

Respiration and losses in stored wheat under different environmental conditions

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Abstract

An automatic electrolytic respirometer has enabled replicated determinations of respiration rates in 25 g samples of grain at different constant temperatures (15–35°C) and water activities (0.65–0.95 a_w). Respiration increased linearly with temperature up to 35°C and with time at water activities above 0.90 a_w but not at lower water activities. At high water activities, germination was decreased and microbial respiration predominated while at low water activities, germination was maintained and grain respiration contributed to overall respiration rates. Comparisons of oxygen consumption and carbon dioxide production generally gave respiratory quotients less than 1.0 except at 15°C. Moulding was not visible after 7 days at 15°C but increased in intensity from 20–35°C. Up to 0.13% dry matter was lost before grain was visibly mouldy while 0.13–1.24%, depending on temperature and water content, was lost from visibly mouldy grain. Models of differing complexity, that could be incorporated in simulations of near-ambient drying to give greater precision, are being constructed from the data.

Introduction

Safe storage periods for cereal grains are mostly predicted from Kreyger (1972) although his data are based on extrapolations from a few studies in which the safe storage period was limited by the appearance of visible moulding. However, this can be unreliable as a criterion because significant losses can occur before moulding is visible if conditions do not favour sporulation (Seitz et al. 1982b; Armitage and George 1986). Studies suggest that safe storage periods are overestimated by Kreyger (1972) and that a more precise definition of safe storage is required. Computer models simulating near-ambient drying of grain to predict safe drying periods (Sharp 1983; Bowden et al. 1983; Smith and Bailey 1983; Brook 1987) have often been inaccurate (Sanderson et al. 1989) because they lack precise information on mould development and quality loss.

Respiration has long been used to measure metabolic activity in stored produce (Bailey and Gurjar 1918; Milner et al. 1947a,b; Scholz 1962; Kittock and Law 1968; White et al. 1982a, b). Its rate is governed by water availability, temperature, oxygen concentration, microbial contamination, mechanical damage, the conditions and period of previous

storage and by mite and insect infestation (Bailey 1940; Milner and Geddes 1945b; Steele et al. 1969). Microorganisms, especially fungi, are important causes of deterioration (Norman et al. 1941; Christensen 1955) and grain also respire (Hummel et al. 1954) but the relative contributions of these two components to total respiration remain controversial (Pomeranz 1974). Some studies, using maize with 22–27% water content, have suggested that grain respiration greatly exceeds microbial respiration (Seitz et al. 1982a) while others have found relatively low and constant levels of respiration in mould-free wheat grain at 12–35% water content (Larmour et al. 1935; Hummel et al. 1954). Respiration rates may differ with the cultivar (Cantone et al. 1983), age (Kittock and Law 1968) and quality of grain tested, between different methods of determining respiration, the quantity of grain used and the period of the experiment.

Dry matter loss results from the utilisation of carbohydrate during respiration. Consequently, respiration data can also be used to measure dry matter loss. Estimates differ as to how much dry matter loss is allowable before grain is rejected. A loss of 0.5% dry matter, sometimes with no visible moulding, was sufficient to render maize grain unfit for use (Saul and Lind 1958; Saul and Steele 1966; Seitz et al. 1982b). Kreyger (1972) considered grain still to be fit for animal feed with dry matter losses up to 2% and decreased germinability, while for seed he considered 0.5% an acceptable or even a small dry matter loss. Hall and Dean (1978) assumed that up to 1% dry matter loss over a period of 12 months was acceptable in grain for food use and that losses were similar in wheat and maize stored at the same a_w and temperatures (Morey et al. 1981). By contrast, although White et al. (1982a) predicted that wheat at 18.4% water content could be stored safely for 55 days using 0.1% loss as the criterion, visible moulding appeared after 23 days suggesting a limit for acceptability of only 0.04%. If respiration rate is proportional to kernel size (Bailey 1940), a dry matter loss of 0.5% in maize can be equated to a 0.085% loss in wheat (Brook 1987). However, measurement of such small losses directly by weighing is subject to errors because the weight of fungal mycelium on the grain needs to be subtracted from the total dry matter.

