled after respective holding temperatures were achieved and maintained at 95 ± 5%.

Russet Burbank was delivered later on 21st October 2015, loaded and placed at 10 C followed by Lady Claire on 22^nd^ October 2015. Intake respiration was then assessed on 23^rd^ October 2015. Samples were then transferred to warming or cooling regimes as above until all crops occupied the same 8 stores.

Application of CIPC (*ProLong*, UPL, Warrington, WA3 6AE, UK) was made using a Swingfog SN 50 (Swingtech GmbH, Germany) fitted with a 1mm nozzle. Treatments were initially applied at a rate of 32 ml per tonne (16 ppm CIPC), and the stores ventilated between 6 and 7 hours after application. The first application was made on 28^th^ September

2015 (6th November 2015 for Lady Claire and Russet Burbank) with follow up applications of 8 ppm in January of 2016 except at 5 C where further sprout control was not necessary.

Assessments were completed after approximately two, three, five, seven, nine and ten weeks and then monthly, 3 to 7 (see Table 3). On each occasion, the respiration rate of five replicate samples was measured in store using the SBCSR standard operating procedure, each net sealed in a chamber and the CO_2 produced measured.

Statistical analysis

The experimental design was a randomised, repeated measures design with 2 factors 'between' subjects i.e. variety and temperature and one factor 'within' subjects i.e. the storage duration. The statistical significance threshold was set at 5% or less and a parametric Analysis of Variance (ANOVA) was used. All statistical analyses were compiled on SPSS software, version 22.0. Graphs were additionally compiled in MS Excel from resulting Descriptive Statistics and Pivot Tables.

Table 2. Sampling dates for respiration assessments 2015-16.

Occasion		Sampling date by cultivar	
		King Edward, Maris Piper, Melody	Lady Claire, Russet Burbank
0	intake	23, 25 September 15	23 October 15
1	2 weeks	5-6, 8 October 15	9-13, 16 November 15
2	3 weeks	14 October 15	-
3	5 weeks	26-27 October 15	23-25 November 15
4	7 weeks	9-11, 13 November 15	7-9 December 15
5	9 weeks	23-25 November 15	17, 21 December 15
6	10 weeks	7-9 December 15	4-5, 8 January 16
7	3 months	4-5, 8 January 16	1-4 February 16
8	4 months	1-4 February 16	29 February - 3 March 16
9	5 months	29 February -1,3 March 16	4, 7-8 April 16
10	6 months	4, 7 April 16	3-5 May 16
11	7 months	3-5 May 16	-

2.3 Results 2015-16

For operational reasons, King Edward, Lady Claire, Maris Piper and Melody tubers were brought to and held at 9 C prior to the start of the trial and for CIPC treatment. Hence the initial tuber respiration rate was similar for these varieties. The initial respiration rate of Russet Burbank was apparently higher than other varieties because, as it was received after the other varieties, respiration was measured during the period of transfer to final storage temperature rather than from a holding temperature.

Two phases were evident within the respiration rate profiles. From approximately 2-3 months storage onwards respiration rates for temperatures from 1 - 9 C were relatively stable (Tables 3 and 4) whereas from trial start to approximately 2-3 months storage there were marked changes in the respiration rate as the tubers adapted to the different storage temperatures (Figures 3-11). These phases are described separately.

2.3a. Respiration rate, 2 – 7 months' storage (2015-16)

The mean average respiration rates for all varieties across storage duration and temperature is shown in Table 3. The lowest respiration rates were generally at 2.5 C or 5 C and between 3 and 5 months storage duration. The highest rate, excluding 15 and 20 C, was found at 1 C.

Table 3. Mean of all variety respiration rates by storage duration and temperature over the storage period 2-7 months.

Storage temperature (°C)	Storage term (months)						
	2	3	4	5	6	7	Overall mean
	respiration rate (mg CO_2.kg.h)						
1	1.89	1.87	1.83	1.99	2.20	2.51	2.05
2.5	1.66	1.61	1.55	1.53	1.90	1.96	1.70
5	1.61	1.63	1.69	1.65	1.96	2.01	1.76
7.5	1.98	1.75	1.94	1.92	2.20	1.80	1.93
9	1.79	1.71	1.75	1.77	2.06	2.07	1.86
Overall mean	1.79	1.71	1.75	1.77	2.06	2.07	

Lady Claire had the highest and Russet Burbank the lowest mean respiration values (Table 4). There were some problems with Lady Claire tubers with soft rot development, particularly at the warmer temperatures and as described earlier affected tubers were removed from the trial prior to assessment. King Edward, Maris Piper and Melody had similar respiration rates throughout storage. Occasions when sprouting was observed are shown in Annex Tables 2a-e.

