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Improving quality by minimising damage

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¶1. RELEVANCE TO GROWERS AND PRACTICAL SECTION

¶1.1 Application

The purpose of this project was to identify physical characteristics of tubers which might be important in determining susceptibility of potato tubers to internal damage ("bruising, "blackspot") and to relate these to agronomic practice.

The principal findings are:

- ☞ potassium fertiliser application decreases susceptibility to internal damage.
- ☞ application of potassium fertiliser at rates optimal for maximum yield is sufficient to alleviate the effects of potassium deficiency. There is no additional benefit in applying very high rates of potassium fertiliser unless these are required to achieve best growth and yield.
- ☞ there is an indication (Expt 4) that potassium fertiliser applied in years prior to the year of crop growth has an effect on the plant which is different from that for potassium applied in the current year for equivalent soil potassium concentrations.
- ☞ susceptibility to internal damage decreases with increasing rate of nitrogen fertiliser, probably associated with decreasing tuber dry matter content.
- ☞ the effects of irrigation are very variable, but a crop maintained under very dry conditions is likely to produce tubers which are vulnerable to internal damage.
- ☞ Dry matter content showed the best association with susceptibility to internal damage, but none of the tuber characteristics examined provided a good description of susceptibility. Even in combination, they would make poor predictors of damage.
- ☞ An impact of 0.5 Joules is sufficient to cause internal damage. This is equivalent to a 200 g tuber falling 25 cm from a stationary position on to a hard surface.

¶1.2 Summary

¶1.2.1 Purpose
The purpose of this work was:

- ☞ to identify mechanical properties of tubers which could be associated with resistance/susceptibility to internal damage

- ☞ to determine environmental conditions/practices which produce tubers possessing these properties

- ☞ where appropriate, to suggest practices which would reliably lead to the production of tubers which are less susceptible to internal damage.

¶1.2.2 Results and conclusions

One objective of this work was to identify treatments which would reliably reproduce internal damage. In fact none of the treatments used was consistently reliable. As a result, it is impractical to give clear advice as to how agronomic factors are likely to affect the incidence of internal damage in a crop. Of the agronomic treatments examined, potassium fertiliser application was probably the most reliable in that effects were observed in three experiments. Even here, in the fourth and last experiment in 1996, on a site with very low native soil potassium, no effects of applied potassium were observed.
The effects of potassium fertiliser application have been the subject of a number of previous investigations and it has been found to decrease the incidence of internal damage in some cases. This beneficial effect seems to have led to the belief, at least in some quarters, that application of potassium fertiliser is a "good" practice for reducing damage. Inevitably, this has resulted in a tendency towards the view that "more must therefore be better" and its application is sometimes seen as an panacea for internal damage in commercial practice. Our results show that adding potassium fertiliser can reduce susceptibility to internal damage, but that these effects are relatively small and achieved at rates normally recommended for achieving good crop growth (section 2.3.1).

- ☞ **It is unnecessary to apply very high rates of potassium fertiliser in order to reduce susceptibility to internal damage. Optimum rates for maximum yield should be sufficient. If a crop is potassium-deficient, then it is likely that yield, as well as damage susceptibility, will be affected.**

For equivalent soil potassium concentration, plant and tuber concentrations were higher where potassium fertiliser had been applied in previous years rather than in the current year (section 2.2.2). Differences between times of application were also evident in the relationships between tuber dry matter content and potassium concentration.

- ☞ **These observations suggest that recently applied potassium**

behaves differently in some way to that applied in earlier years and that further investigation would be appropriate.

Nitrogen fertiliser was examined in only one experiment. Here both susceptibility to internal damage and dry matter content decreased with increasing application rate. In this instance it is likely that the effect was genuinely due to dry matter content and not to differential tuber development (section 2.2.1). The use of irrigation was effective in providing tubers of different susceptibility only where plants were maintained in a dry regime for the whole of a season. Under these circumstances, tubers were high in dry matter content, of low turgidity and possessed weak tissues (section 2.3.3).
With advancing crop development, tubers became less susceptible to internal damage, though symptoms changed from visible tissue fracture and brown discolouration to less obvious fracture and grey/black discolouration (section 2.3.4).

☞ **Timing of harvest can affect the incidence of internal damage. Older tubers are likely to be less susceptible, though the damaged tissue may be darker.**

With increased duration of storage, there was a slight tendency towards increasing susceptibility, but this was very variable and difficult to detect even with a sample size of 40-50 tubers. This observation and our experience with other experiments leads us to suggest that for effective testing of susceptibility, a sample size of 100 tubers would probably be more appropriate.
We examined tissue strength, tissue toughness, the proportion of cell wall, tuber firmness, relative water content and dry matter content (section 2.2.3). Of these, dry matter content showed the best relationship, but even this was poor. Combination of some variables improved the description, but still inadequately described susceptibility.

☞ **No single tuber property examined could be readily identified with susceptibility to damage.**

This observation is particularly relevant, given the importance attached to water status in some previous work and because tissue strength and fracture properties have not previously been examined.
Impact testing was performed over a wide range of tubers from different conditions and backgrounds. From these many tests, experience showed that an impact energy of 0.5 Joules was often sufficient to cause internal damage and usually produced reasonable discrimination between treatments. From this information it is possible to indicate that tubers of 200 g weight need fall only 25 cm on to hard surface to become damaged internally (section 2.3.9). Figure 15 illustrates this point more fully by relating other weights and heights to this energy level. The shape and nature of the object with which a tuber collides will also have a bearing on the likelihood of damage occurring, as will the shape of the tuber.
The last observations in the previous paragraph are useful to illustrate the importance of recognising the difference between ***incidence*** of damage and ***susceptibility*** to damage. Incidence represents the actual occurrence of damage during the processes of harvesting and post-harvest handling and is dependent on the mechanics of

movement, construction of equipment and shape and weight of tubers. In susceptibility testing, these variables are removed, so that only the responses of tuber tissues are important (see section 2.1 for further explanation).

¶2. EXPERIMENTAL SECTION

¶2.1 INTRODUCTION

Internal damage in potato tubers results from impact with other objects during harvesting and post-harvest handling. When the incidence is moderate to severe, this damage can result in consumer rejection and is therefore unacceptable. It is a serious problem for the potato industry, not least because it cannot readily be observed or predicted and can result in considerable financial penalty.

For a more comprehensive consideration of internal damage, the reader is referred to reviews by Hiller (1985), Burton (1989), Storey and Davies (1992) and McGarry *et al.* (1996). A brief summary of the topic follows.

The symptoms of internal damage are varied. For this reason it is often referred to by different names; for example blackspot, bluespot, greyspot, bruising. Common features of these are that they result from impact and always appear 1-3 mm beneath the surface - though the damaged zone may extend much more deeply. This zone may include visible cracking, though not always, and may be coloured brown, yellow, grey, black, opaque floury-white or a combination of these. The degree of discolouration can vary considerably. Sometimes the entire region is surrounded by a well-defined layer of tissue. The damage may occur as dark lines (often associated with cracking) or as a discrete dark "spot" which may include cavities This variety of response is a source of confusion for both commercial and research purposes. We have, therefore, adopted the use of the term 'internal damage' throughout this report, to include all of these symptoms.

Internal damage observed in commercial practice results from impacts of unknown force on tubers which vary in weight and shape. For this reason it is almost impossible for growers and handlers to make valid comparisons of the susceptibility of tuber tissue to impact damage. This often leads to misunderstandings between research scientists and the industry when discussing the possible origins of the problem. It is essential in the first instance that a proper comparison of susceptibility is made using a device such as a pendulum. Tubers which appear to be "more susceptible" as a result of the harvesting process may actually be heavier or have "sharper" sides and/or ends which concentrate the effect of impact. That is not to minimise the importance of such features. Clearly in a commercial situation they may contribute to the occurrence of internal damage and may in some cases be the cause of differences between tubers of different variety or from different locations. To investigate the problem, susceptibility to damage must be placed on a clearly-defined basis in which the tissues of different tubers are subjected to equivalent levels of mechanical stress. Only then can comparative measurements be made and relationships with other properties of tubers be established. We have done this by using a guided falling bolt during our earlier investigations and subsequently, a specially-designed pendulum.

When a potato tuber suffers an impact there is, initially, an entirely physical process of tissue deformation. Some of the energy transmitted to the tuber is absorbed and spread to a varying degree through the surrounding tissues. Energy not absorbed results in movement of the tuber (if it is not fixed in position) and/or rebound of the striking object. The amount of energy absorbed and its spread through tissues will depend on physical and mechanical properties of cells and cell walls. So characteristics such as tissue turgor, tissue strength, cell size and cell wall thickness may play a part in this initial stage of determining the scope of damage. As a result of tissue deformation, cell wall fracture may occur and this will almost certainly cause cell damage. Damage can also occur without apparent fracture as, for example, in true bruising where the damaged zone simply appears to be black. In such instances, the membranes of the cell may have become damaged as result of cell deformation (squashing), particularly where there is a lot of starch, either as large or many starch grains. As a result of this physical damage, the biochemical processes leading to the formation of melanin can occur because previously separated substrates and enzymes come into contact. It is possible that this "decompartmentalization" of the cell could result from more subtle processes than pure physical destruction. In other words, cells may perceive the impact as a signal of invasion, to which they respond by initiating programmed self-destruction. As yet this is a matter of conjecture, since there is no published evidence supporting this possibility.

Whatever the nature of the biochemical response, there is little doubt that physical and mechanical properties of tubers must influence the occurrence and extent of damage, simply because they affect energy absorption and transmission. This report deals principally with properties of this type.

There is a body of evidence about the effects of environmental factors. Differences in susceptibility of tubers have variously been ascribed to the addition of potassium and nitrogen fertilisers, application or not of irrigation and to different stages of development and maturity both during growth and in store. Many of these reports provide conflicting evidence of effects (see reviews referred to earlier). For this reason, it is important to identify tuber characteristics rather than associated treatments, since under different circumstances, treatments may result in different effects on tuber properties. It is only by examining these tuber properties that causes can be established. Our approach has been to use a number of cultivation practices to create variation in susceptibility and tuber properties and to examine associations between them.

¶2.2 DISCUSSION OF RESULTS

¶2.2.1 Effects of agronomic variables on internal damage

Addition of fertiliser affected the susceptibility of potato tubers to internal damage (Tables 1-4).

Potassium fertiliser decreased susceptibility to damage, but the effect was not large and was limited to lower rates of application. Our experiments suggested that where no potassium fertiliser was added there was indeed a greater incidence of damage, but that this could be alleviated by addition of fertiliser at 200 kg ha^{-1}. There was no evidence to suggest that fertiliser applied at greater rates (e.g. 400-600 kg ha^{-1}) provided additional benefit. Indeed in one of our experiments (No. 4), no differences in susceptibility to internal damage were found between any potassium treatments, even though native soil potassium in untreated plots was extremely low (55 ppm). On the basis of our results and those of others (see McGarry et al., 1996 for references), we believe that tubers from potassium-deficient plants are probably more susceptible to internal damage than those which are potassium-sufficient. However, potato crops need to be provided only with enough potassium to achieve maximum yield. **There is no benefit in applying rates greater than this**. It is misguided to apply "extra" potassium in the belief that it will provide greater protection against internal damage. These conclusions are based on the results of four experiments encompassing a wide range of native soil potassium concentrations and applied rates of fertiliser. Mean tuber potassium concentrations showed very little variation in concentration except in tubers of Expt 1 where they were approximately half that of other experiments. Some small treatment effects on tuber potassium concentration were apparent in Expt 4. Taking the data overall there was, however, no relationship between susceptibility to internal damage and mean tuber potassium concentration. The relationships between applied rate of potassium, soil, plant and tuber potassium concentration observed in Expt 4 are discussed further below (Section 2.2.2).

Nitrogen fertiliser application affects susceptibility to damage: the higher the rate of application, the less susceptible are tubers to internal damage. There was a clear association between treatment means of tuber dry matter content (DMC) and susceptibility. This may in part be due to additional nitrogen slowing the rate of crop development and maturity. However, susceptibility of individual tubers also showed an excellent relationship with DMC of each tuber irrespective of treatment. Further evidence conflicting with an explanation on the basis of maturity is that we also find that less mature tubers with lower DMC are in fact more susceptible to damage (Section 2.3.4). Other workers have variously reported that nitrogen fertiliser increased susceptibility, decreased susceptibility and had no effect (see McGarry *et al,* 1996). Using nitrogen availability could be a useful means of investigating further the mechanism behind the association of dry matter and internal damage.

Varying the amount of irrigation can alter the susceptibility of tubers to damage, but in our experiments it was an unreliable treatment (Tables 5-7). The only notable effect was associated with an extreme treatment. For tubers from plants which were starved of water except for that present in the soil at the beginning of the season (Expt 6), susceptibility to internal damage was markedly increased. However, applying irrigation over different periods of the season (e.g. from planting to full crop cover or from full crop cover to harvest) resulted in very little difference in susceptibility. Tuber water status has been indicated as an important variable in determining susceptibility to

internal damage (see McGarry *et al.*,1996, but also refer to other sections of this report). Whether tuber water status can be markedly affected by irrigation regime, except in the most extreme cases, is a debatable point. Indeed it would be quite reasonable to view effects of water availability during growth as being mediated through changes in metabolism as much as water status. In the case of the DRY treatment in Expt 6 (which was very dry), most tuber properties measured were affected. For other treatments in all irrigation experiments, there were few differences. This may have arisen in part, because water availability in the different treatments was less extreme than anticipated (in spite of data in Fig. 4). In Expt 5, rainfall was not inconsiderable during the season. In Expt 6, rainfall was excluded, but irrigation was applied to dry stages of treatments at a very low soil moisture deficit (SMD) to ensure that the crop did not fail. These measures may have ameliorated the intended simulation of drought conditions. It may be that imposition of more extreme stress at critical stages, such as early tuber development could lead to greater susceptibility.
It is important that changes in susceptibility during development and storage are characterised (Figs 5-9), because comparisons between tubers from other treatments may be obscured by the effects such treatments have on development. Can one be sure that a difference in susceptibility between two varieties harvested at the same time is not due to a difference in tuber development? Our results suggest that young immature tubers are very susceptible and that this decreases with age on the plant. However, the type of internal damage also changes. The symptoms in younger tubers show more cracking and the damage is generally brown rather than grey or black. In older tubers internal damage, even though less frequent, tends to reveal the more classic symptoms of a dark bruise-like spot. During storage the changes which occurred differed between years. In 1994, there was the classic increase in internal damage with longer duration in store. Although this occurred in 1993, changes fluctuated more. Detection of changes was severely limited by the size of the errors associated with each mean. This is an indication that samples larger than 50 tubers were probably necessary to detect differences in this case. A similar conclusion might also be applied to some of the other experimental treatments. In all but one experiment least significant difference was greater than 10% and in several it was close to 20%. Although a research objective would be to find and compare treatments that were different by say 70-100%, discrimination of 10% differences between treatments is desirable.
A number of varieties were used during this work, but there was no specific attempt to directly compare varieties in a consistent manner. It was deemed a strength of the work to include several varieties, in that any characteristic (or characteristics) providing a description or explanation of internal damage should be sufficiently robust to account for varietal as much as environmental differences. Because of the ineffectiveness of environmental factors to give reproducible differences in susceptibility, there would be considerable merit in simultaneously examining a large number of genotypes throughout development and during storage. With extensive and effective impact testing, greater consistency of estimating treatment difference could be achieved.

¶2.2.2 Other observations related to potassium nutrition

The relationships between applied rate of potassium, soil, plant and tuber potassium concentration observed in Expt 4 showed some unexpected results. Firstly, measured soil concentrations for plots where potassium fertiliser was applied were much lower than expected from calculation (Fig. 1). As a result, soil potassium concentrations at the higher application rates were equivalent to the lower end of the native gradient plots (Fig. 2). Secondly, plant and tuber potassium concentrations, while showing some relationship with soil concentration, were clearly very different for the native gradient plots compared with the applied potassium plots. Further, this difference between the two types of potassium treatment was evident in the relationship with DMC (Fig. 3), where, in spite of their higher potassium concentration, tubers from the gradient plots showed no greater DMC, even though the general trend was for increasing DMC with increasing potassium concentration. Quite why soils with similar potassium (i.e. 361 and 723 kg ha^{-1} and G3 and G4) should result in plants with very different tuber potassium and dry matter is difficult to explain. It does however suggest that the time of application of potassium fertiliser is important. For some unknown reason, recently applied fertiliser may not be as effective as that applied some considerable time earlier: in the case of this experiment, about 6 years earlier. Because of practical limitations placed on the use of the experimental site at Wellesbourne, the gradient plots and applied-fertiliser plots were not randomised within the same blocks, although they were in the same field and on similar soil type. There remains the possibility that a consistent difference between these locations was present. Measurement of soil nitrate and phosphorus did not clarify this matter. This apparent difference in effect of time of application of potassium fertiliser is probably worthy of further investigation.