An innovative electrolytic respirometer, designed to monitor respiration in soil, recently became available (Tribe and Maynard, 1989) and has been used to study respiration in cereal grains (Hamer et al. 1991). This enables the continuous monitoring of oxygen uptake and measurement of total carbon dioxide production during experiments with cereal grains at different water activities and temperatures. This paper describes some of the results obtained using this method.

Materials and Methods

Wheat grain

Wheat grain grown at Rothamsted Experimental Station in three seasons (1988–1990) was used in most experiments, but barley, oilseed rape and linseed were also used in preliminary

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experiments. Grain was dried to less than 14% water content (wet basis) after harvest, cleaned and stored at 0–5°C.

Water content and water activity

Water contents were determined by oven drying at 105°C for 16 hours (Pixton 1982). Water activities (a_w) were determined in two to four 5–10 g grain samples at 25°C, using a Humidat IC II (Novasina AG, Switzerland) water activity meter, and equilibrating the sample for approximately 1 hour. As a_w changes with temperature, the following equation (Chen and Morey 1989) was used to predict the correct a_w at each temperature from the 'working' a_w at 25°C (Table 1):

$$a_w = 1 - \exp(-0.000043295(\theta + 41.565)w^{2.111})$$

where a_w = water activity (decimal, 0–1.0), θ = temperature (°C), w = water content (% db). However, this did lead to a calculated a_w at 25°C which differed from those determined from the moisture sorption isotherm.

Rehydration of grain samples

Volumes of sterile distilled water, calculated from the moisture sorption isotherms for each a_w , were added to grain in conical flasks with gentle shaking to ensure uniform incorporation. The flasks were then sealed and equilibrated at 0–5°C overnight with regular thorough shaking. Water contents were confirmed before use.

Assessment of seed quality

Germination testing

Germination of seeds was assessed in inverted 9 cm Petri dishes with 9 cm Whatman No. 1 filter papers placed inside the lids and wetted with 1 mL sterile distilled water for rehydrated grain and 1.5 mL for dry grain, as approved by the International Seed Testing Association (1985). Three replicates of 10, 50 or 100 grains were placed 10 to each chamber, separated equidistantly, and incubated at 20°C in polyethylene bags for 8 days for wheat and 7 days for other seeds before the number of germinated grains was counted. Germination percentages were transformed to logits for statistical analysis.

Visible moulding

Visible mould was classified using an arbitrary scale: 0, no moulding; 1, 1–25% grains moulded; 2, 26–50% grains moulded; 3, 51–75% grains moulded; and 4, >75% grains moulded.

Isolation and enumeration of microflora

Direct plated grains were placed aseptically, 10 grains on each of 3–10 agar plates.

Measurement of grain respiration

A respirometer system, designed by Tribe and Maynard (1989), was used as described by Hamer et al. (1991). Grain samples, hydrated to the required a_w , were placed in glass respirometer tubes sealed at the base with rubber bungs. A Bijou bottle, containing 5 mL 2M sodium hydroxide, was placed on the grain surface and a compensator unit, with approximately the same internal air volume as the glass tube, was connected through a U-tube which contained acid copper sulphate electrolyte, a platinum anode and a copper cathode to

form the electrolysis unit. The tip of the platinum anode was positioned slightly above the electrolyte meniscus to avoid a surge in oxygen production at the start of the experiment. All joints were made both air- and water-tight with silicone rubber compound (RS, Northampton). Treatments were randomised before the tubes were placed into stainless steel racks in groups of 16 in a water bath and the electrodes connected to a computer through a multiplex switching unit. The computer recorded the period of operation of the electrolysis unit, allowing calculation of oxygen consumption. CO₂ evolved during each experiment was determined by titrating NaOH against 0.2 M HCl, first, to pH 8.3 with 0.5% (w/v) phenolphthalein (BDH) indicator in 95% ethanol and then to pH 4.0, using one drop of screened methyl orange indicator. Respiratory quotients (RQ) were calculated from the ratio of CO₂ produced to O₂ consumed. Assuming an RQ of 1.0 and the loss of 0.682 g carbohydrate/g CO₂ released (Rees 1982), dry matter loss was calculated from the mass of CO₂ produced or O₂ consumed.