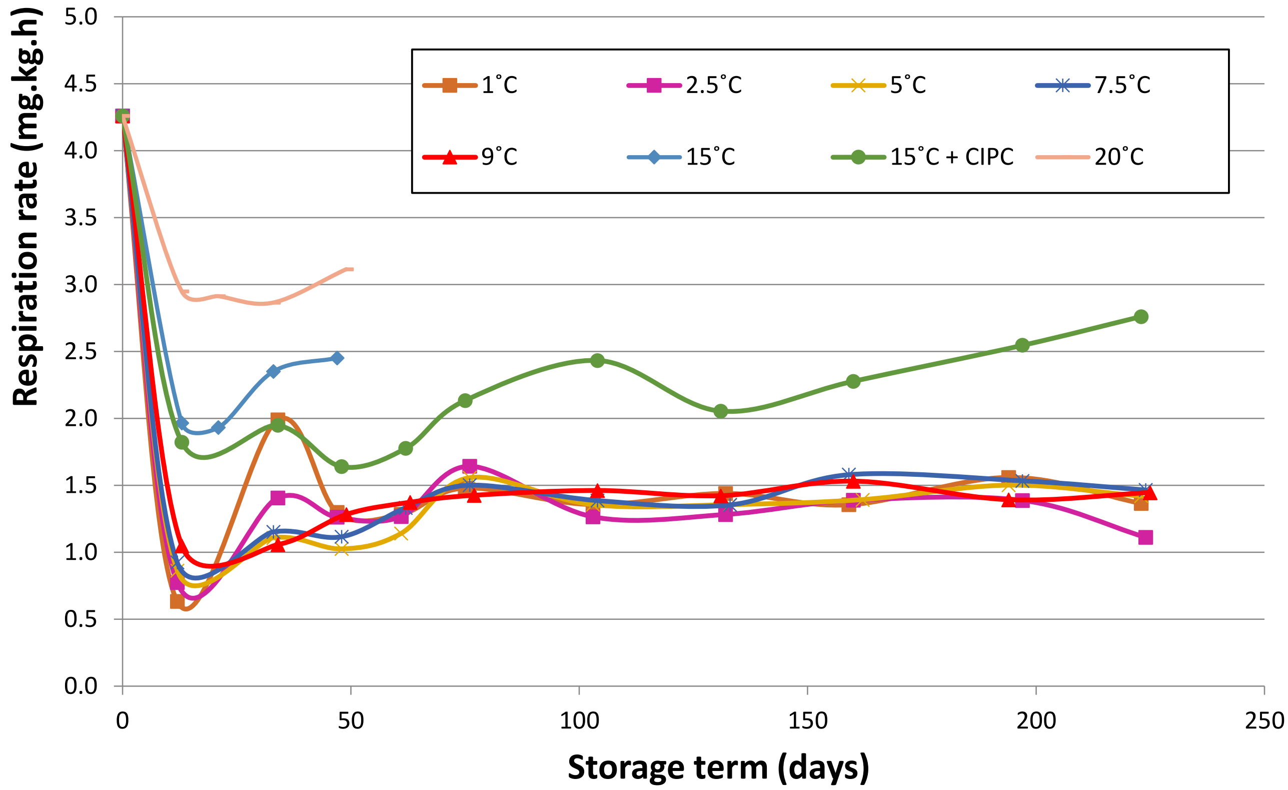
Respiration rates for the five varieties at the different storage temperatures in the trial are shown in Figures 2-6. From approximately 2 months storage for all varieties there was a distinct difference in respiration rate between storage temperatures with those at 15 and 20 C significantly higher in rate than those at 9 C and below (1, 2.5, 5, 7.5 and 9 C) which gradually stabilised to a value generally similar for all these temperatures. Respiration rate at 9 C increased markedly for Lady Claire, Maris Piper and Russet Burbank.
Respiration rates at 20, the highest, and 15 C trials were always higher than those for other storage temperatures. Trials were halted after 3 months because of extensive sprouting despite CIPC treatment.

The results by variety of the ANOVA (Table 5) include the post-hoc Bonferroni pairwise comparisons for the 5 temperatures and the 6 storage durations where ANOVA gave a significant difference based on the F-test ($P<0.05$). All varieties apart from King Edward show highly significant differences ($P<0.001$) between the temperatures, storage durations and their interactions. King Edward shows no significant difference between the temperatures ($P=0.157$) but a highly significant difference between the storage durations ($P<0.001$) and a significant interaction ($P=0.012$).

Significant differences in mean respiration between temperatures are due to pairwise differences of:

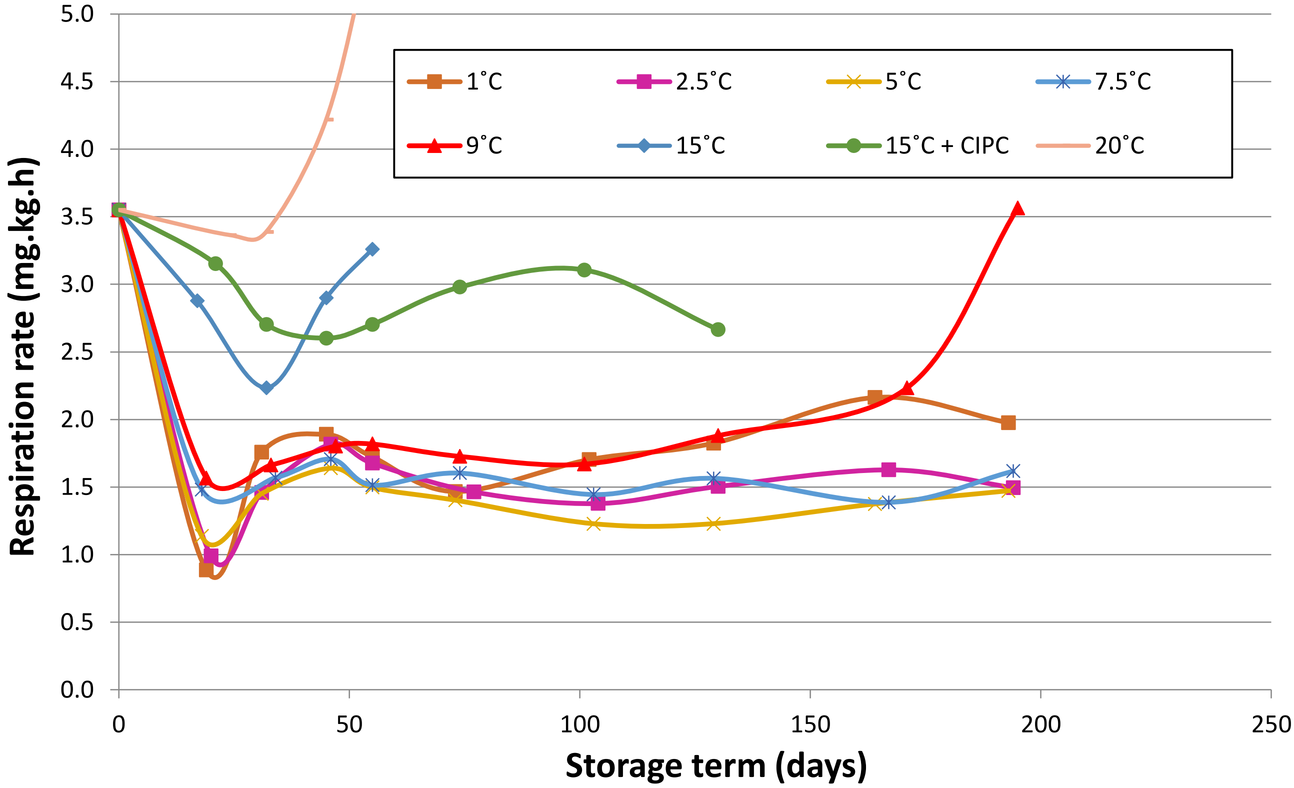
- 9C from all 4 other temperatures Lady Claire, Maris Piper and Russet Burbank.
- 1C NO CIPC from 5C + CIPC Lady Claire and Maris Piper.
- 2.5 NO CIPC v 7.5 + CIPC Melody.
- 5 + CIPC v 7.5 + CIPC Maris Piper and Melody.