¶2.2.3 Relationships between tuber properties and internal damage

A principle purpose of this work was to identify characteristics of tubers which could be associated with susceptibility to internal damage and which might have a mechanistic role (see Tables 8-10 and Fig. 10). In particular, we were concerned with the potential role of rheological properties such as tissue strength and toughness. Tissue strength was measured by its capability to withstand a tensile load before breaking (failure stress, FS). Toughness was measured as the work required to open a crack in the tissue (fracture toughness, FT). Analysis of the data we have collected from a large number of experiments would suggest that neither of these properties alone is even loosely associated with susceptibility to internal damage. No correlation between mean susceptibility and tissue strength or toughness of different treatments could be detected. Nor did analysis of strength and toughness of individual tubers and their responses to impact reveal any indications of importance. Similarly, the fraction of cell wall (measured indirectly as apoplast volume) was not associated with a propensity to damage. Of all the properties that were measured, only DMC showed any association with susceptibility - a feature of many other studies. This was true for correlation analysis of treatment means and for binomial regression analysis based on individual tubers. However, even DMC accounted for only a small proportion of the total variation. This correlation still does not provide an explanation for the likelihood of the occurrence of damage and is not predictive.

There is a strong *prima facie* case for the importance of tuber water status. It might reasonably be anticipated that the more turgid (harder) a tuber, the less energy it will absorb, but the greater will be the impulse load under impact. For softer less turgid tubers the opposite would be true. On this basis alone, one might expect tuber water status to affect the occurrence of internal damage. Our data show little evidence of this. We have been unable to demonstrate good correlation between susceptibility and relative water content (RWC) for data from our field studies. Equally, in laboratory experiments where we deliberately manipulated water content, clear relationships were not forthcoming (Fig 11). The conclusion from our studies is that water status is not a major determinant of susceptibility to internal damage. This is in direct disagreement with the findings of Kunkle and Gardner (1965) and particularly Smittle *et al.* (1974) who published an explicit, though non-quantitative, relationship between these variables.

Combinations of variables in multiple regression accounted for a greater proportion of variation, but also suggested that RWC was not important. Best fit was obtained by combining DMC with FT and FS.

For the two years' data from the study of development and storage of Wilja, significant correlations were obtained between susceptibility to damage and RWC (0.609, $p<0.001$) and DMC (-0.628, $p<0.001$). Each variable accounted for some 35% of variation. In multiple regression analysis, their effects were additive. Other variables (FT, FS, AV and rebound angle) were not related to damage susceptibility. The negative correlation with DMC illustrates the limitations of such variables in explaining or predicting internal damage, given that it is usually positively correlated.

Clearly, to improve our understanding of susceptibility to internal damage it is insufficient to measure essentially mechanical and physical properties of tubers alone. There are other rheological variables which could be included, but relevant biochemical characteristics must also be quantified. Amongst these, as a minimum, polyphenoloxidase activity and the concentrations of free tyrosine should be measured, since respectively, they are the principal enzyme and substrate leading to the formation of melanin, the black pigmentation associated with internal damage.

Following a correlative approach, further progress is unlikely unless a wide range of variables is measured on, as far as possible, a common sample of material. This is because internal damage results from a complex interaction of physical and biochemical factors, any or several of which may be important under different circumstances. A multi-disciplinary approach using skills of several teams is almost certainly necessary to establish the most important characteristics. Multiple regression analyses and possibly the use of neural networks will be necessary to develop predictive models. Such an approach may be appropriate to the comparison of varieties suggested above (Section 2.2.1).

¶2.2.4 Impact testing

Using a pendulum for impact testing is probably as reliable a means as can be achieved (Fig 16). When suitably instrumented, as ours now is, it can supply usable additional information on the physical nature of the tubers during dynamic impact. Recording starting and rebound angles supplies information on the energy required to cause internal damage, indicates the elastic nature of the tuber tissue and enables the calculation of impulse force. By following the movement of the arm, deformation of the tuber and the course of the arm during impact can be monitored. The results obtained from tubers in Expt 4 (potassium, 1996) did not reveal any treatment differences, but the trends in deformation, particularly between testing occasions, were consistent with changes in RWC and in tuber firmness (not illustrated). Routine use of an instrumented pendulum for impact testing in experimental investigation is recommended. A falling bolt is a cheaper, but effective option, if the only data required is presence/absence of damage. The two methods generally show good correlation, but with a falling bolt usually causing greater damage at equivalent potential energies. In our systems, this was because the bolt was unrestrained after impact and thus released all of its energy in multiple impacts until it came to rest. The pendulum possesses a mechanism which preventes the arm from striking the tuber more than once. A falling bolt could be constructed and instrumented to give similar information to that obtained from a pendulum. We generally found that energies in the range 0.4-0.6 Joules were often sufficient to cause internal damage. Increasing impact energy to above 0.7 Joules often caused external damage as well, though this was not always the case. Figure 15 provides information on tuber sizes and drop heights which would produce impacts equivalent to 0.5 Joules.

One of the important features of the method of impact testing is that tuber size should not affect the outcome. For pendulums and bolts, this is true when only the presence or absence of symptoms is considered. However, the size of the damaged zone can be affected. For the same impact energy the volume of damaged tissue is generally larger for smaller tubers (Table 12). This may be related to the amount of surface area which is supporting the tuber on its unimpacted face. We always used half tubers in order to provide a firm flat surface to support the tuber. Clearly the area of this will vary with tuber size and it may be that a large area allows the compression caused by impact of the pendulum head to be more readily absorbed. The bulk of tissue in an uncut tuber would also be greater for larger tubers, but with the additional disadvantage of an inconsistently curved supporting surface. This effect of tuber size on damage volume may be a consequence of the depth of tissue between the impact and supporting surfaces (i.e the thickness of the tuber half), rather than the area of supporting surface. Analysis of some more recently-acquired data (not shown) has provided evidence of a relationship between the depth of the damaged region and the thickness of the tuber half. This further supports the notion that tissue compression on impact may be more readily absorbed by a greater total depth or bulk of tissue between the striking and supporting surfaces.

In assessing tubers for damage, we did not use a scale to record the intensity of damage. This is actually a difficult problem to resolve because of the many hues that can be contained within a damaged zone. However, in some cases symptoms are very feint. We have tended to include these providing they were readily visible. Clearly, subjectivity could intrude here and it may be valuable to devise a more objective means of quantifying this.

¶2.3 RESULTS

¶2.3.1 Effects of potassium fertiliser [Tables 1, 2 & 3]
Susceptibility to internal damage for tubers of cv. Record from a site in Nottinghamshire (Expt 1) was 14 % units less in tubers grown with the addition of 200 kg ha^{-1} K_2O equivalent of potassium sulphate fertiliser compared with no added fertiliser (Table 1). Tubers of cv. Pentland Dell, taken from a low native potassium soil in Hampshire (Expt 2) showed a reduction of 23% compared with untreated controls when potassium fertiliser was applied at 600 kg ha^{-1} K_2O equivalent (Table 1). At a rate of 200 kg ha^{-1}, the increase was not much smaller than this. In tubers of cv. Record grown at Cambridge University Farm (CUF) and harvested on two occasions late in the season (Expt 3), reductions of 16% and 14% units were observed for application of 300 kg ha^{-1} (Table 2). On very low potassium soils (55 ppm K) of the 1996 experiment at Wellesbourne (Expt 4), no effect of additional potassium fertiliser on susceptibility to internal damage for cv. Cara was observed (Table 3). This last experiment included a wide range of treatments from 0 to 723 kg ha^{-1} of added K_2O equivalent as potassium sulphate fertiliser and three native soil concentrations ranging from 80 to 180 ppm potassium ("gradient plots" G3, G4, G5). The apparently greater susceptibility of the longer-stored tubers in Expt 4 is partly due to the lower temperature of tubers at the later testing date. However, preliminary susceptibility testing to establish conditions for the full test on the second occasion (data not presented) included the conditions used on the first occasion and demonstrated that an increase in susceptibility to internal damage had taken place during storage.
In Expts 1, 2 and 3, application of lower rates of potassium fertiliser reduced susceptibility to internal damage when compared with untreated tubers (though not always significantly). With the exception of one case (Expt 3, 200 kg ha^{-1}), these reductions in susceptibility at lower rates were not significantly different from those at the highest rates of potassium fertiliser application. Although treatments in Expt 4 were without significant effect on susceptibility to internal damage and on the volume of damage, there were very clear effects on other tuber properties (see below). In this experiment, concentrations of potassium for soils from the recently-fertilised plots (Table 3) were low compared with the higher end of this native range and were lower than expected from calculation (Fig. 1). Incorrectly estimating the applied rate by ignoring the proportional potassium content of the fertiliser does not account for this discrepancy. Soil phosphorus and nitrate levels between the treatments were very similar.
Potassium concentrations in tuber tissue were unaffected by treatment in Expts 1, 2 and 3. However, concentrations in tubers from Expt 1 were about half those from Expts 2, 3,and 4. For the other nutrients analysed, there were significant differences between treatments in Expt 3, but these related to treatment only in the case of magnesium and organic nitrogen at harvest 2. Concentrations of both magnesium and organic-nitrogen increased with additional potassium fertiliser. In Expt 4, tuber concentrations of potassium showed no effect of recently applied potassium fertiliser, though they were significantly higher for the native potassium gradient plots (Fig. 2). There was an observable, though small, increase in plant potassium concentration with increasing rate of applied fertiliser. Furthermore plant potassium concentrations were greater for the gradient plots. These measurements showed a positive correlation with soil potassium concentration for all treatments, but there appeared to be a difference

between the effect of recently applied potassium and that of native potassium at similar soil concentrations. There were also significantly higher concentrations of calcium and magnesium in the plant samples (not shown) from gradient plots than those from recently-fertilised plots. Other examples of nutrients which were greater in concentration for the native gradient plots than for recently fertilised plots were calcium, magnesium (in tuber cortex and pith) and sodium (tuber pith only - data not shown). The relationship between plant potassium and tuber potassium concentrations (not shown) was linear with no obvious deviation of the data points into gradient and applied fertiliser plots.

Effects of potassium fertiliser on other tuber properties are also shown in Tables 1, 2 and 3. For DMC, effects were generally not significant or were very small. In Expt 4, there was a very clear increase in DMC with increasing soil potassium availability (Fig. 3a). Differences in RWC between potassium treatments were larger, but were not consistent with the rate of application, except in Expt 4 where RWC decreased with increasing potassium concentration. Measurements of water potential (WP) in Expt 3 (harvest 1) suggested that higher potassium rates were associated with more turgid tubers, but these measurements were not consistent with those of RWC and this effect was not observed in other experiments. Rate of application had no effect on strength (FS) or fracture properties (FT) of tuber tissue nor on the volume fraction of tissue that constituted apoplast (AV - assumed to be equivalent to cell wall). Interestingly, there was an increase in rebound angle with increasing potassium fertiliser rate in Expt 2. This means that less energy was absorbed by tubers grown at higher potassium rate. There was, however, no apparent relationship of this with mean tuber water status - which might have been expected - and the effect was not observed in Expts 3 and 4. Although, there were significant differences between treatments in deformation and firmness, no consistent trends with potassium treatment or concentration were observed.

Eighteen tubers (six per treatment) from Expt 4 were assayed for polyphenoloxidase activity of tubers by Dr Ewen Brierley, Nottingham Trent University. Means of 0.57, 0.42 and 0.51 µmoles O_2 mg protein^{-1} min^{-1} (lsd, $p<0.05=0.629$) were obtained for treatments 0, 300 and 723 kg ha^{-1} of K_2O equivalent. There were, therefore, no treatment differences, but a very large tuber to tuber variation in activity was observed. The coefficient of variation for PPO activity of the 18 tubers assayed was 100.3%. Detection of treatment differences would therefore require many more tubers than this to be sampled and suggests that other variables such as tubers size may need to be accommodated in an attempt to reduce this variation.

¶2.3.2 Effects of nitrogen fertiliser [Table 4]

The effect of nitrogen fertiliser application on internal damage was investigated in one experiment at CUF, using cv. Cara (Expt 5). A large and significant decrease (34%) in susceptibility to internal damage was observed in tubers from plots treated with 240 kg ha^{-1} of nitrogen fertiliser when compared with tubers from untreated plots (Table 4). This was associated with lower DMC and a slightly higher RWC than in tubers from unfertilised plots. RWC of tubers from this experiment was low (*circa* 74%) because they were impact tested some months after lifting and storage. As with the experiments examining potassium, there were no differences between treatments in FS, FT or AV.

No significant differences in the concentration of organic nitrogen in the tubers were measured, nor in phosphorus, calcium and magnesium. There was, however, a significant raising of the tuber potassium content from 2.5% to 2.9%.

¶2.3.3 Effects of irrigation [Tables 5, 6 & 7 and Fig. 4]
Information on the effects of moisture availability has been obtained from three irrigation experiments, two of which were done at CUF and one at Wellesbourne. The first experiment at CUF (Expt 6), which was completely sheltered from rainfall by polythene tunnels, compared tubers from unirrigated plots (DRY) with those irrigated according to a CUF irrigation schedule (CUFIS) or from a very wet regime (WET). Susceptibility to internal damage was very much worse in DRY tubers than in those from either CUFIS or WET treatments. There were also significant differences between DRY and the other two treatments in many of the other measured variables (Table 5). DMC in tubers from the DRY treatment was considerably greater than that of either irrigation regime and RWC was also much lower than in tubers from irrigated plants. Apoplast volume fraction in tubers from CUFIS and DRY treatments was significantly lower than those from the WET regime. Failure stress of tuber tissue was greatest in CUFIS tubers, suggesting that these may have had stronger cell walls, since they were lower in AV. Tissue from DRY tubers was significantly weaker in terms of failure stress and fracture toughness, though its cell wall fraction was similar to that of CUFIS tubers.
The second irrigation experiment at CUF (Expt 7), using cv. Record, resulted in no significant differences in susceptibility to internal damage even though there were effects of treatment on DMC and RWC and FT (Table 6). RWC of tubers from the unirrigated treatment (W1) of this experiment was greater than RWC for all treatments in Expt 6. Tubers from treatment W2 (irrigation withdrawn after canopy closure) possessed significantly lower RWC than this. Plants which were irrigated throughout (W4) or irrigated from canopy closure onwards (W3) produced tubers with significantly higher RWC than W1. Effects of irrigation treatment on mechanical properties (FS and FT) in this experiment were few and very small.
Irrigation treatments in Expt 8 (at Wellesbourne) were applied with the intention of repeating the large differences observed Expt 6. Profiles for SMD derived from an evapotranspiration model, illustrate that treatment differences were achieved (Fig. 4). However, in contrast to Expt 6, there were no significant differences in susceptibility to internal damage between the treatments (Table 7). A greater proportion of tubers in treatment IR1 (dry) than in the other treatments exhibited damage and this damage comprised a greater volume of tissue, but statistical error (LSD) for these variables was greater in this experiment than in others, diminishing the sensitivity of difference detection. This was in spite of testing 60 tubers per treatment in three replicates of 20. Errors for the other variables (DMC, RWC, FT, FS and rebound angle) were small, but no treatment differences in these physical properties were evident.

¶2.3.4 Changes with development and storage [Figs 5 - 9]
Very broadly, the trends in susceptibility to internal damage with tuber development on the plant and through storage for 1993 and 1994 were similar (Fig. 5a). Younger tubers tended to be most susceptible and as they aged in the crop, became more resistant to the effects of impact. Later in storage, there was an increase in susceptibility, though this did not reach the level of damage recorded for young tubers. The rise in susceptibility that occurred after 200 days in 1993 and after 150 days from

planting in 1994 is also worth noting.The significance of this is uncertain, particularly since in 1993 it occurred after lifting, while in 1994 it preceded lifting. The band of error (95% confidence limits) surrounding the developmental trend was generally of the order of 20% damage. This clearly does not provide a very precise means of discriminating between tubers and only the largest of changes can be detected. Given that in excess of 500 tubers were examined in each year (at least 40 tubers on each occasion) it amply illustrates the numbers required to achieve effective detection of treatment effects on susceptibility to damage. Trends in the volume of damage resulting from impact were also somewhat variable (Fig 5b), but suggested a decline during maturity on the plant with a slight rise at or after lifting and a steady increase during storage.