Results

Respiration of wheat and barley grains and oilseeds

Respiration of grain of three cultivars of wheat and one each of barley, oilseed rape and linseed were compared over 14 days at 0.88–0.90 a_w and 25°C. Grain of wheat cvs. Avalon and Riband consumed O₂ at a similar rate over the experimental period but that of cv. Rendezvous, harvested a year earlier, consumed significantly less ($p \leq 0.05$) O₂ (Fig. 1). Also, barley grain cv. Magie consumed significantly less O₂ than wheat cvs. Avalon and Riband but did not differ significantly from wheat cv. Rendezvous. The oilseeds, especially linseed, consumed significantly less O₂ than the cereal grains. Generally, there was a linear relationship between O₂ consumption and time for both cereal grains and oilseeds, with correlation coefficients of 0.9980 for wheat cv. Avalon, 0.9959 for wheat cv. Rendezvous, 0.9979 for wheat cv. Riband, 0.9944 for barley cv. Magie and 0.9992 for rapeseed cv.

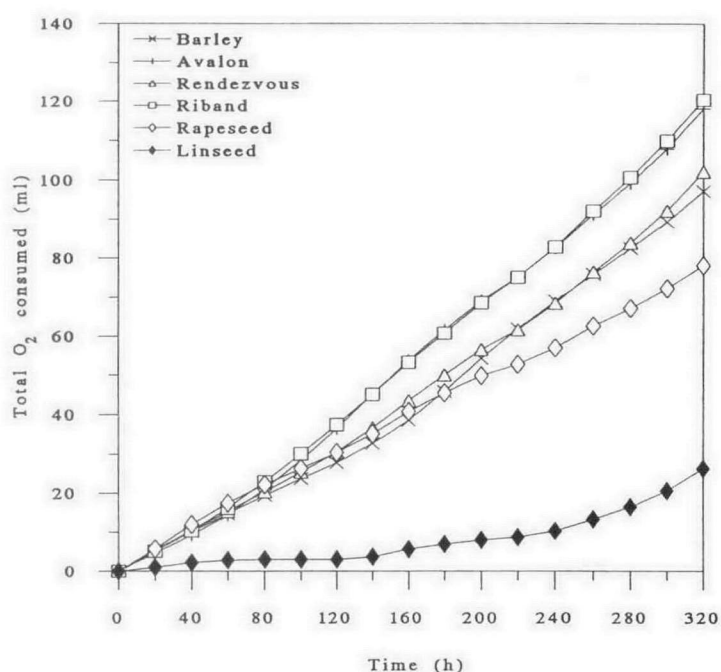


Fig. 1. Patterns of O₂ consumption by barley, wheat (cvs. Avalon, Rendezvous and Riband), rapeseed and linseed grains at 0.88–0.90 a_w and 25°C.

Samourai. However, respiration of linseed cv. Antares was slow initially but then more rapid, giving a linear correlation coefficient of only 0.9142 but a third order polynomial correlation coefficient of 0.9972. Based on these data, the dry matter loss calculated for wheat cv. Avalon was 0.743%, for cv. Rendezvous 0.605% and for cv. Riband 0.724%, and for barley 0.566%. Germination was decreased during storage of all six seed types, but the difference was only significant ($p \leq 0.05$) with cereal grains. The mean percentage germination of the wheat varieties decreased from 99.0–99.3% to 71.1% (cv. Avalon), 47.5% (cv. Riband) and 65.8% (cv. Rendezvous) and of barley grain from 95.3% to 74.4%. By contrast, germination of rapeseed decreased from 100% to 99.2% and of linseed from 99.6% to 96.7%. More cereal grains than oilseeds were visibly mouldy.

The effect of environment on respiration of naturally contaminated wheat grain

The respiration of wheat grain cv. Avalon was determined at water activities from 0.70 to 0.95 a_w (in steps of 0.05 a_w) and at temperatures from 15 to 35°C (in steps of 5°C) over periods of 160–165 hours. Except at 35°C, each experiment was repeated at least once. Oxygen consumption in wheat grain increased with increasing temperature (Fig. 2) and a_w (Fig. 3). At 15–25°C, a_w affected the way in which respiration changed with time: below 0.90 a_w there was an initial lag in respiration before activity increased, while above 0.90 a_w respiration increased linearly with time. Also, the total amount of O_2 consumed by wheat grain over 7 days increased in a nonlinear fashion with a_w and temperature. In the ranges tested, respiration was most rapid at 0.95 a_w and 25–35°C and least at 0.80 a_w and 15°C. CO_2 production followed similar patterns to O_2 uptake.