Figure 2. Respiration rates of King Edward tubers at the different storage temperatures for the duration of the trial



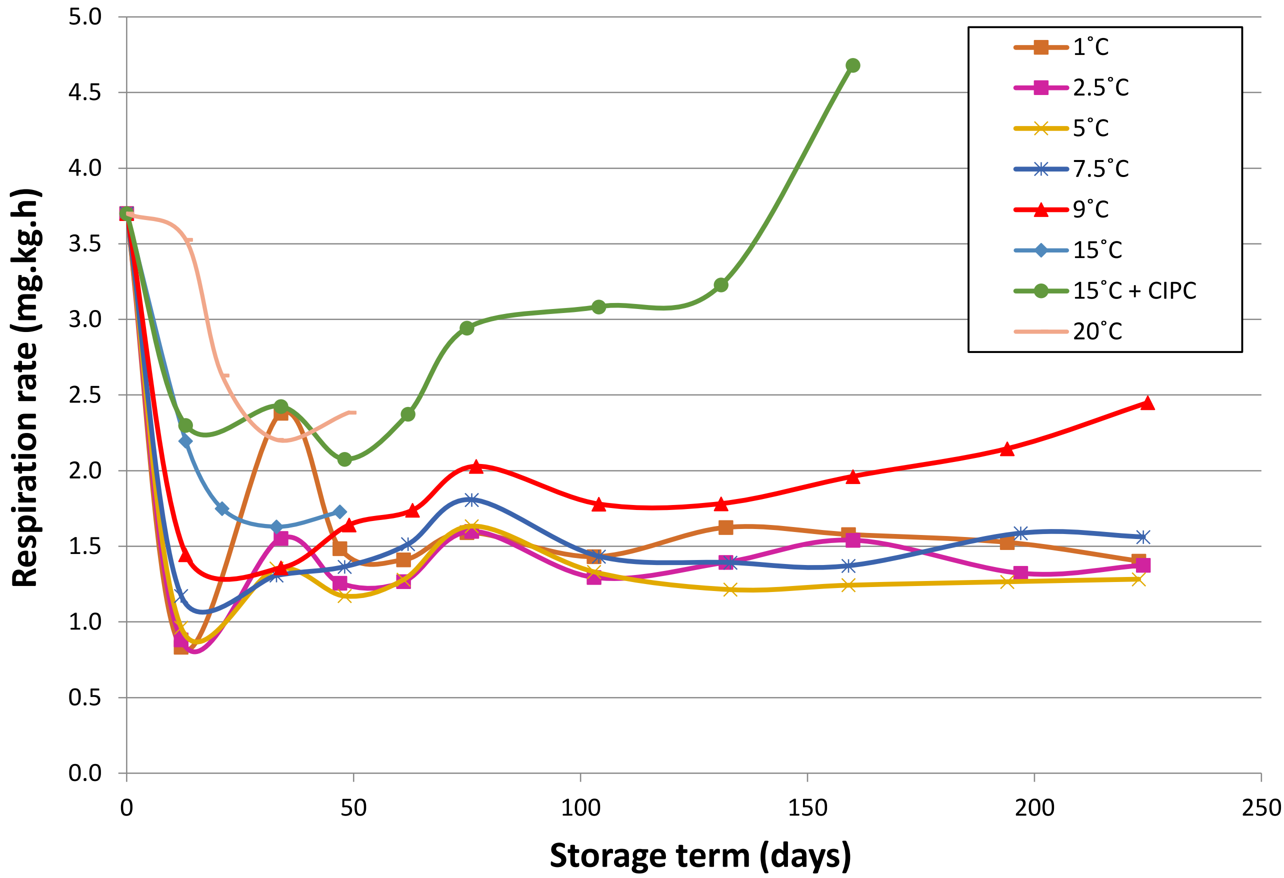
Note: 15 and 20 C CIPC free trials were halted early because of excessive sprouting.

Figure 3. Respiration rates of Lady Claire tubers at the different storage temperatures for the duration of the trial