DMC remained fairly constant at around 20% throughout the period of the experiment in 1994 (Fig. 6). This differed from the early phase of development in 1993 when DMC continued to increase, reaching a final level of about 22%. The very much hotter weather of the summer in 1994 resulted in much more rapid advancement of the crop, so that by the time tubers were taken for the earlier harvests, they were fairly mature. Indeed one important difference in cultivation practice between the two years was that in 1994 the canopy senesced and dried very early, so foliar desiccation was unnecessary. In 1993, chemical desiccation was used prior to lifting. The pattern of RWC in the two years was very similar (Fig. 6), starting high and steadily declining throughout development and storage. The only difference between the years in RWC was that the decline appeared more rapid in 1994, though the final levels were not dissimilar.

Levels of FS and FT were very similar between the two years (Fig. 7). Failure stress, however, showed a quite different trend during storage: in 1994, the tissue weakened with time after about 200 days from planting (approx. 50 days from lifting). This weakening did not coincide with the increase in susceptibility to damage (at 280 days), but preceded it. In 1993, there was no evidence of tissue weakening; in fact at this time it actually strengthened. Given that around this time internal damage susceptibility was increasing, it would appear that other factors are more important. Tissue toughness showed a general decline with tuber age (Fig. 7), though these changes were relatively small. Estimates and trends in AV (Fig. 8), were very different in the two years after 150 days from planting. The very great rise to 20% at 225 days is extremely difficult to explain. An unavoidable change in operator took place at 170 days, but the method employed was very similar to that used prior to this and estimates obtained between 280 and 350 days are similar to those of earlier samples. If these values are correct, then they represent a large increase in cell wall volume at a time when there was very little change in bruising susceptibility. Also the reduction in FS that took place during this time, is difficult to reconcile with increased AV since one might reasonably expect the tissue to be stronger if it contained a greater proportion of cell wall.

Use of a pendulum in 1994, permitted the recording of rebound of the pendulum arm after impact with the tuber. The greater the amount of energy absorbed by the tuber, the smaller the angle of rebound. The trend illustrated in Fig. 9 shows that rebound angle tended to increase with time as the tubers matured in the crop and aged in store. Thus the amount of energy absorbed decreased over this time. The early drop in rebound angle (more energy absorbed) between days 111 and 126 coincided with a decrease in damage while the tubers were growing. However, apart from this, trends in rebound angle and thus energy absorbed did not relate to the susceptibility of tubers to damage. [e.g. later increases in angle were accompanied by increases in susceptibility.] Differences in energy absorption by the tubers, represented by the range of rebound angles presented in Fig. 9 is approximately equivalent to 0.03 Joules or 6% of impact energy of 0.5 Joules.

¶2.3.5 Relationships between internal damage and tuber properties [Tables 8, 9 & 10 and Fig. 10]

One of the principal purposes of this work was to identify characteristics that may predispose tubers to internal damage. Association of characteristics with the occurrence of damage and/or the amount of damage are useful ways of indicating the relative importance of variables. The data from the various experiments have therefore been examined by linear correlation, multiple regression and by binomial regression techniques.

Simple linear correlation between the means of variables for a range of experiments in which only mature tubers were examined (Table 8), has shown that none of the variables accounts for a large amount of the variation (Fig. 10). A significant relationship between susceptibility to internal damage and DMC was observed, but this accounted for only 16% of variation in treatment means. **Combining these variables to assess their collective contribution can account for up to 57% of the variation (Table 9) and suggests that DMC in combination with the rheological properties of tissue strength (FS) and toughness (FT) may be relevant. As a predictive model, however, this would not be successful and it should be emphasised that this is describing the variation in averages only and not the full variation of the data.** In Expt 4, which was not included in this analysis, there was treatment variation in both DMC and RWC, with no significant effect on susceptibility to internal damage.

A similar 'global' examination of the data from data from Expts 9 and 10 ("development and storage") suggests a greater degree of correlation between average internal damage and DMC, but this is negative rather than positive, i.e. greater susceptibility at lower dry matter. A strong positive correlation was observed between internal damage and RWC. The tubers in this study varied considerably in age and included mature tubers which had experienced lengthy storage. Other variables which are age-related are therefore likely to have had considerable influence. No significant relationships were observed with FS, FT, AV or rebound angle (Table 10).

In addition to evaluation of the relationship between mean data, binomial regression was used to identify the presence/absence of relationships between those tubers which succumbed to damage and other tuber characteristics irrespective of treatment. Briefly, this has so far revealed no further evidence of a role for tissue strength and toughness, nor for water status, but has served to corroborate the importance of dry matter. For example in Expt 5 (nitrogen fertiliser), there was a strong association between susceptibility to damage and DMC within each nitrogen treatment and the effects of treatment could be entirely accounted for by changes in dry matter content. In Expt 4 (potassium treatments, 1996), deformation of the tuber on impact and rebound of the pendulum arm after impact were not affected by treatment in any consistent manner and, in the absence of treatment differences for internal damage, no relationships with susceptibility could be discerned.

Tuber firmness (measured inversely as surface deformation - see Methods) was introduced only in 1996 (Expt 4, potassium) as a possible way of more reliably determining the effects of different water status in whole tubers. No relationship with damage could be established because treatments did not result in differing susceptibilities in this experiment. It did, however, show a negative relationship with mean relative water content (data in Table 3) between occasions, though for the different treatments within occasions very little relationship was observed. A negative relationship might be expected on the basis that the greater is RWC, the more turgid and, therefore more firm, is the tuber. A similar pattern was evident for the relationship between firmness and rebound angle of the pendulum, illustrating that less energy was absorbed by more firm, turgid tubers. For firmness and tuber surface deformation during impact, there was a positive correlation between the treatment means within the second occasion and between occasions. Although both measurements are similar in that they determine the extent of surface displacement, one is under dynamic impulse and the other is effectively under static loading.

¶2.3.6 Manipulation of tuber water status [Figs 11 & 12]
The water status of stored tubers was varied in four experiments (Expts 11-14), either by wetting or drying tubers over short periods of time. The purpose of this was to provide tubers of varying firmness as a result of changes in turgor potential of the cells, because there were strong indications in the literature that this had a major effect on internal damage. Mean RWC for the various treatments indicated that they were effective in altering tuber turgor. Taking all of the data from these experiments collectively, no overall relationship between the susceptibility to internal damage and RWC could be determined (Fig. 11). Only in Expt 11. was there any suggestion of a consistent relationship between these variables. In this instance damage decreased with increasing RWC (and thus turgor). The alterations in water status had clear effects on mechanical properties of the tubers. Energy absorbed by tubers (estimated from rebound of the pendulum arm) and the toughness (FT) of tuber tissue both decreased with increasing RWC, and thus turgor (Fig. 12a and 12b).

¶2.3.7 Variation in cell morphometry in tubers from irrigated and unirrigated plants [Table 11 and Fig. 13]
Plants grown in the glasshouse at Wellesbourne (Expt 15) provided tubers which had received either ample or insufficient water during growth. Some of these tubers were used for the provision of data on cell dimensions and others were subjected to pendulum impact. This resulted in no internal damage in any of the tubers irrespective of treatment. Measurement of cell dimensions also showed no difference in overall means (Table 11). Cell dimensions showed a gradient of increasing size as distance into the tuber from the surface increased (Fig. 13), but no differences in cell dimensions between treatments were observed. However, cells from more than 0.7 mm below the tuber surface of unirrigated plants were significantly more circular than those of irrigated plants. The difference between treatments was of the order of 6%.
Measurements of cell wall thickness revealed thicker tuber cell walls for plants which were well irrigated. This difference was present in cells located deeper in the tissue, but not in cells of the skin layer.
Cell size was also measured for 'inner' and 'outer' zones of tubers from the zero and 723 kg ha^{-1} potassium treatments of Expt 4, but no treatment differences in size were

observed.

¶2.3.8 Effect of tuber size on susceptibility to internal damage in falling bolt tests and a comparison of damage induced by pendulum and falling bolt [Table 12 and Fig. 14]

It is important in impact testing for susceptibility to damage, that gross physical properties such as size, shape and weight do not influence the outcome. For this reason it is preferable to hold tubers in a fixed orientation and inflict a known impact rather than to drop tubers on to a hard surface. The latter method clearly is mass dependent and there is uncertainty about the location of impact unless the tuber is guided. In pendulum and falling bolt testing, the weight of tuber should have no effect. It is possible, however, that for tubers of different size there are differences in curvature of the surface which will affect the impact area and therefore the stress experienced. Also, the area of the face of the tuber on the side opposite to the impact site will vary with size and this may affect the spread of shock waves away from the impact site. In our system this face was usually the cut surface of a half-tuber.

We have investigated the effect of impacts from a pendulum on tubers over a range of fresh weights from 80 g to 280 g (Table 12). There was no correlation between the incidence of susceptibility and weight for these data and no effect on the presence of internal damage was detected when analysis of variance was applied to tubers classified into three size grades. There was also no significant correlation between the sizes of individual tuber and the volume of internal damage, but damage volume was significantly less in tubers classified as large when compared with small and medium-sized ones. Parameters defining shape clearly indicated that smaller tubers were generally more spherical than large ones and their surfaces more curved.

In 1993/94, impact testing was achieved using a guided, falling bolt, while a pendulum was being developed. Its manufacture by HRI Technical Services was completed by the end of April 1994. Data for the comparison of the pendulum and falling bolt were taken from impact testing at 0.5 Joules on cv. Wilja during development and storage. The variation in the proportion of tubers showing damage is due to variation with time and development of the tubers and not to the application of different impact energies. A satisfactory linear relationship (Fig. 14) was obtained between the incidence of internal damage caused by the two methods. Though there is a hint of curvilinearity in the relationship, the correlation is sufficiently good for us to be able to make reasonable comparison between experiments in which the bolt was used and ones where the pendulum was used. There was a tendency for the bolt to cause greater damage than the pendulum at all levels of damage (*cf* the 1:1 line on the graph). This is almost certainly because the bolt inflicted multiple impacts until it finally came to rest. Thus, all of the energy from the falling bolt was transferred to the tuber. In pendulum testing, the arm was restrained after rebounding from the first impact to provide information on energy absorption and on restitution.

¶2.3.9 Energies causing internal damage: relationship with tuber mass and drop height [Fig. 15]

As we gained experience in impact testing, the level of impact energy required to cause internal damage became apparent. Generally we have found that an impact delivering 0.5 Joules of kinetic energy to be sufficient to inflict damage. Sometimes less than this is necessary. Levels as low as 0.3 Joules are usually insufficient. We have used greater energy levels (up to 0.75 Joules) but this often results in additional external cracking. From a practical point of view it is the minimum energy input which is relevant. We have used the requirement of 0.5 Joules to construct a simple graph (Fig. 15) which illustrates equivalent "drop heights" for tubers of different mass to experience similar levels of impact energy. The graph thus permits an appreciation of the likely impact tubers experience when moving under the influence of gravity. Thus a tuber of mass 100 g will be subjected to an impact energy of 0.5 Joules when falling from half a metre, while it requires only a 25 cm drop to achieve the same energy for a 200 g tuber. Tubers weighing 100 g and 200 g are representative of tubers with a diameter of approximately 50 mm and 70 mm respectively.

Clearly there are many other factors that affect the outcome in terms of the likelihood of internal damage. Not least among these will be the part of the tuber which breaks the fall. An end or edge is likely to suffer greater mechanical stress than a flat face.

¶2.4 EXPERIMENTS

¶2.4.1 Potassium fertiliser

Tubers were obtained from four experiments at different sites.

Expt 1. In 1993, cv. Record was grown by staff form CUF, on a site in Nottinghamshire. The crop was planted in a soil of potassium index 3 and treated with three levels of potassium sulphate fertiliser (0, 100 and 200 kg ha^{-1} K_2O equivalent) replicated three times. After lifting at the end of September, samples were transported to Wellesbourne where they were stored at 6°C until impact tested and analysed for other characteristics on 10 November 1993. In this experiment the numbers of tubers tested from each treatment were 45 (0 kg ha^{-1}), and 69 (100 and 200 kg ha^{-1}). The tubers were halved and each half used for impact testing at ambient temperatures (approx 20°C). After ranking for tuber weight, half-tubers were allocated to one of six impact energy levels, 0.23, 0.35, 0.47, 0.59, 0.70 and 0.82 Joules, delivered by a falling bolt. The average response was determined by accumulating data over all impact levels. The incidence of internal damage increased with impact energy with between 40% and 60% of tubers showing damage at 0.35-0.47 Joules.

Expt 2. In 1994, cv Pentland Dell was grown by CUF staff at a site in Hampshire. The crop was planted in a soil of potassium index 1 and treated with four levels of potassium sulphate fertiliser (0, 150, 300 and 600 kg ha^{-1} K_2O equivalent) replicated in three blocks. After lifting at the end of September, samples were transported to Wellesbourne where they were stored at 6°C until 30 November 1994, when they were impact tested. Samples of 30 tubers per treatment (60 impacts on half tubers) were tested at ambient temperatures (approx 20°C) using impact energies of 0.5 and 0.65 Joules delivered by the pendulum.

Expt 3. In 1994, cv. Record was grown at CUF in an experiment examining a factorial combination of potassium fertiliser application rates (0, 100, 200 and 300 kg ha^{-1} K_2O equivalent) and irrigation treatments in a split plot design replicated three times. Potassium treatments were randomized within irrigation treatments. For our examination of the effect of potassium fertiliser on internal damage we used tubers from irrigation treatment W4 only (see Expt 7, section 2.4.3 for further explanation). The crop was planted in a soil of potassium index 5. Two harvests were taken. The first on 2 September 1994 and the second on 29 September 1994 when the crop was finally lifted. On each occasion samples were transported to Wellesbourne where they were stored at 6°C until 4 October 1994 and 24 January 1995 respectively, when impact testing at ambient temperatures (approx 20°C) was done. Samples of 39 tubers (fresh weight 100-200 g) per treatment were tested. These were halved to obtain 78 impacts evenly divided between impact energies of 0.3, 0.5, 0.7 Joules delivered by a pendulum. Samples for DMC and RWC were taken from 13 half tubers used in testing at 0.3 Joules. The same number was randomly taken from those tested at 0.7 Joules for measurement of FS and FT.

Expt 4. In 1996, cv Cara was grown at Wellesbourne on a low fertility site (Wharf Ground), where six different rates of potassium sulphate fertiliser (0, 120, 241, 363, 482 and 723 kg ha^{-1} K_2O equivalent) were applied to a soil with a native potassium concentration of 55 pm (potassium index 0). In addition, plots of potatoes were also planted in a different area of the same field, on a series of native soil potassium gradients set up in 1990. Soil samples were taken from all plots and analysed for nitrate-nitrogen, phosphorus and potassium. Tubers were planted on 14 May and harvested after natural haulm senescence, on 18 November and stored on polystyrene trays in boxes at 4°C. Treatments of potassium freshly applied to plots were fully randomised within three blocks. Plots on established gradients of potassium were systematically arranged within five blocks, of which only three (treatments G3, G4, G5) were harvested for impact testing. Adjacent blocks comprised gradients which ran in opposite directions. Plots in both areas included adequate guards to ensure that intrusion of adjacent treatments into harvested areas was prevented. The crop was regularly irrigated throughout growth.

The haulm of two entire plants per plot were taken on 20 September 1996 as samples for analysis of potassium and other mineral nutrients. Three tubers per plot were taken from store on 14 February 1997 and used collectively to provide samples of tissue for separate mineral nutrient analyses of pith and cortex.

Tubers weighing between 100 g and 200 g were selected for impact testing. Ten tubers per plot from each of the 27 plots were impact tested for the first time on 18 December 1996 at room temperature (approx 20°C). The second occasion was split by block into sessions on 14 April 1997 (block 1) 17 April 1997 (block 2) and 28 April (block 3). For these sessions, tubers were tested at 10°C. On both occasions impact energies of 0.5 Joules were used. Because very little internal damage was caused on the first occasion in December, a preliminary trial of all but the zero K treatment was done with 0.4 Joules and 0.7 Joules on tubers at 10°C and room temperature (approx 20°C) prior to the second series of tests. This indicated that the lower energy level was suitably discriminating, but that a better response was obtained at the lower temperature. The higher energy level resulted in damage to most of the tubers.

Impact characteristics of pendulum head penetration and rebound were measured on one half of each sliced tuber. The other half was used for estimates of tuber firmness RWC and DMC of cortex and whole tuber.