CO_2 and O_2 data from experiments with wheat grain cv. Avalon were used to calculate respiratory quotients (RQ) over the range of conditions studied. RQ values were generally in the range 0.5 to 1.5 (Table 2) but were consistently larger at 15°C than at higher temperatures, especially at low a_w . The mean RQ, calculated from all data, was 1.11 ± 0.228 . Because this agrees closely with published results giving RQ close to

1.0, a value of 1.0 was used in calculating dry matter loss from O_2 data.

Dry matter losses (Table 3) mirrored trends in respiration rates. Calculated dry matter losses were greatest at 0.95 a_w and 25–35°C, ranging from 1.187 to 1.239%, and least at 0.80 a_w and 15°C with 0.007%. Losses increased markedly with temperature from 15 to 25°C but then changed little up to 35°C. Table 3 also shows conditions that allowed visible moulding of $\geq 1\%$ grains during 7 days incubation. Visible moulding could occur with very little loss in dry matter. For instance, at 0.85 a_w and 25°C, visibly moulded grain had lost 0.13% dry matter.

Temperature and a_w were closely interrelated in determining the occurrence of visible moulding after 7 days incubation. As temperature increased, a wider range of a_w permitted visible moulding. At low a_w , moulding was visible only at high temperatures. For instance at 0.80 a_w , visible moulding was seen only in samples incubated at 35°C. At 0.85 a_w , only samples incubated at 25°C or above were visibly moulded, with the area of seed surface colonised increasing as temperature increased, while at 0.95 a_w , there was visible moulding even at 15°C.

Usually, the predominant moulds were *Penicillium* and *Eurotium* spp., especially at higher temperatures, but *Fusarium* spp. colonised grain at 0.90 and 0.95 a_w . *Aspergillus* spp. were found in all grain except at 0.95 a_w /15/20°C, *Eurotium* spp., in all except at 0.90 a_w /30°C and 0.95 a_w /15, 25 and 35°C, and *Penicillium* spp. in all a_w at 15–20°C and 0.90–0.95 a_w /25–30°C. *Alternaria* spp., already present at the start, were subsequently only isolated after incubation at 0.90 a_w /15°C and 0.95 a_w /15 and 20°C and *Cladosporium* spp. at 0.85–0.95 a_w /15°C and 0.90–0.95 a_w /20°C. *Rhizomucor* spp. occurred mostly in samples incubated at 0.95 a_w /30°C and 35°C. Fungi isolated at 0.90 a_w /20°C were identified to species where possible. Most *Aspergillus* spp. were *A. candidus* and *A. versicolor*, most *Eurotium* spp. were *E. amstelodami* although a few were *E. repens* and *E. rubrum*, and most *Penicillium* spp. were *P. brevicompactum* Dierckx with *P. chrysogenum* Thom, *P. crustosum* Thom, *P. granulatum* Bainier and *P. hordei* Stolk also isolated.

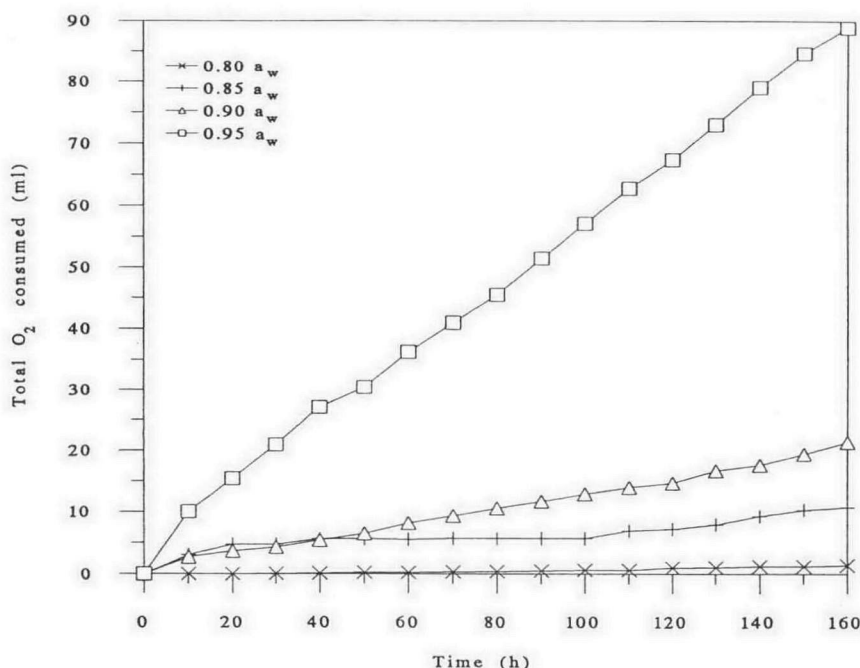


Fig. 2. The effect of a_w on the respiration of wheat grain cv. Avalon at 20°C.