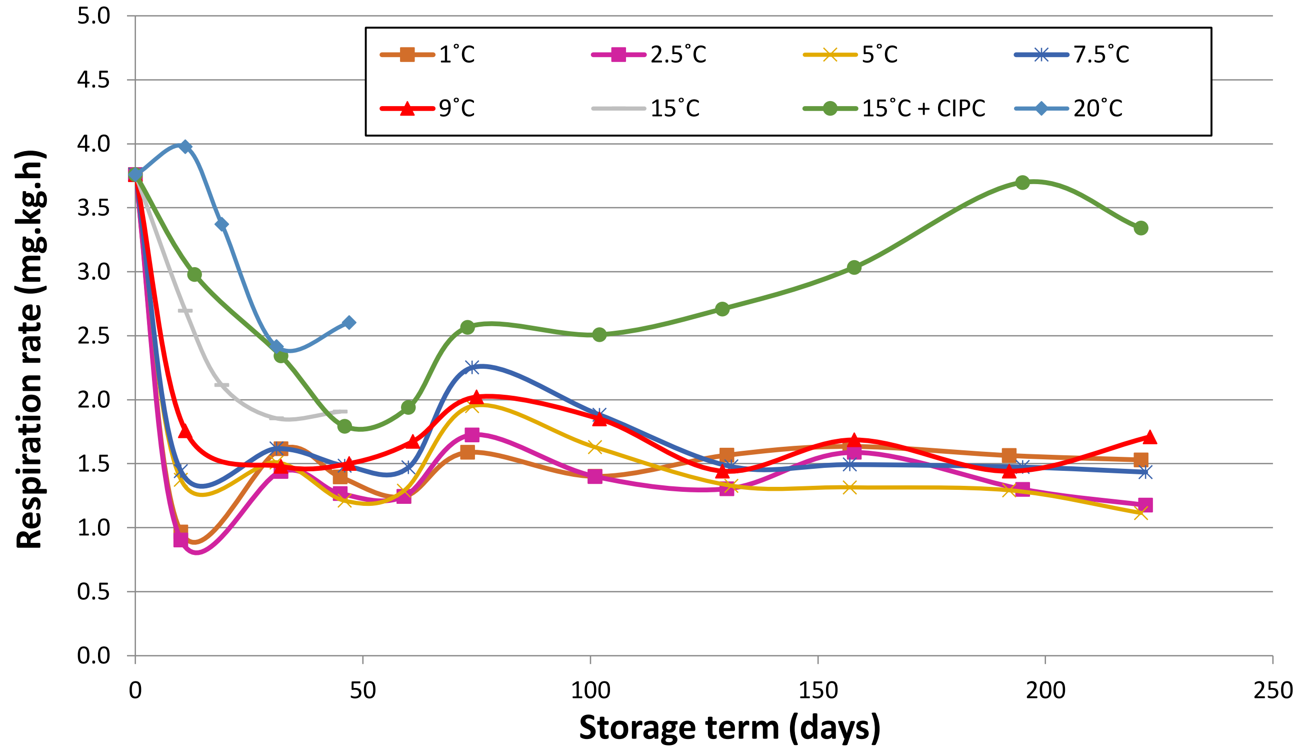
Note: 15 and 20 C trials were halted early because of excessive sprouting.

Figure 4. Respiration rates of Maris Piper tubers at the different storage temperatures for the duration of the trial



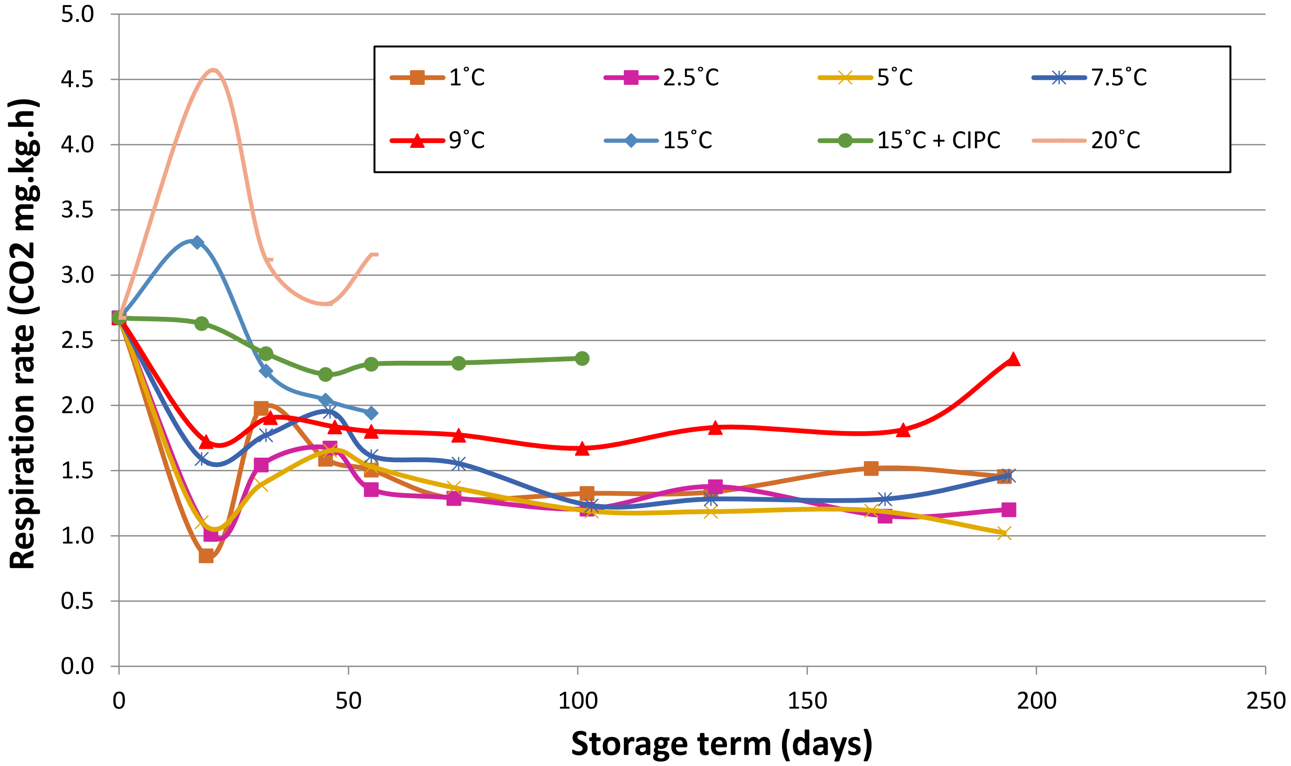
Note: 15 and 20 C CIPC free trials were halted early because of excessive sprouting.

Figure 5. Respiration rates of Melody tubers at the different storage temperatures for the duration of the trial



Note: 15 and 20 C CIPC free trials were halted early because of excessive sprouting.

Figure 6. Respiration rates of Russet Burbank tubers at the different storage temperatures for the duration of the trial



Note: 15 and 20 C trials were halted early because of excessive sprouting.