Samples were taken from four tubers each of the 0 kg ha^{-1} and 723 kg ha^{-1} potassium treatments for anatomical assessment. Measurements of about 100 cells for each tuber were made at two depths (approx 0.5 and 3 mm beneath the surface). On 21 April 1997, samples of two tubers per plot for each of treatments 0, 361 and 723 kg ha^{-1} and the three blocks (18 tubers in total) were transferred to Dept of Life Sciences, Nottingham Trent University for analysis of PPO activity.

¶2.4.2 Nitrogen fertiliser

Expt 5. Tubers for this investigation were taken from a crop of cv. Cara grown at CUF in 1993 and treated with 0, 120 and 240 kg ha^{-1} nitrogen fertiliser in an experiment comprising three blocks. Samples were lifted on 1 September 1993 and stored at 6°C until they were tested on 19 and 25 January, 1994.

Thirty-nine tubers (78 halves) per treatment were examined. Eighteen halves were allocated for measurement of mechanical properties. Impact testing was done at room temperature (approx 20°C) on the remaining 60 half-tubers per treatment (20 impacts per energy level) with a falling bolt at impact energies of 0.3, 0.5 and 0.65 Joules. Analysis of susceptibility to internal damage was based on the proportion of damaged tubers accumulated over all test energies.

¶2.4.3 Irrigation
Three experiments were done. Two at CUF, in 1993 and 1994, and one at Wellesbourne, in 1995.

Expt 6. In 1993 tubers of cv. Cara were grown in polythene tunnels to prevent interference from rainfall. There were three treatments, which were, in order of increasing water availability; no irrigation (DRY), irrigation according to a CUF irrigation schedule (CUFIS) and frequent watering (WET). These were replicated within each of the three tunnels. Tubers were harvested on 1 September 1993 and stored at 6°C until 19 January 1994, when they were impact tested at room temperature (approx 20°C). For each treatment 30 tubers (in 100-200 g range) were cut into halves and 45 half-tubers were tested at impact energies of 0.35, 0.59 and 0.82 Joules using a falling bolt (15 per energy level). Samples from these same tubers were also used for estimating DMC and RWC The remaining 15 half tubers per treatment were used for measurement of fracture toughness, tensile strength and apoplast volume. Analysis of susceptibility to internal damage was based on the proportion of damaged tubers accumulated over all test energies.

Expt 7. In 1994, tubers of cv Record were planted at CUF in an unsheltered experiment examining the effect of irrigation and potassium nutrition on dry matter content and yield (see Expt 3, section 2.4.1). Irrigation treatments were as follows: rain-fed only (W1), rain-fed plus irrigation until full crop cover (W2), rain-fed until full crop cover as in treatment W2 and then rain-fed plus irrigation until harvest (W3) and rain-fed plus irrigation throughout (W4). Treatments were fully randomised within three blocks with potassium treatments applied within irrigation plots. In all treatments, except W1, the allowable soil moisture deficit during the "irrigation" phase was 25-30 mm, at which point crops were irrigated with 20 mm of water. Samples for impact testing were taken on two occasions from only those plots which received 100 kg ha^{-1} potassium fertiliser. The first was on 2 September 1994 and the second on 29 September 1994. These were stored at 6°C until they were tested on 20 September 1994 and 13 February 1995 respectively. Forty tubers from each treatment (80 impacts on half-tubers) were impact tested at room temperature (approx 20°C) using the pendulum to deliver energies of 0.3, 0.5 and 0.7 Joules.

Expt 8. In 1995, the following irrigation regimes were imposed on a crop of cv Cara grown under mobile rain shelters: no irrigation (IR1), irrigation until full crop cover (IR2) irrigation from full crop cover to harvest (IR3), and irrigation throughout growth (IR4). Irrigation was provided whenever soil moisture deficits (SMD) exceeded 30 mm for treatment IR4 and for the irrigated periods of IR2 and IR3. For treatment IR1 and unirrigated periods of treatments IR2 and IR3 water was provided when SMDs were greater than 70 mm. The crop grew in the open except when rain was expected when the covers were pushed into place over the crop. Irrigation was provided by seep hose laid between rows. The system was calibrated to deliver specified amounts by timed application. All treatments were replicated and randomised in three blocks. Tubers were lifted on 17 November 1995 and stored at 4°C, until impact tested on 5 December 1995. Samples of 20 tubers per plot (60 tubers per treatment) were taken for estimating susceptibility to internal damage using the pendulum and an impact energy of 0.5 Joules. Of these, samples of ten tubers per plot were used for DMC, RWC, FS, and FT.

¶2.4.4 Development and storage

Commercial potato crops of cv. Wilja, grown at Wellesbourne in 1993 and 1994, were sampled to follow changes in susceptibility to internal damage and other tuber characteristics with crop development and during storage.

Expt 9. In 1993, testing began at 100 days from planting (on 2 April, 1993) and continued through to harvest at 175 days. All samples were hand-dug to reduce the likelihood of mechanical damage. Effects of size on tuber characteristics were taken into account by using tubers in the range 100-200 g at each harvest. Impact testing was done at laboratory temperature (approx. 20°C) by dropping a guided bolt on to individual tubers from heights between 10 and 35 cm above the tubers to accommodate possible differences in response with age. The crop was lifted on 24 September 1993, 175 days after planting and stored in bulk in a straw-insulated clamp in a barn, at ambient temperatures. After 260 days from sowing (85 days after lifting, 21 December, 1993) samples were removed to a store held at 4°C. Testing of the tubers for damage susceptibility and sampling for the other characteristics continued at approximately monthly intervals throughout the winter of 1993/94. Sample sizes varied. For estimating susceptibility to damage, DMC and RWC, between 40 and 60 tubers were taken at all occasions. For FS, FT and AV, sub-samples of between 40 and 45 were taken from these tubers during crop development and 30 during the storage phase.
Susceptibility to internal damage was assessed using a range of impact energies from 0.23 to 0.7 Joules delivered by falling bolt at room temperature. Three energy levels were used on each occasion, but the full range was not always covered. Susceptibility to internal damage was thus expressed as % of internally-damaged tubers interpolated for an impact energy of 0.5 Joules using binomial regression on drop height. Measurement of the following tuber properties were made on samples of tissue from the same tubers as those used in the impact tests: RWC, DMC, FT, FS and AV.

Expt 10. In 1994, the very hot conditions resulted in very rapid growth and a crop that matured very quickly. Timings of samples were based on those of 1993 and as a result only a few samples were taken before the crop was lifted on 6 September 1994. Tubers were stored in a clamp at ambient outdoor temperatures until 20 December 1994, when samples were bagged and placed in a store at 4°C.
Impact testing was done on 40 tubers (100-200g) for each harvest. Respective tuber halves were subjected to falling bolt and pendulum methods at equivalent impact energy of 0.5 Joules. The set of tuber properties measured was the same as in Expt. 9, with the addition of rebound from pendulum testing. These were made on the same tubers as those used in impact testing.

¶2.4.5 Manipulation of tuber water status

In a series of experiments, the water status of potato tubers was deliberately manipulated by drying to reduce tissue turgor or wetting to increase tissue turgor. Tubers were then impact tested and some other tuber properties measured. These manipulations were done on four separate occasions using tubers of several varieties.

Expt 11. In September 1993, tubers of cv Maris Piper (100 - 200 g fresh weight) which had been stored for nearly 12 months at 5°C, were cut in half and eighteen half tubers per treatment left with their cut surfaces in contact with purified water (approx 5 mm deep) for 72, 48, 24 or 0 hours in a polythene enclosure. Contact with water was then removed and the tubers allowed to equilibrate, similarly enclosed, for a further 3 days. Temperature during the entire procedure was 10°C. Tuber halves were removed from the cold room at the end of treatment and impact tested with the falling bolt at an energy of 0.59 Joules. Samples of tubers were taken to estimate RWC and DMC.

Expt 12. In March 1994, tubers of cv Wilja, which had been stored since lifting at the end of September 1993, were subjected to similar rehydration treatments as in Expt 11. There were six soaking treatments: 7, 5, 4, 3, 2, 1 and 0 days and 20 tuber halves were allocated to each treatment. Impacts were delivered by falling bolt at an energy of 0.59 Joules. Samples were taken for estimating RWC and DMC.

Expt 13. In May 1995, tubers of cv Wilja, which had been stored since lifting on 6 September 1994, were used for manipulation of water status. Thirty tuber halves were allocated to each of five treatments for manipulation of water status. Tubers were subjected to soaking, as previously described, for 0, 1 and 3 days or allowed to dry in ambient air conditions for 3 and 7 days prior to impact testing. Impacts were delivered by the pendulum at an energy of 0.5 Joules and rebound angles recorded. Samples of tubers were taken for measuring RWC, DMC and FT.

Expt 14. In January 1996, tubers of cv Cara which had been stored since lifting on 17 November 1995, were subjected to 0, 3 and 7-day soaking periods and 3 and 7-day drying periods. Thirty-two tuber halves were allocated per treatment and impact tested with the pendulum at an energy of 0.5 Joules. Samples of tubers were taken for measuring RWC, DMC and FT, FS and WP.

¶2.4.6 Variation in cell morphometric properties

Expt 15. In 1994, tubers of cv Record were planted in pots on 14 April and grown in a glasshouse/polytunnel until 17 October when they were lifted and stored at 10°C. Plants of both treatments were well watered during early growth to ensure that sound productive plants were produced. During this time, compost was regularly added to the pots to simulate earthing up as the stems elongated. Once tuberization had begun, half of the pots were hand-watered frequently, when the compost appeared dry, and half were hand-watered only when the plants showed visible signs of wilting. On 21 March, 30 tubers of each treatment were subjected to impact of 0.5 Joules from a pendulum. Ten tubers from each of the two treatments were used in preparing samples for anatomical study. Measurements of cell dimensions were made on over 10,000 cells taken from 10 layers representing a 5 mm depth beneath the tuber surface. Cell wall measurements were made on 350 cells over the same region.

¶2.4.7 Tuber size and internal damage

Tubers of cv. Wilja which had been stored in an outdoor clamp at ambient temperatures from 24 September 1993 were removed to storage at 4°C on 21 December 1993. On 23 February 1994, tubers were individually weighed, graded and sub-sampled by weight selection into three categories (small, medium and large).

Impact testing was done at room temperature (approx 20°C) with a falling bolt inflicting impacts of 0.35, 0.59 and 0.82 Joules. For each impact energy, 24 half-tubers (from 12 tubers) per size-class were tested, giving a total of 216 impacts on 108 tubers.

¶2.5 METHODS

¶2.5.1 Storage

Unless stated otherwise, tubers were lifted by hand and placed on polystyrene trays in cardboard apple boxes for subsequent transport and storage. This was done to minimize accidental damage to the tubers before impact testing. Storage was usually between 4°C and 10°C.

¶2.5.2 Impact testing

Information on impact testing relevant to most experiments is recorded here. Specific details are given with each experiment. Except where stated otherwise, all impact testing was carried out at room temperature (approx. 20°C) on tubers from cold store which had been allowed to equilibrate prior to testing. Tubers were weighed prior to testing and samples taken from those with weights of between 100-200 g. If more than one impact energy was to be used, tubers were ranked by weight and representatives of similar weight randomly allocated to groups which were to be impacted at different impact energies (drop heights or angles). Testing at different impact energies was an important feature, particularly in the earlier experiments, since it is not possible to know prior to testing what energies will be suitably discriminating between susceptible and resistant tubers. This procedure was used less in some of the later experiments as our experience increased. Results are presented as averages over the energy levels used. Prior to impact testing tubers were halved along their length and usually both halves were impact tested. RWC and DMC were assessed using cores from one half of each tuber. Samples from unimpacted parts of the other half were saved for measurement of FS, FT, AV and water and solute potential as appropriate.
Impact testing was done either with a falling bolt (earlier experiments) or the pendulum.

¶2.5.2.1 Falling bolt

This comprised a 239 g coach bolt moving in a vertical, clear plastic tube. The tube acted as a guide to ensure that the bolt did not stray off course once released. It could be raised or lowered to accommodate tubers of different size and was marked with various distances from its lower end so that release height was determined with reference to the tuber surface. Impact energy (in Joules) was calculated as the product of bolt mass, height above the tuber surface and acceleration of gravity (assumed to be 9.81 ms^{-2}).

¶2.5.2.2 Pendulum

The pendulum was designed and made by Mr Paul Springer of HRI Technical Services, in collaboration with Dr Tony McGarry, in 1994. In 1996, further development was done by HRI Technical Services to enable instrumentation of the pendulum. Mechanical modifications for this were designed and made by Mr Steven Coggins. Electronic specification, development and installation was done by Mr Martin Holdsworth.
The pendulum used to test for susceptibility to internal damage was specifically designed to ensure that each tuber received only one impact and that the rebound of the head was measured (Figure 16). The construction of the arm and striking head

determined that the pendulum was compound in type. As a consequence, it was necessary to estimate the moment of inertia of the pendulum arm from the masses and locations of its components. This enabled the estimation of an "effective length", which was shorter than the actual length of the pendulum arm. The implications of this were taken into account in calculating impact forces and kinetic energies. Rationalisation of theoretical calculations and the operation of the pendulum in practice was achieved by measuring the speed of the head over the final 16 mm of its travel before impact using a photoelectric device built by Chemical Engineering Dept, Birmingham University. Much of the theoretical physics related to this was carried out by Mr Nick Parsons. For work done in 1996 only, the pendulum was upgraded with instrumentation to record the movement of the arm from release to rebound. A rotary potentiometer was linked via a toothed belt to the fulcrum of the pendulum arm enabling the angle from vertical to be measured as a voltage. This was recorded using proprietary interfacing hardware (Amplicon 226) and software (Signal Centre 2). This system permitted the depth of penetration of the head into the tuber to be recorded and more precise and reliable records of rebound. Complete traces of arm movement during impact were saved for further analysis if required.
Impact energy was calculated as the product of the moment of inertia of the compound pendulum arm, acceleration of gravity and cosine of starting angle, while allowing for the distance from centre of mass to the axis of rotation and for the angle between the centre of mass and the vertical at impact.

¶2.5.3 Assessment of internal damage
After impact, half-tubers were incubated at room temperature (approx. 20°C) for 2 days for the response to develop. Assessment determined the presence or absence of visible internal damage and included measurement of the maximum length and breadth of damage in slices taken successively from the outside of each tuber. The depth of damage was measured as the collective thickness of slices showing damage. Volume of damage was estimated from these measurements. Descriptive comments of each damage response were also made.

¶2.5.4 Relative water content (RWC) and dry matter content (DMC)
RWC is the weight of water present in tissue before incubation in pure water, relative to that present after incubation in pure water. It is assumed that tissue incubated in water will reach full turgor, so RWC gives an indication of the turgidity of tissue. In all experiments prior to 1996, cores (15 mm diameter) of tuber taken from a tuber which had been impact-tested, were sliced (approx. 3 mm thick), weighed, incubated in water for 24 h at room temperature and then reweighed. These cores would thus have included tissue from both pith and cortex.
DMC of this same tissue was estimated from the weight of this tissue after it had been oven-dried for more than 24 h at 90°C and the original fresh weight.
For experiments in 1996, RWC was estimated using three 3 mm thick disks per tuber of cortex tissue only. These were sliced from 9 mm cores of the complete half-tuber and incubated for 24 hours at 5°C in pure water. Measurements of fresh and dry weights were done, as above, to give RWC and DMC for the cortical tissue only.
One unsliced core was retained, weighed and dried for estimation of "tuber" DMC.

¶2.5.5 Water potential (WP)
Water potential was measured by dewpoint hygrometry of tuber cortex tissue using Wescor C52 chambers. A 3 mm thick disc taken from the cortical region of a 9 mm diameter core of tuber was placed in each chamber and equilibrated for 3 hours before measurement.

¶2.5.6 Apoplast volume fraction (AV)
This is an estimate of the volume fraction occupied by extracellular material and, where air spaces are very small and sparse, is an approximation of the cell wall fraction. It was estimated by cutting two discs of tuber tissue (7 mm diameter by 1 mm thickness) from the cortex of tubers and incubating them at <5°C for 2-4 h in a solution of radioactive mannitol of known activity. Mannitol does not readily penetrate the cell membrane and the low incubation temperature ensures minimal metabolic activity. The radioactivity and weights of the discs were measured and the fraction calculated as the ratio of radioactive concentration in the discs to that of the solution.

¶2.5.7 Failure stress (FS)
Failure stress indicates the collective strength of the tissue sampled. It is the force per unit cross-sectional area (MPa) required to break the specimen. This was measured on a piece of tuber tissue (20-22 mm long by 2 mm square section) taken from the cortical region. The length of the test piece ran parallel to the surface of the tuber in a heel-to-rose-end direction. The ends of this tissue were glued to a card to give an actual specimen length of 17.5 mm and a 1 mm notch made in the central region of the sample. It was then subjected to tension imposed at a constant rate of 1 mm min^{-1} by an Instron mechanical tester, until the test piece broke. Stress was estimated from the load at failure and the cross-sectional area of the test piece.