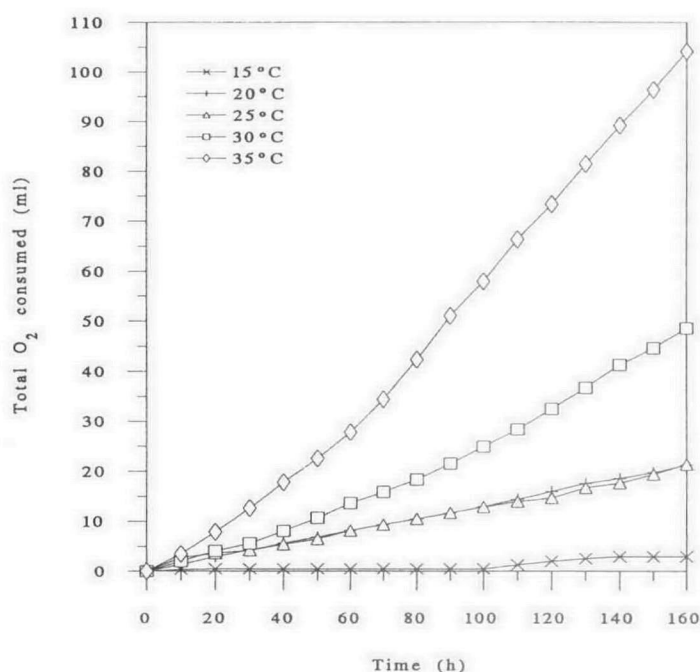


Fig. 3. The effect of temperature on respiration of wheat grain cv. Avalon at 0.90 *a_w*.

Germination of seeds stored with >0.85 *a_w* decreased significantly during 7 days at all temperatures except 30°C. The greatest loss of germination, compared with control grain stored with <0.65 *a_w*, occurred in samples incubated at 0.95 *a_w*, the highest *a_w* tested. At this *a_w* germination was significantly less (*p*≤0.05) at 25°C than at all other temperatures. Germination at 0.80 and 0.85 *a_w* and 15°C did not differ significantly (*p*≤0.05) from the control at any temperature. Unexpectedly, germination showed no significant change from that of control grain after incubation at 30°C, while at 35°C germination was decreased significantly (*p*≤0.05) only in samples stored at 0.95 *a_w*.

Modelling

The full data set was subjected, with generous help and advice from Prof. Martin E. Nellist and Mr R. White of Silsoe Research Institute, to a range of mathematical tests in attempts to produce mathematical models of the respiration of moulding wheat grain over the range of environmental conditions examined. It was assumed that respiration rate was linear with time under all conditions. The stages of the modelling processes were as follows:

- a) The predicted *a_w* of grain samples for each *a_w*/temperature combination was calculated using the equation of Chen and Morey (1989) as above.
- b) Respiration data were converted to mg O₂/day/kg dry grain and divided by incubation temperature (Schmidt and Jacobsen 1982) to give R/θ, where R is respiration and θ is temperature, in units of mg O₂/day/kg dry matter /°C. Figure 4 shows that ln(R/θ) increased linearly with increasing predicted *a_w* (*R*²=0.9594).
- c) Respiration and water content could be related in the equation:

$$R = \frac{a_1 + a_2t}{Y(1 + \exp(-(a_5 + a_6t + a_7\theta)(w - a_8)))}$$

Table 1. Actual *a_w* at different temperatures after preparation of stated *a_w* at 25°C.