Table 4. Individual variety respiration rates means across storage duration and temperature

	Storage temperature (°C) and treatment	Storage duration (months)						
Variety		2	3	4	5	6	7	Overall Mean
King Edward	1, no CIPC	1.96	1.87	1.76	1.82	1.94	2.14	1.91
	2.5, no CIPC	1.70	1.53	1.39	1.41	1.69	1.77	1.58
	5, + CIPC	1.46	1.48	1.48	1.51	1.64	1.81	1.56
	7.5, + CIPC	1.68	1.49	1.66	1.69	1.87	1.87	1.71
	9, + CIPC	1.84	1.83	1.69	2.00	2.03	2.20	1.93
Overall		1.73	1.64	1.60	1.68	1.83	1.96	
Lady Claire	1, no CIPC	2.42	2.58	2.64	3.11	3.81	4.38	3.16
	2.5, no CIPC	2.08	1.93	2.00	2.08	2.80	3.04	2.32
	5, + CIPC	2.06	2.08	2.50	2.61	3.37	3.46	2.68
	7.5, + CIPC	2.74	2.84	2.96	2.85	3.57		2.99
	9, + CIPC	2.64	2.78	3.00	3.60	3.95		3.19
Overall		2.39	2.44	2.62	2.85	3.50	3.63	
Maris Piper	1, no CIPC	1.92	1.76	1.71	1.76	1.78	1.85	1.80
	2.5, no CIPC	1.60	1.56	1.55	1.46	1.72	1.70	1.60
	5, + CIPC	1.47	1.54	1.48	1.39	1.58	1.61	1.51
	7.5, + CIPC	1.79	1.43	1.68	1.65	1.94	1.83	1.72
	9, + CIPC	2.26	1.79	1.87	2.05	2.13	2.28	2.06
Overall		1.81	1.62	1.66	1.66	1.83	1.86	
Melody	1, no CIPC	1.71	1.64	1.66	1.73	1.79	2.28	1.80
	2.5, no CIPC	1.66	1.72	1.56	1.55	1.77	1.76	1.67
	5, + CIPC	1.72	1.77	1.74	1.60	1.89	1.84	1.76
	7.5, + CIPC	2.12	1.61	1.89	1.86	1.90	1.84	1.87
	9, + CIPC	2.28	1.99	1.96	2.12	2.09	2.02	2.08
Overall		1.90	1.74	1.76	1.77	1.89	1.95	
Russet Burbank	1, no CIPC	1.47	1.48	1.35	1.54	1.67	1.88	1.56
	2.5, no CIPC	1.25	1.31	1.25	1.14	1.50	1.52	1.33
	5, + CIPC	1.34	1.30	1.25	1.16	1.33	1.35	1.29
	7.5, + CIPC	1.59	1.39	1.53	1.55	1.73	1.65	1.57
	9, + CIPC	1.85	1.65	1.58	1.81	1.80	1.84	1.76
Overall		1.50	1.42	1.40	1.44	1.61	1.65	

Significant differences in mean respiration between months of storage duration are due to pairwise differences that are not always consistent from variety to variety (Table 5).

- Month 2 was different from at least 2 other months in all varieties.
- Month 6 was different from Month 3 in all varieties.
- Month 6 was different from Month 2 in King Edward, Lady Claire and Maris Piper.
- Month 7 was not measured in 2 varieties and was different from Months 2, 3 and 4 in Maris Piper.

Table 5. ANOVA of respiration rate in 2015/6 for Months 2-7 in storage including post-hoc Bonferroni pairwise comparisons

				Significant Bonferroni comparisons (P<0.05)	
Variety	**Temp.**	**St. Du.**	**Temp. * St. Du.**	**Temp. (°C)**	**Storage Durations**
King Edward	0.157	<0.001	0.012	n/a	M2 v M5 M6 v M2, M3, M4
Lady Claire	<0.001	<0.001	<0.001	1 v 5, 7.5 9 v 1, 2.5, 5, 7.5	M2 v M3 M5 v M3, M4 M6 v M2, M3, M4, M5
Maris Piper	<0.001	<0.001	<0.001	1 v 5 5 v 7.5 9 v 1, 2.5, 5, 7.5	M6 v M2, M3 M7 v M2, M3, M4
Melody	<0.001	<0.001	<0.001	2.5 v 7.5 5 v 7.5 9 v 2.5, 5	M2 v M3, M5 M3 v M4, M6, M7
Russet Burbank	<0.001	<0.001	<0.001	9 v 1, 2.5, 5, 7.5	M2 v M3, M4 M3 v M6
NS: Non-significant result (P>0.05). Significant results : * (P<0.05) ** (P<0.01) *** (P < 0.001)					

2.3b. Respiration rate, intake to 2 months' storage.

For storage temperatures 1-9 C and, for some varieties for 15 and 20 C, e.g. King Edward, there appeared to be a number of phases of respiration prior to the approximately stable respiration rate after 2-3 months.

The first phase was a steep decrease in rate over an initial period (approx. 14 days) during which tubers were brought from 9 C to their final storage temperatures at 1 C/day. This decrease was found irrespective of the final temperature and was observed even in those samples already at the final temperature (9 C). The largest decrease was found for tubers at the lowest final storage temperatures of 1 and 2.5 C.

The second was an increase in rate from 14 days to approx. 30 days generally with the largest increase found at the lowest final storage temperatures of 1 and 2.5 C. The respiration rate then generally reduced over the next approx. 30 days to a value close to a stable storage value. For King Edward, Maris Piper and Melody there was a further apparent increase and decrease in respiration rate peaking at approx. 75 days before a relatively stable storage value was attained.

Figure 12 shows the mean respiration rates after 33 days' storage. At these time points the respiration rate at 1 C was generally very similar to that at 15 and 20 C, and significantly higher than at intermediate temperatures. Strikingly, the rate at 1 C later during storage decreased to around the same level as at 9 C.