¶2.5.8 Fracture toughness (FT)
Fracture toughness measures the energy required to achieve crack propagation through a tissue and is expressed as Joules m^{-2}. Very brittle material will tend to have low energy and is therefore not "tough". Toughness was measured on a block of cortical tuber tissue (5x5x3 mm) in which the longer dimensions ran parallel to the surface of the tuber. The test piece was placed under a wedge (angle, 30°) which was driven into it at a constant speed of 1 mm min^{-1} by an Instron mechanical tester, until stable crack propagation occurred ahead of the wedge. The initial stage of the process prior to crack propagation, when the tissue was being separated by the wedge and energy was being stored in the flanks of the block, was ignored. Energy required to achieve fracture was calculated from the stable portion of the trace which occurred after this stage.

¶2.5.9 Tuber firmness
Half tubers of which the other half had been used for impact testing, were subjected to surface compression at a rate of 1 mm min^{-1} with an 8 mm Magness-Taylor tool fitted to an Instron materials tester cross-head. The tool was driven into the uncut surface of tubers placed cut-side down on a firm support table, until a load of 30 N was achieved. The probe was then withdrawn. This procedure generally led to a displacement of no more than 2 mm and did not result in visible surface damage. Estimates of tissue displacement were taken at compression loads of 10 N, 20 N and

30 N. The greater the displacement, the less firm is the tissue.

¶2.5.10 Mineral analysis.

Tuber samples from cortex and pith were oven-dried at 90 °C and milled to a fine powder. Haulm samples were oven-dried at 105 °C, broken, milled and sub-sampled. Soil samples were air-dried and ground to <2 mm particle size. Analyses for nitrogen, phosphorus, potassium, calcium and magnesium were done by HRI's analytical laboratory at Wellesbourne.

¶2.5.11 Anatomical studies.

Samples were taken from the outer 6 mm of tubers and fixed in buffered glutaraldehyde solution. After dehydration in an ethanol series, they were infiltrated with L.R.White's resin, again through a stepped concentration series, and cured in an oven at 60°C. Sections were prepared on a microtome at 5-10μ, dried and adhered to slides on a heater and stained with methylene blue and safranin. Images were captured using a Datacell Mirager system and measurements made using Optimas image analysis software.

Tissue samples from irrigation Expt 15 (watering treatment) were examined as two 3 mm segments arranged in a profile which was normal to the tuber surface. The profile was charted by viewing successive fields (approximately 0.75 mm in length) and counting at least 30 cells for each position. The total number of cells in this database was 10,600. Tissue samples from Expt 4 (potassium) were sectioned parallel to the tuber surface at two depths (0.5-1 mm and 3 mm) and 752 cells were measured.

¶2.6 PUBLICATIONS

McGarry, A., Hole, C.C., Drew, R.L.K. and Parsons, N. (1996). Internal damage in potato tubers: a critical review. Post Harvest Technology. **8**, 239-258

Hole, C. C., Drew R. L. K. and Parsons, N.R. (1996) Relationships between internal damage in tubers and tuber properties as affected by agronomic factors. In Abstracts of Conference Papers. 13th Triennial Conference of European Association for Potato Research, 14-19 July, Veldhoven, The Netherlands.

¶2.7 PRESENTATIONS

Hole, C.C. Bruising and tuber damage. Workshop session, 4th Annual Cambridge Potato Conference of CUPGRA, 15/16 December 1993.

Hole, C.C. Control of bruising. Workshop session, 6th Annual Cambridge Potato Conference of CUPGRA . 11/12 December, 1995.

Hole, C.C. Field Factors affecting bruising. Research for your future. A Conference for Potato Growers and the Industry organised by the Potato Marketing Board. Keele Conference Park, 22 April 1996.

Hole, C.C. Agronomy, tuber physical properties and susceptibility to bruising. Potato Marketing Board Workshop on Bruising and damage, NIAB Cambridge, 8 July, 1996.

Hole, C. C. Relationships between internal damage in tubers and tuber properties as affected by agronomic factors at the 13th Triennial Conference of European Association for Potato Research, 14-19 July, 1996 Veldhoven, The Netherlands.

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Table 1. Effect of potassium fertiliser on susceptibility to internal damage and other tuber properties. Expts 1 and 2.

Expt	Tuber property	Rate of potassium fertiliser application, kg ha^{-1} K_2O					lsd p=0.05
		0	100	150	200	600	
Expt 1	**Internal damage %**	**70**	**59**		**56**		12.8
Soil K index = 3	DMC %	25.9	24.7		24.7		0.69
	RWC %	85.4	83.7		86.4		0.89
	AV %	14.1	14.4		14.6		2.29
	FT J m^{-2}	360	390		367		57.7
	FS MPa	0.55	0.54		0.56		0.09
	K conc	1.1	1.2		1.2		0.12
	Org-N conc %	1.0	1.1		1.0		0.20
	P conc %	0.24	0.27		0.23		0.031
	Ca conc %	0.022	0.028		0.020		0.0052
	Mg conc %	0.074	0.083		0.072		0.0105
Expt 2	**Internal damage %**	**63**		**47**	**47**	**40**	17.6
Soil K index = 1	DMC %	23.6		23.6	23.6	23.0	0.6
	RWC %	82.8		82.7	80.7	81.7	0.8
	WP MPa	-1.3		-1.3	-1.4	-1.3	0.14
	AV %	20.5		20.8	18.5	18.5	2.84
	FT J m^{-2}	384		354	348	355	26.7
	FS MPa	0.46		0.48	0.44	0.47	0.04
	K conc %	2.3		2.1	2.3	2.2	0.54
	Rebound,°	14.6		15.0	15.3	15.6	0.28

Expt 1. Internal damage was estimated as the proportion of tubers showing damage accumulated over impact tests with falling bolt at a range of energies (0.23, 0.35, 0.47, 0.59, 0.70 and 0.82 Joules).
Expt 2. Internal damage was inflicted using a pendulum and estimated as the proportion of tubers showing damage accumulated over energies of 0.3. 0.5, and 0.7 Joules.
Mineral nutrient concentrations are for tuber tissue

Table 2. Effect of potassium fertiliser on susceptibility to internal damage and other tuber properties. Expt 3.

Harvest	Tuber property	Rate of potassium fertiliser application, kg ha^{-1} K_2O				lsd p=0 05
		0	100	200	300	
Harvest 1	**Internal damage %**	**52**	**42**	**51**	**37**	12.5
	Volume* cm^3	0.49	0.37	0.55	0.55	0.134
Soil K index	DMC %	24.1	24.6	23.5	24.4	0.96
= 5	RWC %	84.5	83.3	85.9	83.9	1.23
	WP MPa	-0.81	-0.86	-0.76	-0.78	0.067
	AV %	*	*	*	*	*
	FT J m^{-2}	439	429	458	454	48.2
	FS MPa	0.62	0.57	0.58	0.54	0.07
	Rebound,°	13.8	13.8	13.6	13.7	0.21
	K conc %	2.6	2.6	2.6	2.6	0.15
	Org-N conc %	1.3	1.2	1.5	1.2	0.18
	P conc %	0.23	0.23	0.23	0.24	0.061
	Ca conc %	0.025	0.025	0.025	0.030	0.0065
	Mg conc %	0.095	0.101	0.089	0.097	0.0041
Harvest 2	**Internal damage %**	**63**	**56**	**71**	**49**	12.0
	Volume* cm^3	1.01	0.65	0.85	0.80	0.200
Soil K index	DMC %	23.2	22.1	23.4	23.4	1.20
= 5	RWC %	85.2	84.1	87.3	84.6	1.23
	WP MPa	-1.4	*	*	-1.4	0.08
	AV %	19.3	*	*	19.6	2.08
	FT J m^{-2}	426	399	406	434	39.4
	FS MPa	0.51	0.47	0.48	0.48	0.04
	Rebound °	14.5	14.7	14.9	14.8	0.20
	K conc %	2.4	2.5	2.4	2.6	0.21
	Org-N conc %	1.2	1.4	1.5	1.6	0.13
	P conc %	0.26	0.30	0.22	0.28	0.049
	Ca conc %	0.037	0.033	0.029	0.032	0.0052
	Mg conc %	0.082	0.102	0.106	0.118	0.0123

Internal damage was inflicted using a pendulum and estimated as the proportion of tubers showing damage accumulated over impact energies of 0.3. 0.5, and 0.7 Joules.
Mineral nutrient concentrations are for tuber tissue.
* 'Bruise' volume

Table 3. Effect of potassium fertiliser on susceptibility to internal damage and other tuber properties. Expt 4.

Tuber property	Potassium treatment, kg ha^{-1} K_2O (where appropriate)									lsd (p=0.05)
	0	120	241	361	482	723	G3	G4	G5	
Stored for 39 days										
Internal damage %	**17**	**7**	**10**	**17**	**0**	**7**	**40**	**10**	**17**	**16.9**
Volume* cm^3	*	*	*	*	*	*	*	*	*	*
DMC of tuber %	19.8	19.6	20.2	21.7	20.6	22.3	20.1	20.8	20.7	1.00
DMC of cortex %	22.3	22.1	22.7	24.0	23.2	24.4	21.7	22.5	22.9	1.11
RWC %	82.7	82.2	81.7	81.4	80.4	80.8	80.1	78.5	78.4	0.62
Firmness mm	1.37	1.37	1.33	1.35	1.37	1.41	1.34	1.32	1.35	0.041
Deformation, mm	5.89	5.96	5.82	5.89	5.82	5.89	5.96	5.82	5.89	0.090
Rebound °	16.3	16.3	16.1	16 0	16.4	16 7	16.1	16.2	16.4	0.43
Stored for 110 days										
Internal damage %	**80**	**73**	**77**	**67**	**83**	**77**	**80**	**73**	**70**	**21.9**
Volume* cm^3	0.70	0.69	0.67	0.75	0.63	0.88	0.79	0.82	1.24	0.398
DMC of tuber %	18.5	18.5	19.1	20.4	19.7	20.9	18.9	20.5	20.1	1.14
DMC of cortex %	22.1	21.5	23.0	23.8	23.8	24.9	22.1	24.0	22.8	1.26
RWC %	77.0	76.3	76.1	75.3	75.9	74.4	75.4	74.2	74.3	0.98
Firmness mm	1.71	1.69	1.63	1.70	1.68	1.84	2.02	1.81	1.85	0.113
Deformation, mm	5.98	5.93	5.93	5 93	5.92	6.02	6.16	5.98	6.08	0.136
Rebound °	15.1	15.3	15.1	15.1	15.1	15.2	15.0	14.9	15.2	0.30
Soil K ppm	57	67	62	86	72	110	85	108	183	30.5
Plant K %	1.63	1.6	1.4	1.7	2.2	2.2	3.9	4.6	5.3	1.09
Tuber cortex:										
K %	2.00	2.18	2.01	1.99	2.26	2.19	2.60	2.85	3.11	0.487
P %	0.47	0.43	0.40	0.40	0.39	0.36	0.41	0.44	0.44	0.077
Org N %	1.75	1.37	1.48	1.28	1.25	1.18	1.27	1.17	1.27	0.470
Ca %	0.062	0.045	0.050	0.046	0.051	0.041	0.060	0.052	0.054	0.0161
Mg %	0.082	0.083	0.077	0.086	0.086	0.094	0.112	0.118	0.131	0.0212
Na %	0.113	0.117	0.103	0.091	0.114	0.073	0 162	0.159	0.118	0.0644

* 'Bruise' volume. Mineral nutrient concentrations are for tuber tissue.

Firmness is for displacement of tuber surface by 30N load. Larger values represent softer tissues.

Impact testing was done at 0.5 Joules and temperatures of approx. 20°C and 10°C for 1st and 2nd occasions respectively. See text for further comment.

Table 4. Effect of nitrogen fertiliser on internal damage and other tuber properties. Expt 5.

Tuber property	Rate of nitrogen fertiliser application, kg ha^{-1}			
	0	120	240	lsd (p=0.05)
Internal damage %	**52**	**45**	**18**	16.3
DMC %	23.2	23.6	21.2	0.98
RWC %	73.7	74.5	74.6	0.99
AV %	15.2	16.4	15.0	2.27
FT J m^{-2}	383	362	381	62.5
FS MPa	0.49	0.51	0.52	0.053
K conc %	2.5	2.7	2.9	0.29
Org-N conc %	0.85	0.86	0.94	0.319
P conc %	0.37	0.40	0.38	0.051
Ca conc %	0.033	0.038	0.037	0.0065
Mg conc %	0.097	0.100	0.099	0.0130

Internal damage was estimated as the proportion of tubers showing damage accumulated over impact tests with falling bolt at energies of 0.3, 0.5 and 0.65 Joules.

Table 5. Effect of irrigation (no rainfall) on internal damage and tuber properties. Expt 6.

DRY - No irrigation at all, CUFIS - Irrigation by CUF schedule, WET - frequent irrigation

Tuber property	Irrigation treatment			lsd p=0.05
	DRY	CUFIS	WET	
Internal damage %	**82**	**36**	**36**	16.2
DMC %	25.6	21.5	21.2	0.94
RWC %	77.9	80.4	82.0	2.22
AV %	11.2	10.0	13.5	1.42
FT J m^{-2}	346	440	437	53.6
FS MPa	0.53	0.68	0.60	0.066
K conc %	1.96	1.73	1.86	0.130
Org-N conc %	1.47	0.70	1.19	0.339
P conc %	0.40	0.41	0.42	0.027
Ca conc %	0.014	0.033	0.020	0.0060
Mg conc %	0.099	0.102	0.107	0.0153

Internal damage was estimated as the proportion of tubers showing damage accumulated over impact tests with falling bolt at energies of 0.35, 0.59 and 0.82 Joules.
Mineral nutrient concentrations are for tuber tissue.

Table 6. Effect of irrigation (+rainfall) on internal damage and tuber properties. Expt 7.

Tuber property	Irrigation treatment				lsd p=0.05
	W1 (Rain only)	W2 (Rain + early irrigation)	W3 (Rain + late irrigation)	W4 (Rain + irrigation throughout)	
HARVEST 1					
Internal damage %	**65**	**60**	**58**	**62**	9.4
Volume† cm^3	0.78	0.94	0.73	0.76	0.171
DMC %	24.3	27.1	23.7	24.5	0.94
RWC %	83.6	77.3	86.1	85.5	1.78
WP MPa	-0.76	-0.89	-0.79	-0.83	0.075
AV %	12.8	12.1	13.0	13.6	1.27
FT J m^{-2}	508	454	491	514.6	52.3
FS MPa	0.61	0.64	0.66	0.67	0.068
Rebound °	14.7	14.2	15.1	15.1	0.27
K conc %	2.6	2.5	2.5	2.6	0.16
Org-N conc %	1.3	1.4	1.2	1.4	0.15
P conc %	0.25	0.25	0.21	0.25	0.027
Ca conc %	0.025	0.022	0.030	0.031	0.0035
Mg conc %	0.095	0.098	0.096	0.088	0.0076
HARVEST 2					
Internal damage %	**72**	**76**	**67**	**63**	13.6
Volume† cm^3	0.92	1.00	0.83	1 09	0.182
DMC %	23.8	25.7	22.7	23.5	1.55
RWC %	80.1	76.0	82.9	82.0	2.01
WP MPa	*	-1.6	*	-1.4	0.17
FT J m^{-2}	431	425	445	436	49.4
FS MPa	0.49	0.50	0.50	0.54	0.043
Rebound °	13.5	13.1	13.8	14.0	0.28
K conc %	2.5	2.5	2.6	2.5	0.28
Org-N conc %	1.5	1.4	1.3	1.4	0.35
P conc %	0.22	0.23	0.24	0.30	0.043
Ca conc %	0.031	0.026	0.029	0.033	0.0059
Mg conc %	0.089	0.086	0.104	0.102	0.0182

Internal damage was inflicted using a pendulum and estimated as the proportion of tubers showing damage accumulated over impact energies of 0.3. 0.5, and 0.7 Joules

Mineral nutrient concentrations are for tuber tissue.

† Bruise volume

Table 7. Effect of irrigation (no rainfall) on internal damage and tuber properties. Expt 8.