<i>a_w</i>	Temp. (°C)	Actual <i>a_w</i> (after Chen and Morey, 1989)				
		15	20	25	30	35
0.80		0.73	0.75	0.78	0.80	0.84
0.85		0.80	0.82	0.85	0.89	0.90
0.90		0.93	0.94	0.95	0.94	0.97
0.95		0.99	0.99	1.00	1.00	1.00

Table 2. Effects of *a_w* and temperature on respiratory quotients of wheat grain cv. Avalon over 7 days.

<i>a_w</i>	Temp. (°C)	Mean respiratory quotient ± SEM				
		15	20	25	30	35
0.80		5.13 ± 0.91	0.68 ± 0.13	0.45 ± 0.04	0.61 ± 0.04	0.84 ± 0.04
0.85		2.50 ± 0.70	0.34 ± 0.07	0.54 ± 0.21	0.87 ± 0.07	0.67 ± 0.11
0.90		1.81 ± 0.39	0.75 ± 0.11	0.54 ± 0.17	0.90 ± 0.01	0.82 ± 0.03
0.95		1.18 ± 0.24	0.73 ± 0.02	0.59 ± 0.09	0.90 ± 0.07	1.02 ± 0.09

Table 3. The effects of *a_w* and temperature on calculated dry matter loss in wheat grain cv. Avalon after incubation for 7 days.

<i>a_w</i>	Temp. (°C)	Predicted dry matter loss (%) after 7 days:				
		15	20	25	30	35
0.80		0.007	0.02	0.039	0.061	0.133 ^a
0.85		0.018	0.027	0.130 ^a	0.161 ^a	0.372 ^a
0.90		0.085	0.226 ^a	0.436 ^a	0.347 ^a	0.774 ^a
0.95		0.517 ^a	0.762 ^a	1.21 ^a	1.187 ^a	1.239 ^a

^a Samples were visibly mouldy after 7 days incubation.

where: R=cumulative O₂ consumption (mg O₂/kg dry matter), t=time (hours), w=water content (14.5–27.0% wb), θ=temperature (15–35°C), $Y=(1+\exp(a_3(a_4-\theta)))$, a₁=345.83, a₂=125.2, a₃=0.1737, a₄=20.33, a₅=0.9143, a₆=-0.001036, a₇=-0.013634, and a₈=24.38 (Nellist, personal communication).

Discussion

Although there were some problems initially in adapting the electrolytic respirometer and its software to measure grain respiration, once these were successfully overcome, it was possible to collect a very large data set. The preparation required for each experiment restricted their size to 32 treatments, instead of the maximum 128 possible with the apparatus, but it still enabled a range of treatments to be replicated several times on each occasion and was much easier to use than many alternatives. It also enabled continuous computer monitoring of oxygen consumption while avoiding the errors of earlier systems that depended on changes in liquid levels in manometer arms (Peterson et al. 1956; Von Scherer et al. 1980), absorption of CO₂ into alkali (Beare et al. 1990; Pazout and Pazoutova 1989; Bailey 1940; Steele et al. 1969) or Haldane gas analysers (Milner and Geddes 1945a; Christensen et al. 1949) and which allowed few samples to be studied simultaneously. A big advantage of the electrolytic system was that it allowed both O₂ consumption and CO₂ production by respiring grain to be measured although CO₂, unlike O₂, could only be analysed at the end. The instant response of the electrolysis cell to pressure changes in the unit was important because it prevented the accumulation of inhibitory concentrations of CO₂ and allowed greater CO₂ production (Larmour et al. 1935; Bailey 1940; Pomeranz 1974).