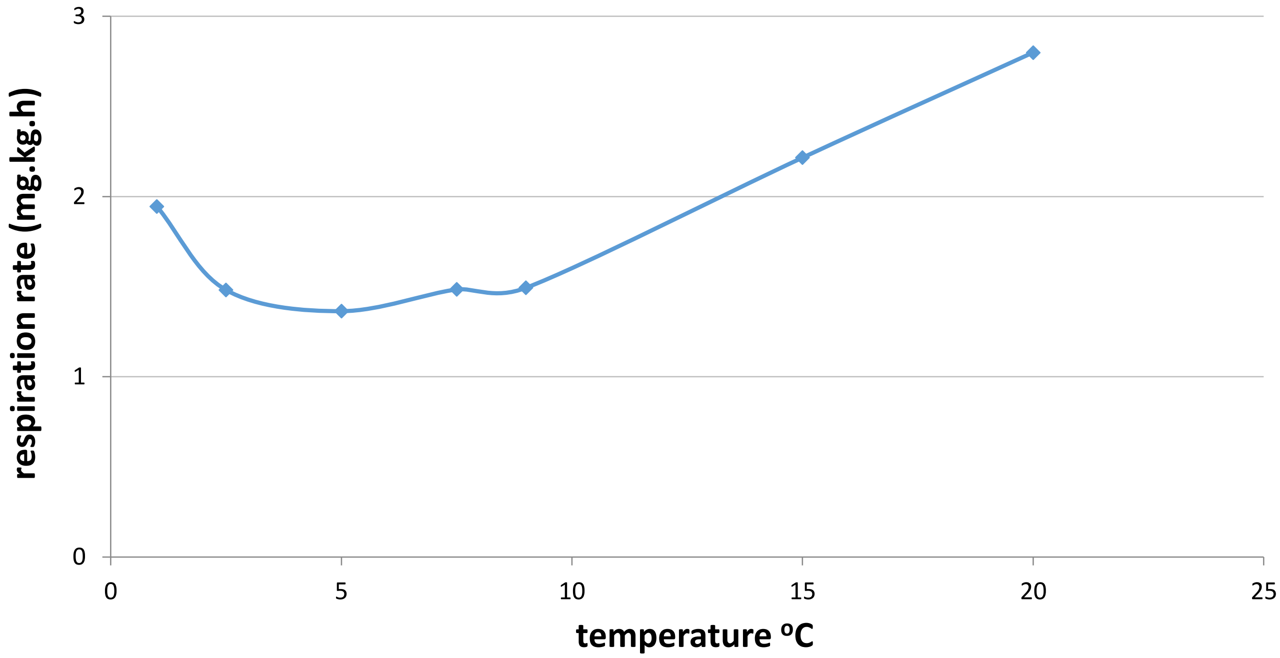
2.3c. Respiration rate and sprouting at temperatures 15 C and above

The highest respiration rate was always found at 20 C (Figures 2-6). High rates were also measured at 15 C, approx. intermediate between that at 20 C and the lower temperatures.

In the absence of CIPC sprouting was evident within 2 - 8 weeks at 20 C and 15 C (for 2014-15 Annex Tables 1a-e and, for 2015-16, Tables 2 a-e). At later storage durations, sprouting also occurred at 15 C with only a single CIPC application (3 months Lady Claire; 4 months Maris Piper; 3 months Russet Burbank) and, during 2014-15 at 9.0 C +CIPC (Lady Claire).

However, sprouting was not necessarily associated with an increase in respiration rate. For example during 2015-16 at 15 C + CIPC and 2014-15 at15 C the respiration rate of King Edward increased over the storage period without sprouting being recorded whereas in Lady Claire respiration did not significantly alter over the period during which sprouting was observed 3 and 4 months, 2015-16 and 2014-15.

Figure 12. Mean respiration rate of five cultivars at different storage temperatures after 33 days of storage



2.3d. Comparison between trials 2013-14, 2014-15 and 2015-16

Allowing for 5.5 C (2013-14) and 5.0 C (2014-15, 2015-16) to be similar enough temperature treatments for useful comparison between years, there were three temperature treatments with long storage durations common to both years:

Year 1 (2013-14): 2.5 C +/ - CIPC, 5.5 C + CIPC, 9 C + /- CIPC

Year 2 (2014-15): 2.5 C - CIPC, 5 C + CIPC, 9 C +CIPC

Year 2 (2015-16): 2.5 C - CIPC, 5 C + CIPC, 9 C +CIPC

The overall mean respiration rates for these temperatures are shown in Table 6.

Table 6. Overall mean respiration rates during storage at the different storage temperatures for the trial years.

	Overall mean respiration rate ($mg\ CO_2/kg/h$)		
Storage temperature (°C)	**2013-14**	**2014-15**	**2015-16**
2.5	2.30	1.71	1.70
5.5/5.0	1.99	1.79	1.76
9	2.15	2.17	1.86

ANOVA results by variety (Table 7) show the significance in the differences of the years, storage treatments, storage duration and the two-way interaction of storage treatment with storage duration.

Apart from storage duration for Russet Burbank (P=0.112), there are very significant results (P<0.01) in almost all aspects and the post-hoc Bonferroni analysis shows the significant differences between the 3 temperatures (2.5-CIPC, 5/5.5+CIPC and 9+CIPC) and between the 6 storage durations.

Table 7. Significance of factors for ANOVA compiled by variety.

Factors					Significant Bonferroni comparisons (P<0.05)	
Variety	**Year**	**St. Temp.**	**Year* Storage *Temp**	**Storage Duration**	**St. Temp. (°C)**	**Storage Durations**
King Edward	<0.001	<0.001	0.019	<0.001	Not calculable	M6 v M2, M4 M7 v M2, M4, M5
Lady Claire	<0.001	<0.001	0.034	<0.001	9+ v 2.5-, 5/5.5+	M2 v M3 M5 v M3, M4 M6 v M2, M3, M4, M5
Maris Piper	<0.001	<0.001	<0.001	<0.001	2.5- v 5/5.5+ 2.5- v 9+	M2 v M3 M3 v M4, M5, M6 M4 v M6 M7 v M2, M4, M5, M6
Melody	<0.001	0.002	<0.001	<0.001	2.5- v 9+ 5/5.5+ v 9+	M2 v M3 M3 v M4, M5, M6, M7
Russet Burbank	0.001	<0.001	<0.001	0.112	2.5- v 9+ 5/5.5+ v 9+	M5 v M6

For each of the 3 temperature treatments, the mean respiration by variety and year across the 6 storage terms is shown in annex Figure 5a-c. The ANOVA showed highly significant differences (P<0.001) between mean values for the years, varieties, storage durations and the interactions of variety with years. There were 4 aspects of interest. Post-hoc Bonferroni analysis shows some significant differences between the 5 varieties and between the 6 storage durations.