Tuber property	Irrigation treatment				LSD p=0.05
	IR1 (Dry)	IR2 (Wet/Dry)	IR3 (Dry/Wet)	IR4 (Wet)	
Internal damage %	**63**	**42**	**52**	**45**	17.8
Volume, cm^3	0.54	0.36	0.43	0.37	0.239
DMC %	18.4	17.5	18.7	17.9	1.01
RWC %	74.9	74.3	74.8	74.4	0.77
FT J m^{-2}	300	305	319	313	33.6
FS MPa	0.71	.70	0.68	0.68	0.025
Rebound °	15.7	15.7	15.5	15.6	0.23

Impact tested with pendulum using energy of 0.5 Joules
Mineral nutrient concentrations are for tuber tissue

Table 8. Correlation between susceptibility to internal damage and single variables.

Tuber property	% variance accounted for	Correlation coefficient, r	Significance
Dry matter content %	15.6	0.43	$p < 0.050$
Relative water content %	7.9	0.33	NS
Fracture toughness Jm^{-2}	3.5	0.26	NS
Failure stress MPa	0	-0.19	NS
Apoplast volume fraction %	0	0.18	NS

Data from Expts 1, 2, 3, 5, 6 & 8.

% internal damage normalised to 0.5 Joules and all % variables subjected to angular transformation.

Table 9. Association of variables with susceptibility to internal damage - multiple regression

Regression model	Variance accounted for, %	Variance ratio	Significance of change
DMC + RWC + FS + FT	56.7	10.2	-
RWC + FS + FT [DROP DMC]	30	10.1	$p < 0.01$
DMC + FS + FT [DROP RWC]	52.7	3.0	NS
DMC + RWC + FS [DROP FT]	31.2	9.9	$p < 0.01$
DMC + RWC + FT [DROP FS]	22.9	11.5	$p < 0.01$

Data from Expts 1, 2, 3, 5, 6 & 8

% internal damage normalised to 0.5 Joules and all % variables subjected to angular transformation.
Data for AV not included because it was collected from fewer tubers than other variables and showed little correlation - see Table 8.

Table 10. Correlation between susceptibility to internal damage and single variables.

Tuber property	% variance accounted for	Correlation coefficient, r	Significance
Dry matter content %	34.2	-0.61	$p < 0.001$
Relative water content %	36.7	0.63	$p < 0.001$
Fracture toughness Jm^{-2}	4.5	0.30	NS
Failure stress MPa	0	-0.12	NS
Apoplast volume fraction %	0	-0.04	NS
Rebound angle,°	0	-0.13	NS

Data from Expts 9 & 10. Internal damage normalised to 0.5 Joules

Table 11. Summary of cell morphometry for tubers of well-watered and poorly-watered plants. Expt 15.

Treatment	WET	DRY	lsd (p=0.05)
<u>Cell variables</u>			
Area μm^2	10,544	10,387	2,032
Breadth µm	99.2	99.3	9.2
Length µm	142.1	141.5	12.2
Perimeter µm	399.0	393.9	29.2
Circularity (circle = 12.6)	18.8	18.0	1.08
<u>Cell wall variables</u>			
Thickness			
"skin" layer	1.89	1.93	0.15
"below "skin"	2.10	1.90	0.07
<u>Tuber variables</u>			
DMC %	21.7	22.0	1.52
RWC %	71.9	70.7	2.18
Rebound °	14.3	14.6	0.5
Internal damage	0	0	-

Table 12. Effect of tuber mass on susceptibility to internal damage determined by pendulum: Incidence and dimensions of internal damage.

Tuber class	Small (80-100g)	Medium (130-180g)	Large (200-280g)	lsd ($p<0.05$)
Internal damage %	56	50	46	14.8
Damage volume cm^3	0.33	0.32	0.20	0.112
Curvature m^{-2}	540	370	270	145
Correlation coefficients	Damage vs	Tuber size	-0.068	
	Damage volume vs	Tuber size	-0.130	

Figure 1. Relationship between soil potassium concentration (measured in 1997) and concentration expected from calculation for plots to which fertiliser was applied in Expt 4. Line illustrates 1:1 relationship.

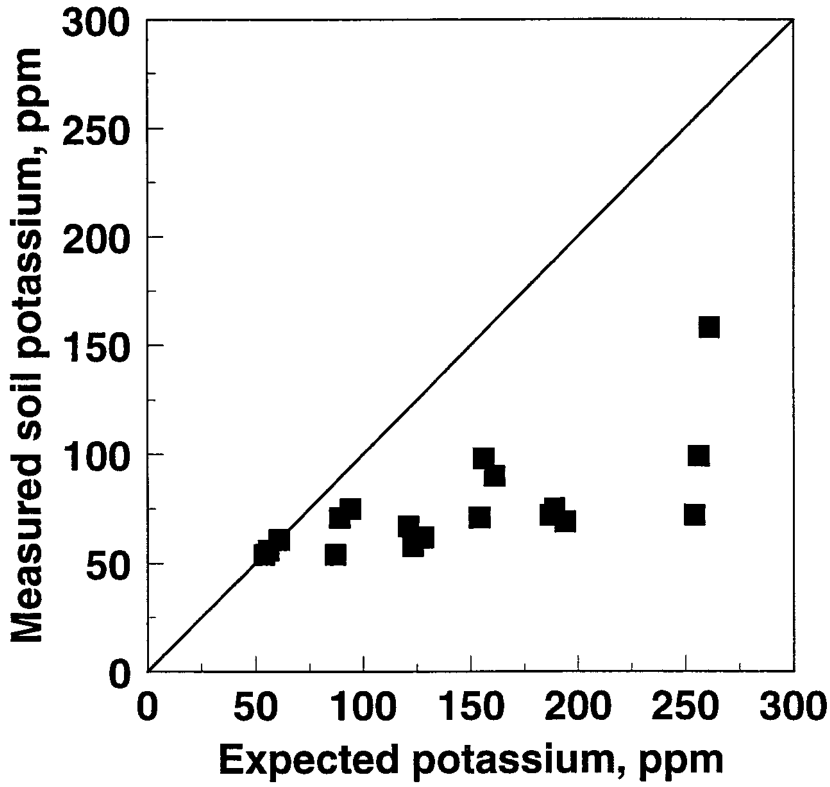


Figure 2. Variation in haulm and tuber potassium concentrations with soil potassium concentrations for treatments in Expt 4. Treatments for gradient plots which were set up in 1990 are identified (G3, G4, G5). Unlabelled points represent applied fertiliser treatments. □, haulm potassium; ● tuber cortex potassium.

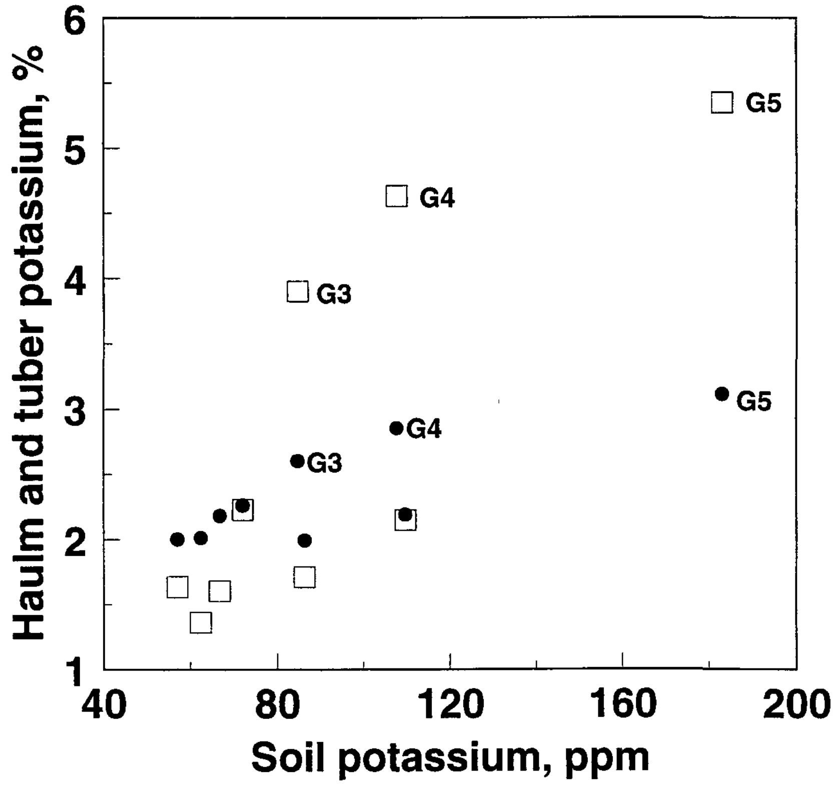


Figure 3. Tuber cortex dry matter content versus a) soil, b) haulm and c) tuber cortex potassium concentrations. DMC measured on two occasions [■,18 December 1996; □,17 April 1997] : Expt 4. Treatments for gradient plots which were set up in 1990 are identified. Unidentified points represent applied fertiliser treatments.

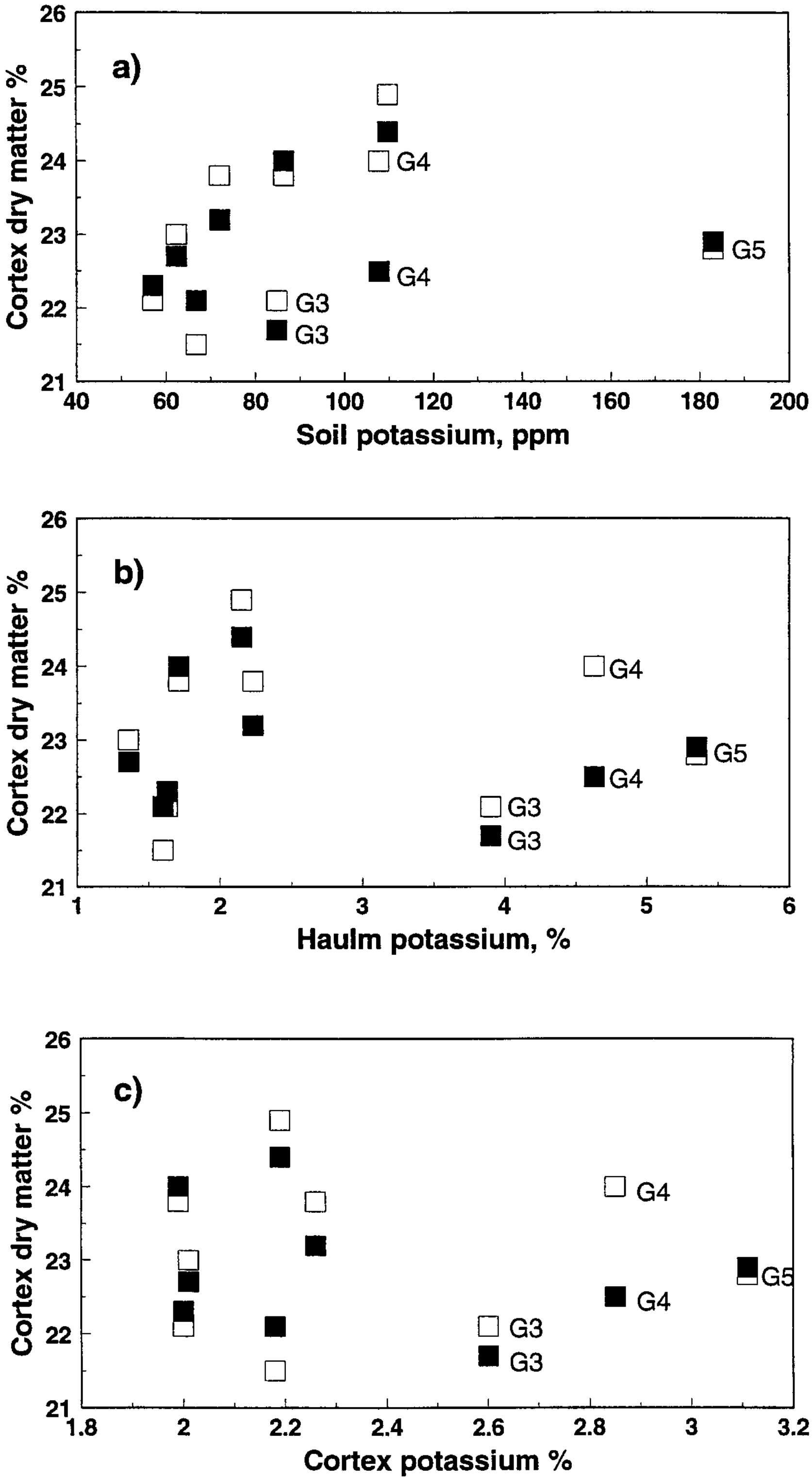


Figure 4. Trends in soil moisture deficits during the growing period for the four treatments of Expt 8.

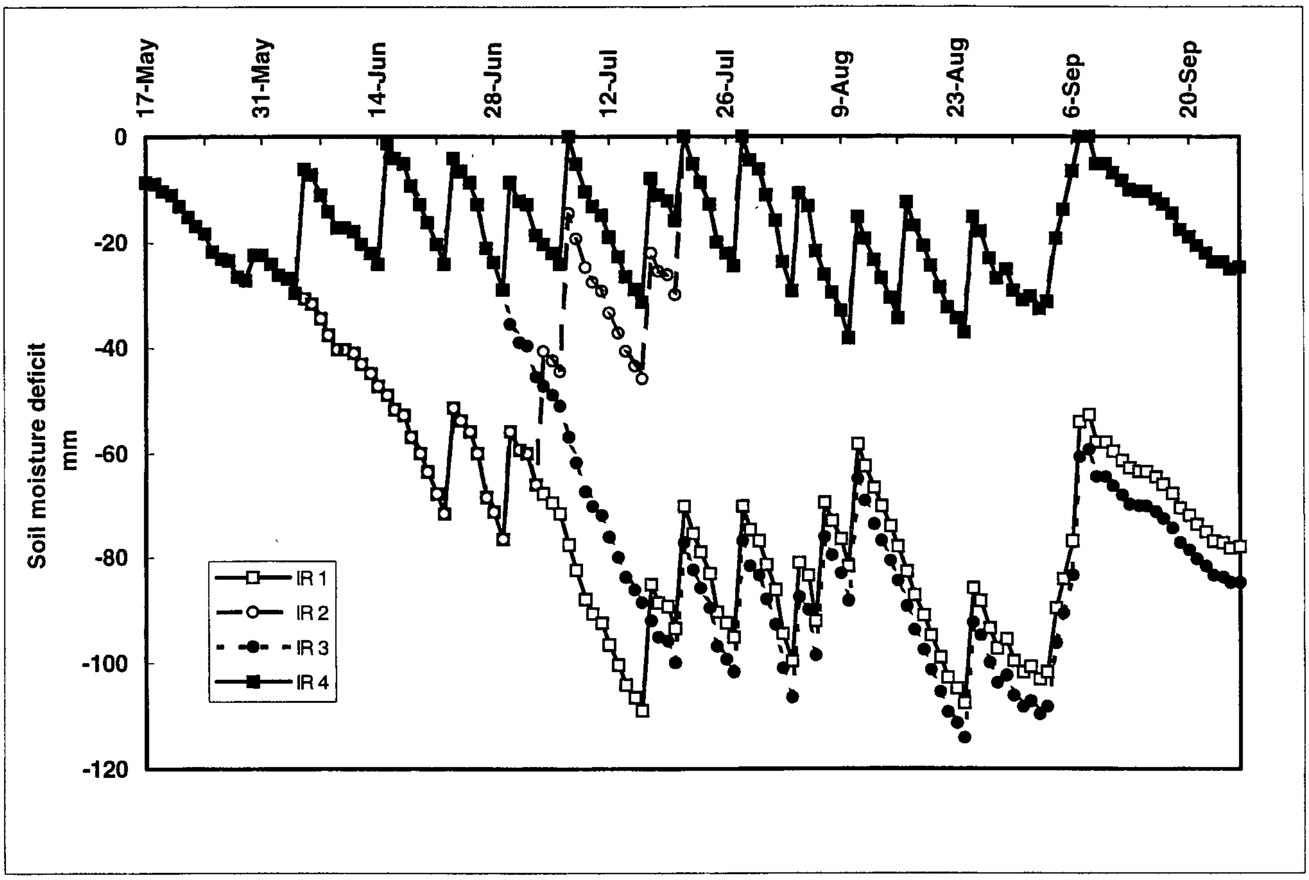
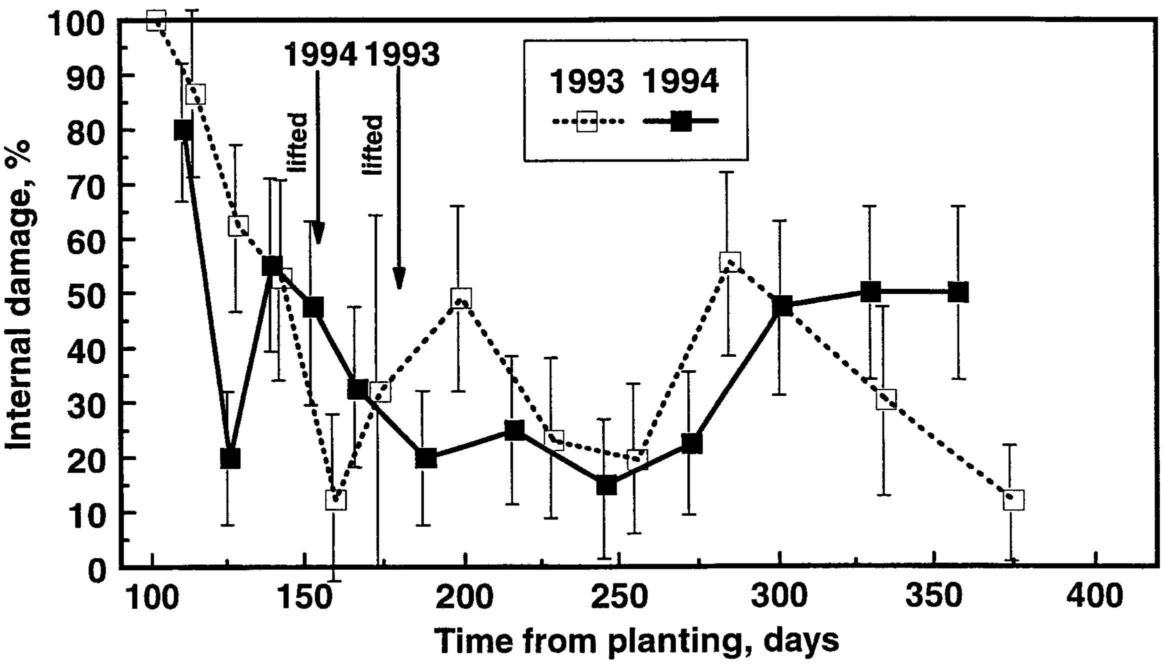