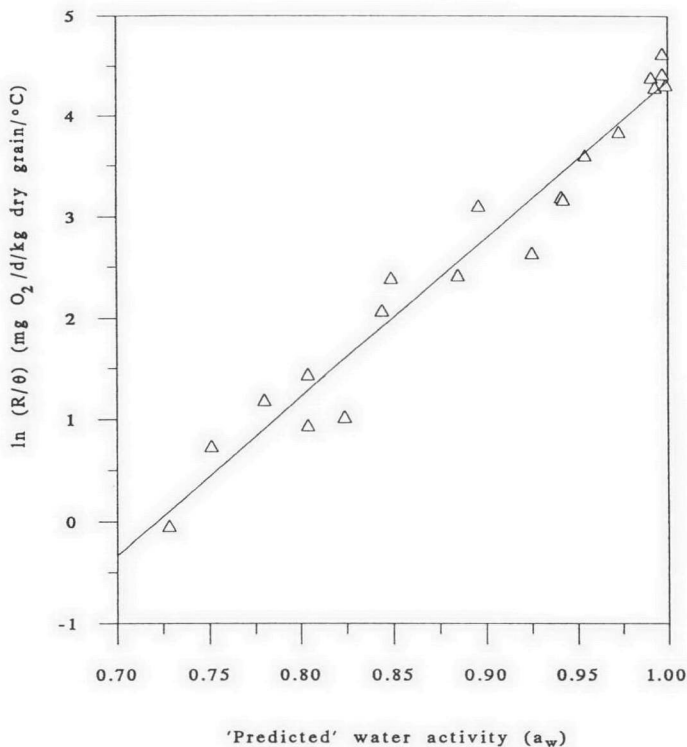


Fig. 4. The effect of temperature-specific ('predicted') a_w on the ratio of O₂ consumption rate (R) to temperature (θ) in wheat grain, cv. Avalon, over 7 days incubation at 0.80–0.95 a_w and 15–35°C.

It was perhaps surprising that oilseeds consumed significantly less O₂ than cereal grains, despite their greater surface area:volume ratio which should have allowed more rapid gas exchange with the atmosphere. However, Bailey (1940) has suggested that respiration is proportional to kernel size. Linseed appeared to have a longer lag phase before the respiration/time relationship became linear and it would appear that linseed could safely be stored for longer than rapeseed or cereal grains. Wheat cv. Rendezvous had been stored for one year more than other wheat cultivars tested and although it carried more *Eurotium* spp., it consumed less O₂ over 14 days than the other cultivars. Kittock and Law (1968) have similarly shown 17% less respiration in wheat grain stored for two years than in that stored for only one year. The data on respiration of barley grain support Kreyger's (1972) conclusion that barley can be stored for longer than wheat.

It is likely that respiration/time relationships are normally sigmoid with an initial lag phase, an exponential phase and then a plateau or declining phase when nutrient reserves are exhausted. The lag and exponential phases were evident in wheat with <0.90 a_w at 15–25°C, as described by Peterson et al. (1956) and Fernandez et al. (1985) but at higher temperatures and a_w, the lag phase was extremely short and only the exponential part of the curves was evident. This gave a linear relationship with time as found by Seitz et al. (1982b) for dry matter loss. Figure 5 compares our respiration data with other published data. Milner et al. (1947b), Scholz (1962) and Kittock and Law (1968) described respiration rates that were much faster than in our experiments and outside the range of Figure 5. In one of these studies, at least (Kittock and Law 1968), the seed had germinated and produced shoots. White et al. (1982a) found slower respiration than that in other studies but was sampling only three times weekly at 20°C and five times at 30°C which may have allowed to accumulate of CO₂ to inhibitory levels. Otherwise, results are similar to our own.