Across the 3 years, for 2.5C No CIPC and 5-5.5+ CIPC, pairwise significant differences were found between all 3 years. However, for 9C+CIPC, 2013/14 was significantly different from 2014/1, which in turn was significantly different from 2015/16.

2.3e. Comparison between trials 2014-15 and 2015-16

The trials conducted in years 2014-15 and 2015-16 were, as close as possible, direct repeats and a comparison can be made between all varieties, storage temperatures and durations. Mean respiration for each of the years, variety, storage temperature and storage term are shown in annex Figures 6a-e. ANOVA results by storage treatment (Table 8) showed high significance (P<0.001) for the years, varieties, storage durations and the interactions of variety with years.

Post-hoc Bonferroni analysis showed significant differences between the 5 varieties and between the 6 storage durations. For all 5 storage treatments, the mean for variety Lady Claire was always significantly different from the mean for the other 4 varieties (Table 8).

Table 8. Significance of factors for ANOVA compiled by storage temperature.

P-values of Factors					Significant Bonferroni comparisons (P<0.05)	
Storage Treatment	**Year**	**Variety**	**Year * Variety**	**Storage Duration**	**Variety**	**Storage (Months)**
1C No CIPC	<0.001	<0.001	<0.001	<0.001	LC v all 4 others MP v RB	M2 v M5, M6 M3 v M5, M6 M4 v M5, M6
2.5C No CIPC	<0.001	<0.001	<0.001	<0.001	LC v all 4 others RB v MP, Mel	M6 v all 4 others
5C + CIPC	<0.001	<0.001	<0.001	<0.001	KE v RB LC v all 4 others MP v Mel Mel v RB	M6 v all 4 others
7.5C + CIPC	<0.001	<0.001	<0.001	<0.001	Mel v KE, RB LC v all 4 others	M2 v M3 M6 v all 4 others
9C + CIPC	<0.001	<0.001	<0.001	<0.001	KE v LC, MP LC v all 4 others	M5 v all 4 others M6 v all 4 others

There were some differences in the initial respiration rates from the start of the trial to approx. 2 months (Figures 2-6 and Annex 2014-15 Figures 2-6). The major difference was that, except for Russet Burbank, during 2014-15 the initial respiration rate for tubers at lower storage temperatures 1, 2.5 and 5 C increased rather than fell as during 2015-16, Some differences in methodology between years may have had an impact on these results.

However in both years similar shaped “U” shaped graphs for respiration rates at 14 -33 days were observed with respiration rates at 1 and 15 C higher than those at intermediate temperatures (combined varieties Figure 12). Respiration rates for the individual varieties are shown in Annex Figures 3a-e (2014-15) and Annex Figures 4a-e (2015 -16).

3. Discussion

Methodology

A number of precautions were taken to help reduce variability of measurement. The same tubers were used for each measurement (statistically "repeated measures"). Crops were graded by hand to remove unsuitable and undersize (<45mm) tubers. A sample of approx. 3kg (approx. 15-20 tubers) was placed in loosely tied nets to allow gentle movement from store position into the plastic box for measurement. Variation was measured by five in-store replicates. At each sampling occasion, tubers were inspected and, where necessary, defective tubers removed without being replaced.

Burton (1989) described different phases of respiration rate from harvest through long term storage. An initial high, and rapidly declining rate of respiration from harvest/immature tubers; a dwindling rate of mature tuber respiration until, at the start of sprout growth, an increase in rate.

Early storage period

Burton (1989) re-compiled previous respiration measurements (Burton *et. al.* 1955) of three varieties, including King Edward, recorded after about one month at various storage temperatures. The "U" shaped curve is shown in Figure 1 of the introduction of this report. Similarly shaped curves were obtained at 15 days 2014-2015 and 33 days of storage 2015-2016.

However, it was evident prior to these time points during 2015-16 that there was a rapid decrease in respiration rate particularly for tubers at the lowest temperatures (Figures 2-6). Workman *et al.* (1979) studied the response of four varieties including Russet Burbank to various temperatures with respect to respiration and other parameters. Tubers were held at 20 C for 48 hours prior to the temperature being decreased daily sequentially through 16, 10, 5, 2.8 and finally 0 C. After reaching 0 C the temperature was maintained for an additional 50 days with respiration measured daily. The respiration rate of each variety decreased with each decrease in temperature with the minimum rate occurring at 0 C. The rate then started to increase reaching a maximum after 10 - 15 days at 0 C, depending on the variety. Thereafter, respiration slowly decreased with that of Russet Burbank decreasing more than the others. Graphs of the Russet Burbank respiration rate recorded during their trial over the 50 days are very similar to those obtained with the variety during 15-16 of this trial. The reason for this early decrease is unknown. Possible reasons for this response not being observed during the 2014-15 trial (Annex Figures 2a-e) were the approx. 2 week later start of the trials in 2014-15 and the timing difference for the start of assessments between the two years.

The increase in respiration rate in response to cold temperature "cold-induced respiratory burst" (Craft 1963) has been well studied. Burton (1974) showed that it was unnecessary to have extreme temperature changes to obtain the 'respiratory burst', or to change from a low to a high temperature. Subsequently there have been many studies describing the changes required for response and protection of tubers from low temperature stress. Examples include maintenance of redox balance under stress situations, reduction in production of damaging reactive oxygen species (Cosso *et al.* 2003).