Figure 5. Changes in a) susceptibility to internal damage and b) volume of damage zone, during development and storage of cv. Wilja tubers. (Expts 9 and 10.)
Means are based on damage estimated at 0.5 Joules impact energy.In a), bars show 95% confidence limits estimated from binomial regression. In b), they show lsd (p=0.05) for comparing means within years.

a)



b)

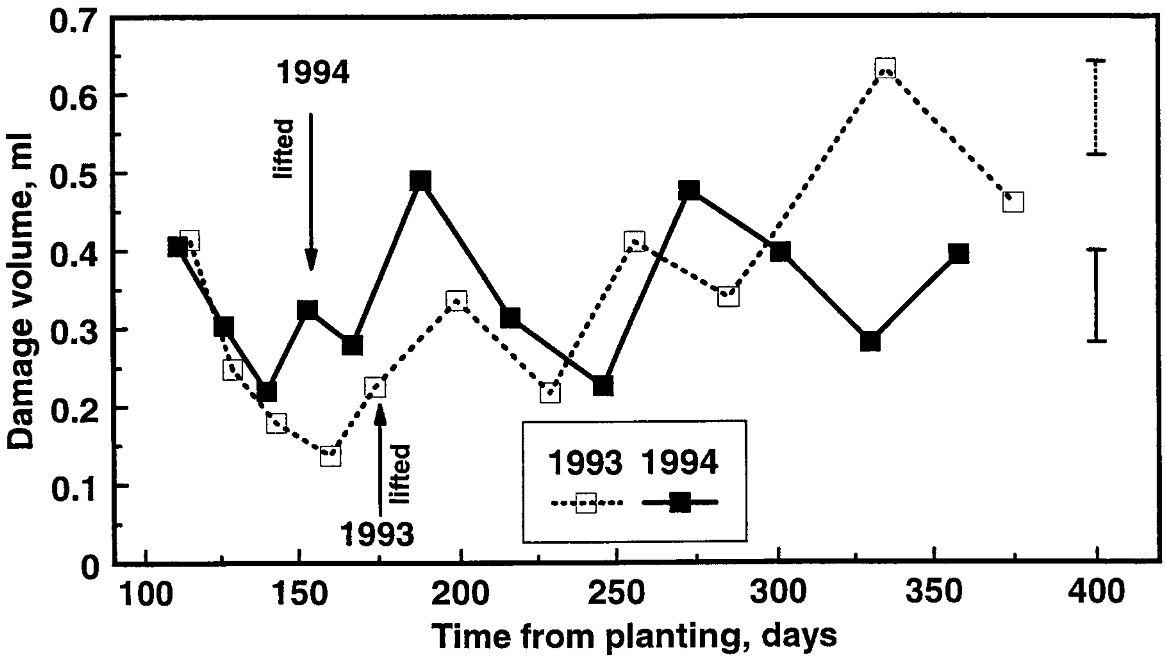


Figure 6. Changes in dry matter and relative water contents during development and storage of cv. Wilja tubers. (Expts 9 and 10.)
Bars show lsd (p=0.05) for comparison between harvest means within a year.

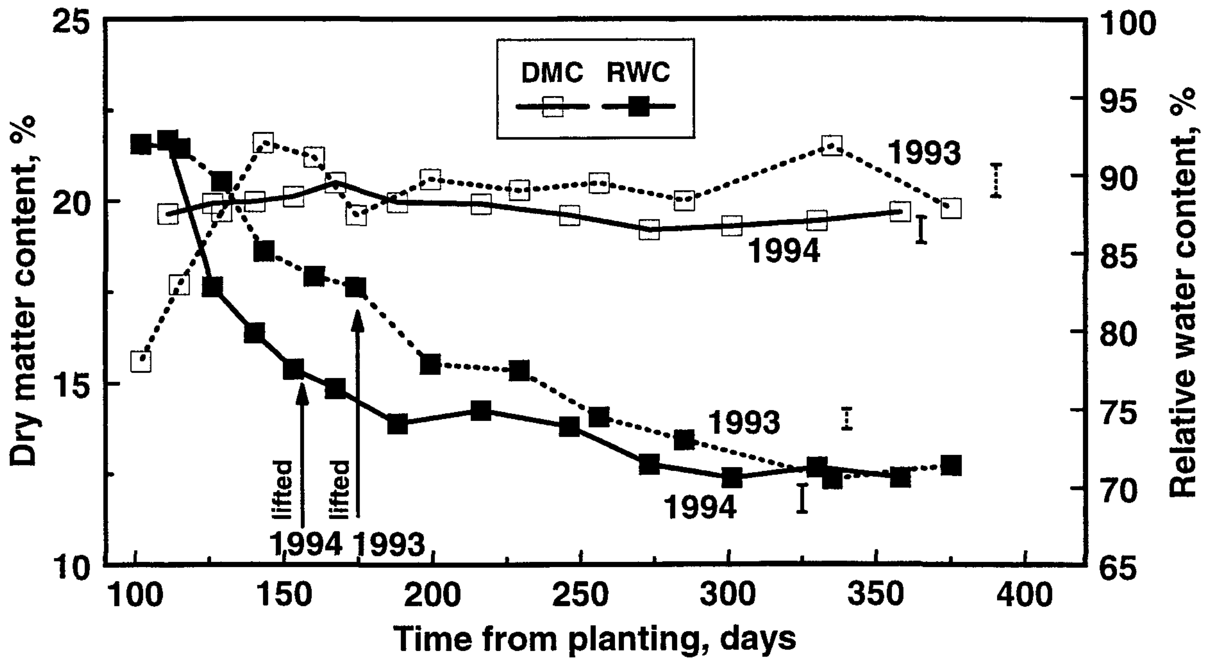


Figure 7. Failure stress and fracture toughness during development and storage of cv. Wilja tubers. (Expts 9 and 10.)
Bars show lsd (p=0.05) for comparison between harvest means within a year.

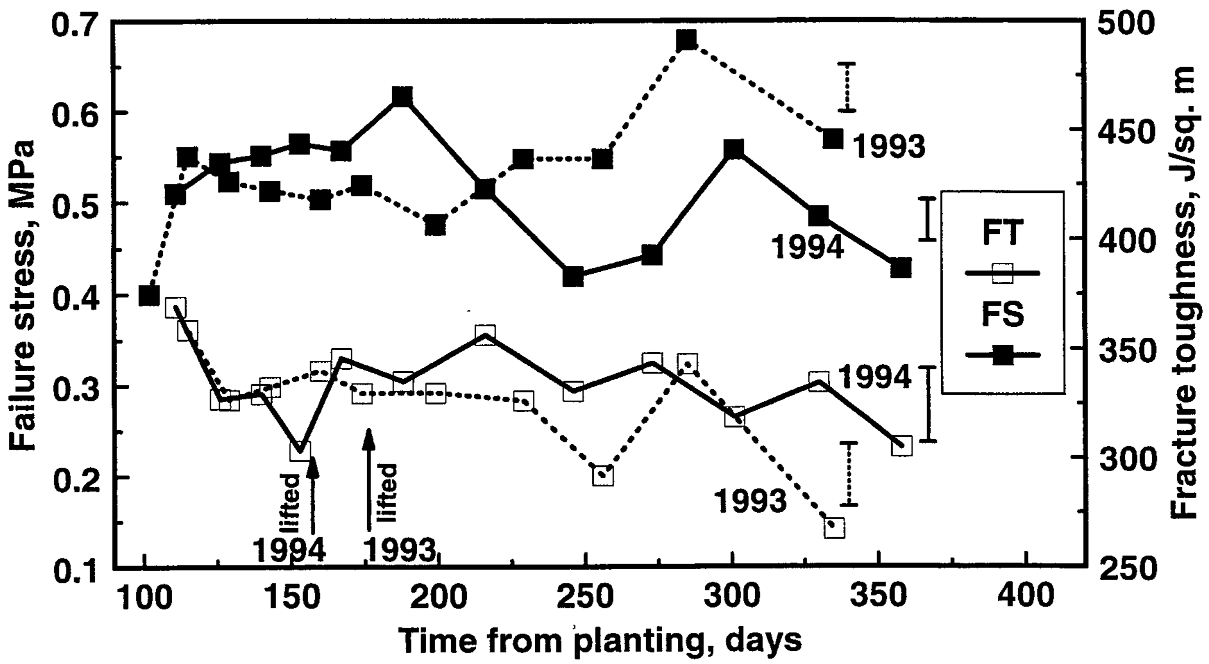


Figure 8. Changes in apoplast volume fraction during development and storage of cv. Wilja tubers. (Expts 9 and 10.)
Bars show lsd (p=0.05) for comparison between harvest means within a year.

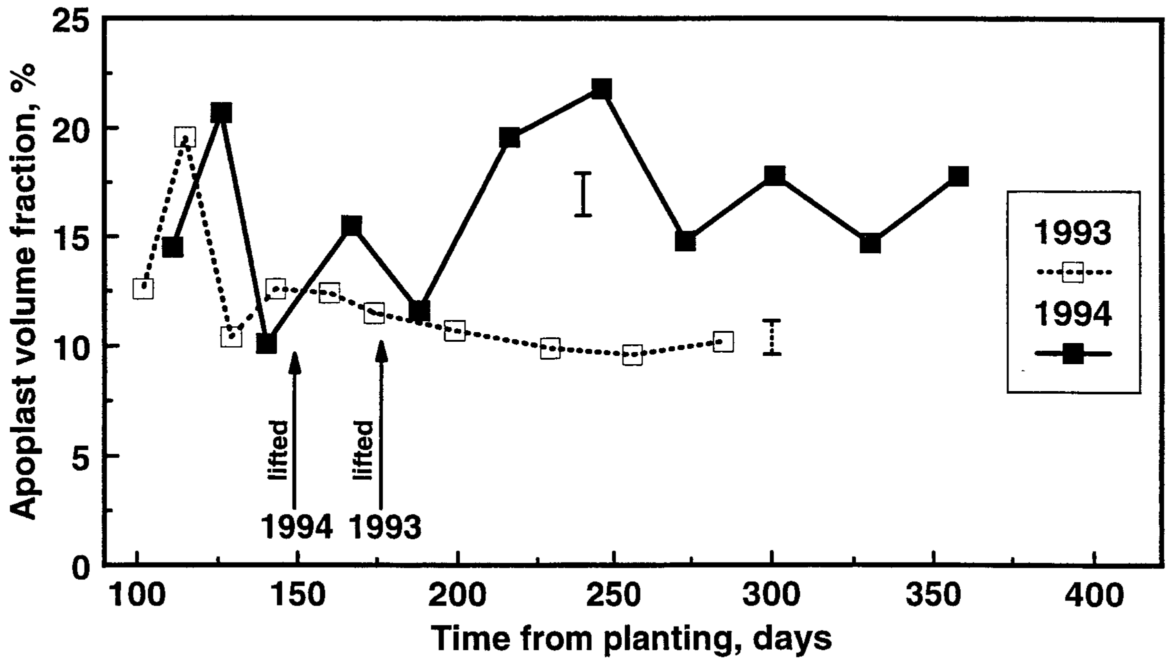


Figure 9. Changes in rebound angle during development and storage of cv. Wilja tubers. (Expt 10, 1994)
Bars show lsd (p=0.05) for comparison between harvest means.

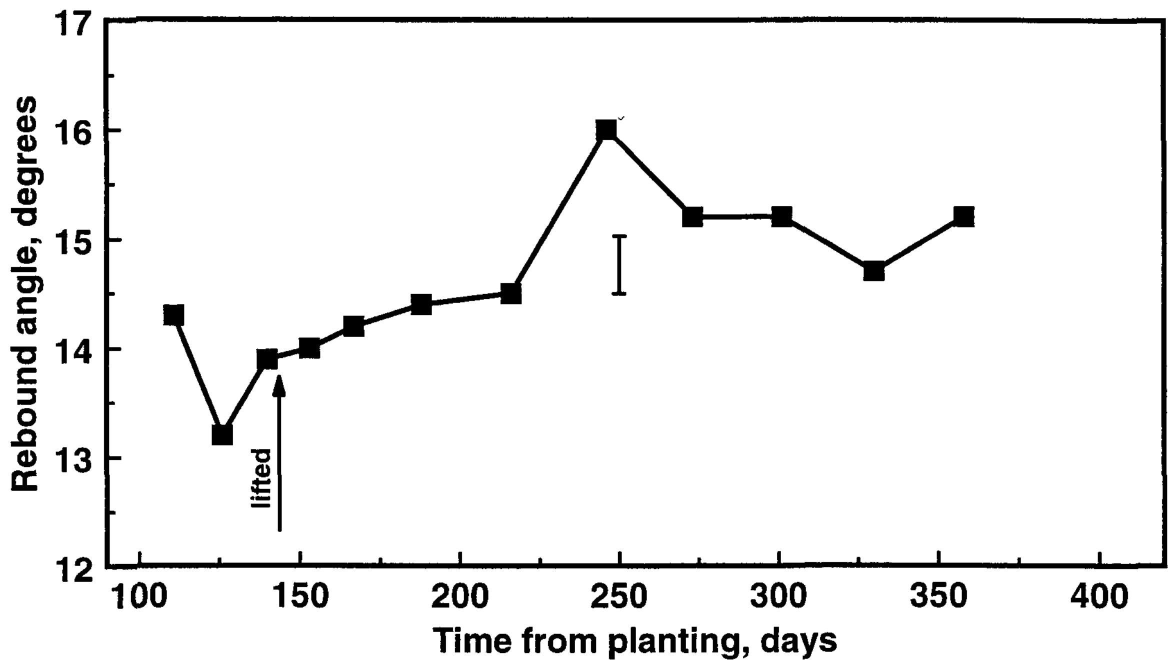


Figure 10. Relationships between treatment means of internal damage and a) dry matter content, b) relative moisture content, c) fracture toughness and d) failure stress. Data from: Expt 1,O; Expt 2,◊; Expt 3,□; Expt 5,✳; Expt 6,◆ ; Expt 7,■
Internal damage normalised to impact energy of 0.5 Joules.