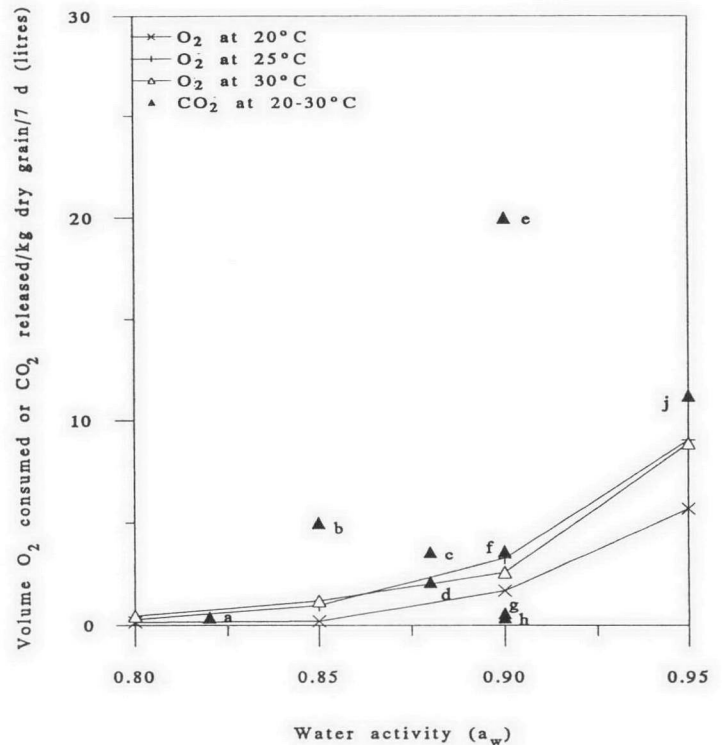


Fig. 5. Respiration of wheat grain, cv. Avalon, measured over 7 days in an electrolytic respirometer compared with published data. Key: a, Bailey, 1940; b, e, Scholz, 1962; c, f, Milner et al., 1947a; d, Larmour et al., 1935; g, h, White et al., 1982a; j, Woodstock and Justice, 1967.

There was a linear relationship between \ln (modified respiration/temperature) and increasing a_w (after correction for temperature differences) as found by Schmidt and Jacobsen (1982) with rapeseed. This relationship suggested that it would be feasible to develop a mathematical model of total respiration over a known timescale under defined conditions but the modification of the 25°C a_w values by the correction process illustrates how models can sacrifice accuracy when standardising the whole data set.

Muck et al. (1991), by standardising published growth rates, developed a two-segment linear model of fungal growth in silage which showed that the growth rates of yeasts and fungi increased linearly with a_w below 0.99 a_w but more slowly from 0.99 to 1.00 a_w . The more detailed relationship between respiration, environmental conditions and time that we have proposed is being used to predict consumption of O_2 during storage. The validity of this model is being tested for incorporation into a simulation model of near-ambient grain drying.

The calculated respiratory quotients for wheat grain, cv. Avalon, were mostly <1.0, especially at >0.95 a_w at all temperatures $\geq 20^\circ\text{C}$. However, at 15°C, respiratory quotients decreased from 5.13 to 1.18 as a_w increased from 0.80 to 0.95 suggesting that anaerobic respiration had occurred, although this was unlikely as O_2 was continuously generated in response to its utilisation by samples and the a_w was insufficient to allow rapid metabolism or anaerobic organisms to grow. Published studies (White et al. 1982a; Woodstock and Justice 1967) also mostly give respiratory quotients ≥ 1.0 , even though markedly different detection methods have been used. Respiratory quotients <1.0 could have resulted from errors in measuring CO_2 or O_2 , metabolism of compounds other than carbohydrates, or that CO_2 was being utilised by fungi and not released. It is possible that not all CO_2 was absorbed by the alkali, so that its production was underestimated, or that the titrations, which relied on two visual assessments of colour change by chemical indicators, were not an accurate measure of CO_2 in the alkali. Lipid and protein metabolism would also give respiratory quotients <1.0 while respiration is not 100% efficient (Deacon 1984) and the utilisation of carbon in biomass could decrease the output of CO_2 . In general, the O_2 data have been assumed to be more accurate than CO_2 data.

This study has shown that visible moulding or loss of germinability, both of which could lead to rejection of the grain, can occur with small losses of dry matter. For instance, 0.085% dry matter loss and decreased seed germination occurred within 7 days at 0.90 a_w and 15°C. No moulding was visible but loss of germinability indicated that fungi had perhaps already invaded the grain. Kreyger (1972) suggests that wheat grain can be stored for up to 3 weeks under these conditions with no loss in germination, and for up to 1.5 weeks before moulding is visible and 0.27% dry matter would be lost. Thus germination has decreased more rapidly, before moulding was visible, and dry matter has been lost more slowly than suggested by Kreyger (1972). With conditions Kreyger considered borderline for storage for 14 days, 0.90 a_w /25°C, dry matter loss of 0.371% occurred with decreased germination and heavy moulding. Kreyger (1972) used a value of 1.0% dry matter loss as a general limit for acceptability for safe storage of wheat but even the conservative limit of 0.5% widely used for safe storage of maize grain (Seitz et al. 1982a) appears unacceptable for wheat. If losses in germination are used to indicate unacceptable levels of fungal invasion of grain, a limit of 0.085% dry matter loss, as suggested by Brook (1987), would seem more realistic from our experiments. This can be considered equivalent to 0.5% loss in maize, in relation to husk/seed volume ratio. White et al. (1982a) suggested an even lower level, 0.04%, as the limit of acceptability for wheat

grain storage. Only one treatment in our experiments gave >0.04% loss without visible mould or decreased germination.

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