Dwelle and Stallknecht (1978a) measured rates of oxygen (O_2) consumption midway through the storage season. O_2 consumption was lowest in tissue slices taken from tubers stored at 1.7 and 10°C and highest in slices from intermediate temperatures. In general rates of O_2 consumption were inversely related to rates of CO_2 evolution by whole tubers at those temperatures. These differences again reflect the changes required to respond to and protect from stress.

Mid-storage period

Burton (1989) described the dwindling rate of mature tuber respiration as a feature of mid-storage. Similar results have been demonstrated in the current trial, recorded by Schippers (1999) and at a narrower range of temperatures by Harper (2015). The respiration rate of Majestic stored at 2 C peaked at approx. 30 days and then gradually reduced over seven months storage. However there were differences with, for example, a "U" shape curve when stored at 10 C with the minimum at approx. three months storage (Burton 1974a).

Dwelle and Stallknecht (1978a) measured the respiration rate of six varieties stored at 1.7, 4.4, 5.8, 7.2 and 10°C, from November to May inclusive. In contrast to our study, in all varieties including Russet Burbank and except for Norchip, respiration measured as CO2 evolution during the first months of storage was generally lowest at 7.2°C (45°F) and higher at the other temperatures studied. The lowest overall rates of respiration occurred at 3 months storage, rates before and after this time markedly decreased and increased respectively. They accurately describe the results with these varieties as a "U" shaped curve. In contrast, and as found in our study, the respiration rates of Norchip for most of the storage season were virtually indistinguishable between the five temperatures.

Rather than being stable flat rates there were obvious fluctuations in the respiration rate of all varieties across the storage period. Burton (1974) similarly described short-term fluctuations in the rate of respiration of ± 20%. In completely undisturbed samples the fluctuation was of the order of ± 10% of the mean value. The cause of the fluctuations is unknown.

Minimum respiration rate

Burton (1989) summarised some of his studies as, the minimum rate could remain steady for a period of several weeks, could differ markedly between different samples, and between different individual tubers within a sample, and in different years and cultivars.
In our trial the minimum respiration was generally at 2.5-5.0 C, around three months storage and could remain steady for up to 2 months. Russet Burbank generally had the lowest respiration rate of the varieties tested.

Sprout Growth

In Burton (1974a), sprouting in early January of Majestic tubers was not associated with an increase in respiration, respiration slightly and gradually increased with a further three months storage. Similarly Dwelle and Stallknecht (1978a) described the limited increase of respiration of Norchip with sprouting. This was in contrast with, for example that of Russet Burbank which showed a "substantial" increase of respiration with sprouting. Overall the result of this study are mixed with respect to respiration rate, sprouting and seasonal reproducibility. During 2014-15 sprouting of Russet Burbank appears to precede a rise in respiration rate.

Differences in rates of respiration of different varieties

Schippers (1977a) reviewed the literature and described numerous examples of studies in which different varieties displayed differences in respiration rate. In his own work (Schippers 1977b) found non-statistically significant differences in respiration rates of six commercial varieties identified although found significant differences between other varieties. Such variation was also found with commercial UK varieties in this study, Russet Burbank generally had the lowest and Lady Claire generally the highest respiration rate. Dwelle and Stallknecht (1978a) demonstrated differences in the pattern of respiration between varieties with, for example, that of Norchip different to that of Russet Burbank.

Differences in rates of respiration between seasons

Differences in individual variety and overall respiration rates were found between seasons in this study (Table 6), findings which have been observed previously. Copp *et al.* (2000) found that while absolute respiration rates varied depending upon growing season and treatment, all cultivars and treatments studied during three storage seasons showed similar respiration profiles and concluded "It is clear from the data that the absolute rate of respiration and the increase in rate in later storage varied considerably with season, cultivar and treatment."

Potential reasons for seasonal variation provided by different authors were summarised by Schippers (1977a) and included for example growth under different conditions e.g. nitrogen availability or geographical location. Other reasons may include differing levels of maturity (Burton, 1964).

Respiration and weight loss

Results from Butchbaker *et al.* (1973) demonstrated that respiration accounted for between 10 and 50% of total weight loss, except when tubers were stored at 100% relative humidity. At a fixed temperature (10 C) the proportion of losses due to respiration compared with vapour losses remained constant over 60 days. Store humidity was the more significant factor influencing any loss. Results from this work indicate that there would be little or no difference in weight loss over temperatures from 2.5-7.5 C for long durations of storage. Harper (2015) found no significant differences in weight loss, for four varieties over six months storage, between storage temperatures of 2.5, 4.0 and 5.5 C.

Higher weight losses could be expected during periods of "respiratory burst" which are more likely either at the start of storage or when tubers are removed from storage.

The limited differences in respiration pattern over the temperature range 1 - 9 C and storage period 2/3 - 6 months would suggest that respiration rate should not impose differential costs as a consequence of temperature. Maintenance of a particular temperature in relation to environmental conditions would be the determining factor of storage cost during this period (Harper 2015).

These findings indicate that, for large parts of the storage period, respiration rates are similar across a wide range of temperatures, more so than previously suggested by the literature (eg Burton 1989). This may therefore offer an opportunity to reduce ventilation and cooling need during the holding period, something which can be more easily achieved with the advent of inverter (speed) controls on much of the new environmental control equipment now found in modern potato stores.

4. Conclusions

Respiration rates during early storage showed similarity to the data Figure 1 (Burton 1989). The high rates of respiration at low temperatures, the “respiratory burst”, are part of the response to, and protection of tubers from, low temperature stress.

From approx. three months’ storage onwards the respiration rates from 1.0 to 9 C temperature were very similar, generally to the end of the storage period. The lowest respiration rates were usually found at 2.5-5 C and at around 3 months’ storage.

Rates at 15 and 20 C increased rapidly during storage and were probably associated with sprouting which became increasingly evident and led to respiration measurements being terminated after 2-3 months.

Differences in respiration rates were found between Russet Burbank, which respired at the lowest rate, and the other varieties and between Maris Piper, King Edward & Melody and Lady Claire which generally respired at the highest rate.

Overall less variation in respiration rate in relation to storage temperature was observed in a range of varieties evaluated than had been previously measured.

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