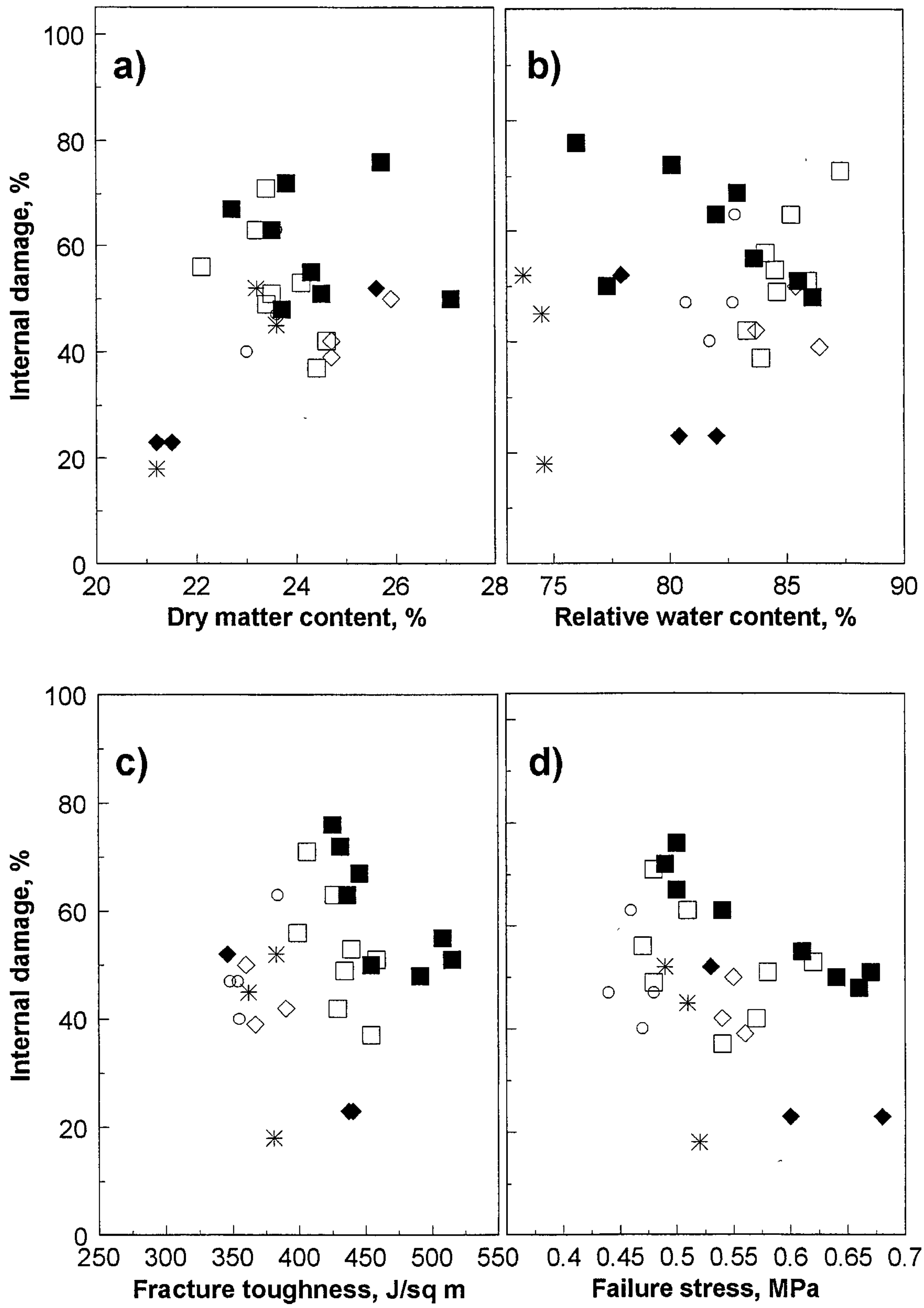
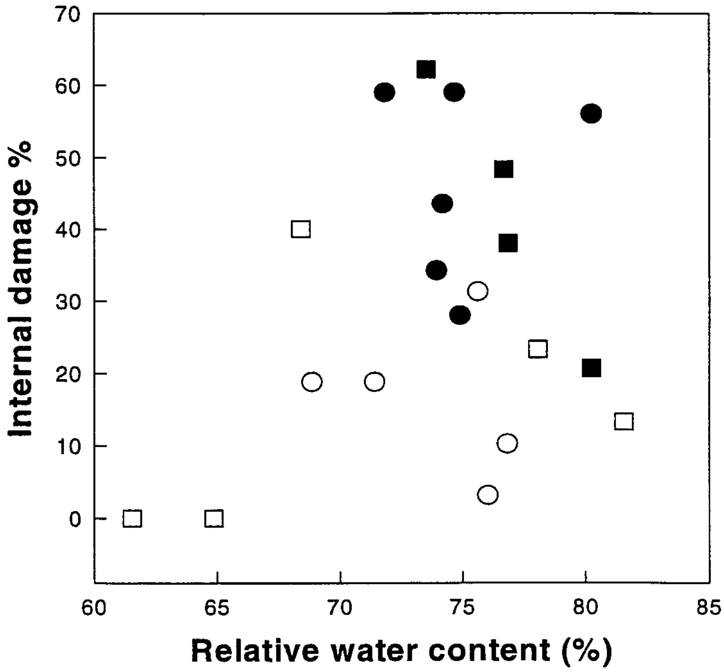
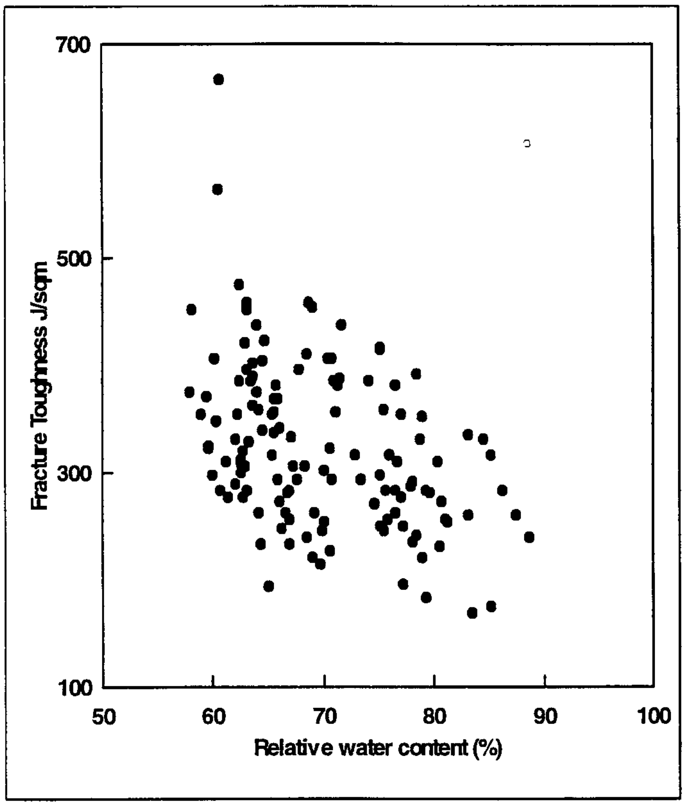


Figure 11. The effect of manipulating relative water content of tubers on their susceptibility to internal damage. Expt 11,■ ; Expt 12,●; Expt 13,□; Expt 14,O.



Relative water contents of 60, 70 80 and 85% are approximately equivalent to water potentials of -0.97, -0.82, -0.67. -0.34 MPa based on a generalised pressure/volume curve for potato tubers.
Data are accumulated from four experiments in which tuber water status was manipulated by drying or wetting over periods of up to 10 days. Impacts were inflicted by guided bolt or pendulum and normalised to a common impact energy of 0.5 Joules.

Figure 12. a) Fracture toughness and b) Energy absorption of tubers versus RWC of tubers from Expt 13.



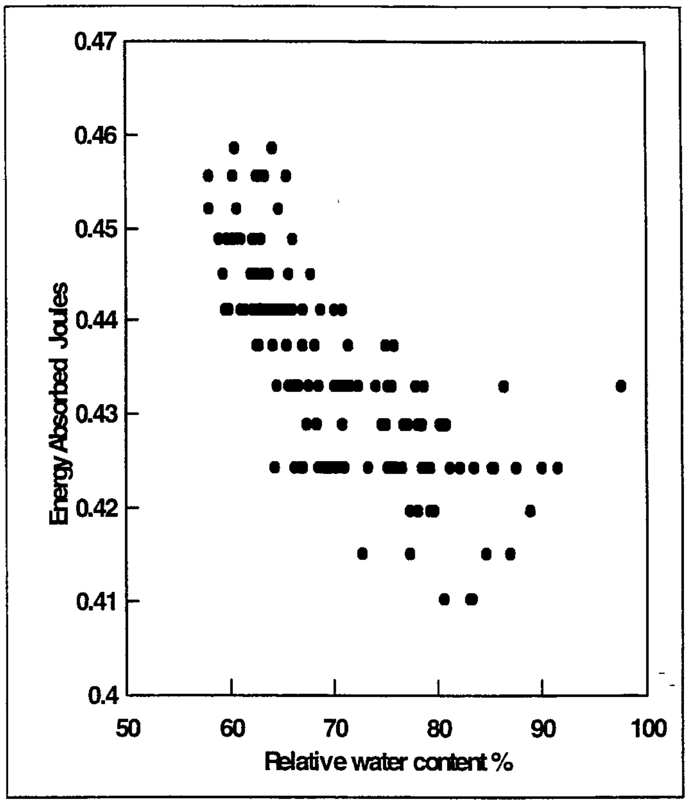


Figure 13 Variation in cell morphometry with distance beneath the skin: a) cell area, b) cell circularity, c) cell length and d) cell breadth. Expt 15.
Bars represent lsd (p=0.05) for comparison of means at each distance.

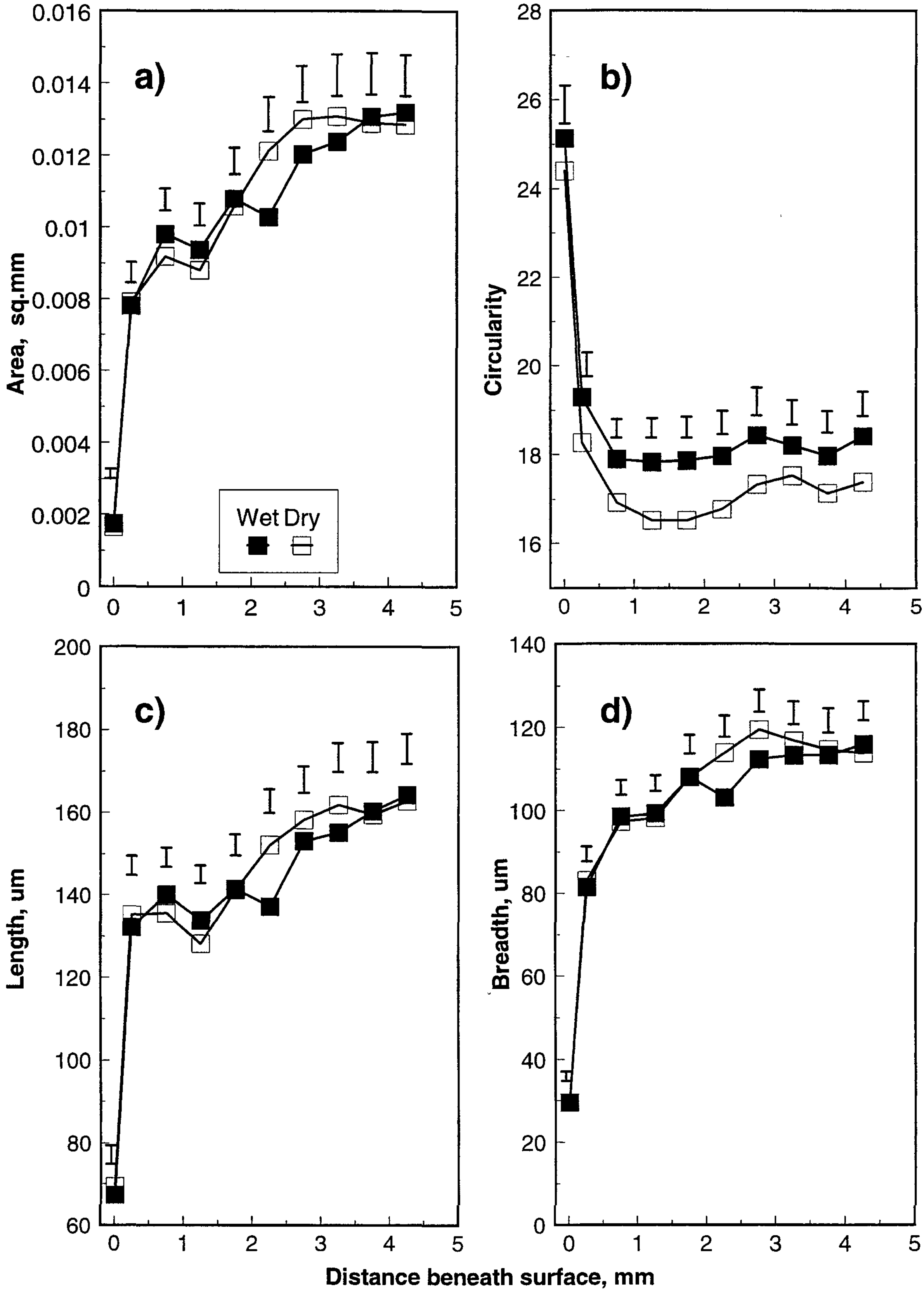


Figure 14. Comparison of internal damage inflicted by pendulum and falling bolt in tubers of cv Wilja tested at 0.5 Joules. Expt 10

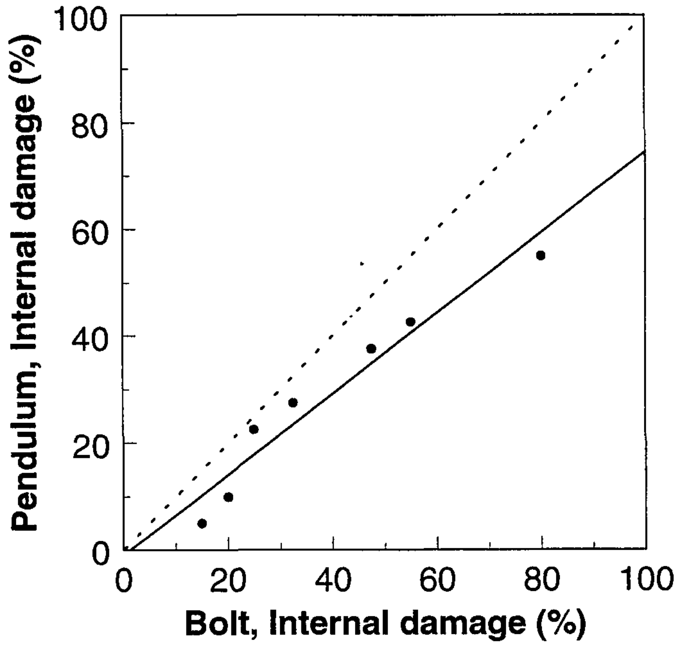


Figure 15. Energy levels for objects of different mass falling under gravity from different heights.

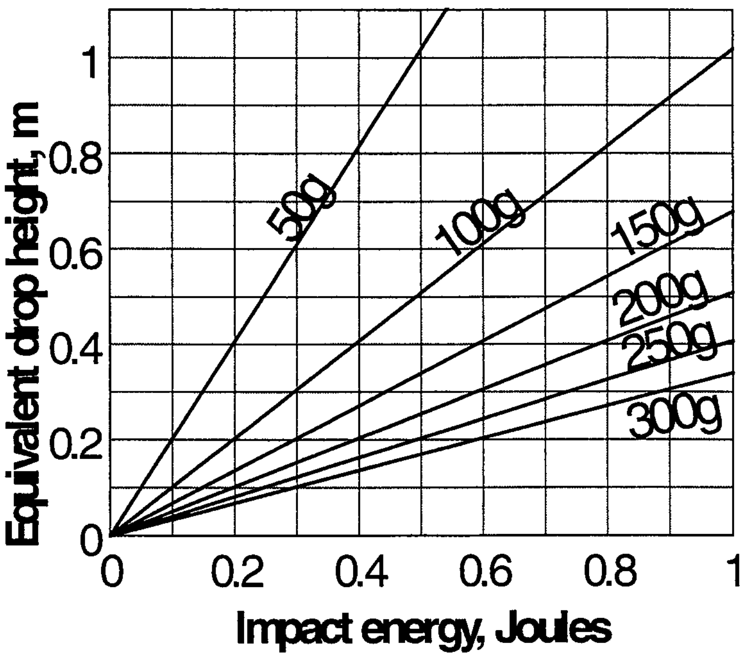


Figure 16. Pendulum used to determine tuber susceptibility to internal damage. Shown with modifications to enable movement of pendulum arm to be recorded.