Preface

There have been major changes in arable and horticultural production over the past few years, with a greater emphasis on the justification of crop protection management and more effective use of good husbandry techniques, both for seed protection and production.

Since the third Symposium on Seed Health and Treatment in 2001, there has been more information available on the technology of seed testing and treatment, the interpretation of results and improvements in seed production to lessen the risks of seed-borne pathogens. There have also been developments with new pesticides, a very desirable aspect in view of the current changes in pesticide registration criteria in the EU.

Production of high-quality seed continues to be the vital foundation for successful cropping. Seed testing remains an essential tool in the selection of high-quality seed. The results of these tests enable decisions to be made on the use of seed and the necessity of seed treatments for reliability of seedling establishment and control of seed-borne pathogens or seedling pests.

New pesticide actives are also in demand as older materials become less effective or environmental pressures or user safety become even more scrutinised. Without the regular developments and introduction of new products, we will be unable to adapt to the changing environment of new pest or disease pressures or national strategies in crop protection and food supply.

Delivery of pesticides to crop or seed has also changed. Formulations and seed treatments are continually being improved to ensure accurate targeting of the pest or disease and to maximise operator safety from seed processing to seed drilling.

The efficacy of new pesticides or treatments is being tested for a wider range of targets and crops, and successful trialling leads to more opportunities for protection, particularly of minor crops. The justification for the use of seed treatments will continue to be an issue, and seed testing and interpretation of results will play an even more important role in the future.

This Symposium Proceedings brings together current knowledge of seed production and protection, and the contents provide an important discussion forum both for current technologies and for those that will still be required in this changing environment.

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Chairman, Symposium Programme Committee
February 2009

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Requirements and demands on seed for peas and beans in the UK

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Summary

Seed for peas and beans is a major cost of crop production, and seed quality is an important issue in reliable plant establishment. The upward trend in farm saving of pulse seed in the UK increases the risk of pests and diseases and the production of high-quality vigorous seed. This paper outlines the main issues pertaining to pea and bean cropping and the requirement for seed of high provenance.

Introduction

Pulse crops in the UK comprise peas for vining or fresh market, peas for combining, field beans (*Vicia faba*), and lupins. In total around 200,000 ha are cropped annually. The main crops are field beans with both autumn-sown (winter beans) and spring-sown beans occupying around 70,000 ha each, and peas for combining at around 25,000 ha (Anon., 2008).

Seed for most of the vining peas for freezing or fresh market is imported from seed-producing areas in Eastern Europe or the USA, although a proportion is produced in the UK. Field bean and combining pea seed is almost all produced in the UK. The area had shown a decline over recent years due to low prices and competition from other break crops, but with the very recent increase in nitrogen fertiliser costs, and an increase in the demand for high quality peas and beans for premium markets, the area of combinable pulses is set to increase for 2009 and beyond.

Seed quality

A specific requirement for vining pea seed is its reliability in establishing a satisfactory population when sown early in the spring, when soil is cold and the likelihood of rain is high. The ability of a seed to survive these conditions is related to the characteristic known as seed vigour. In vining peas, seed vigour is assessed in the laboratory using the electrical conductivity test. This measures leachates from seed that has been immersed in water for 24 h (Anon., 2009a). The vigour is related inversely to the conductivity of the water. In the field, such 'leaky' seeds attract soil-borne pathogens, particularly *Pythium* spp., which infect the damaged areas of the cotyledon associated with the leakage and result in pre-emergence seedling mortality. Damage can be caused to the testa during harvesting and handling of dry seed, and such damage is associated with high conductivity levels in the testa (Biddle, 1981).

Seed health

Seed-borne diseases include the fungal pathogens *Ascochyta* spp. and *Mycosphaerella pinodes*. In peas, both pathogens result in seedling failure or leaf and pod spot disease, which can result in yield or quality loss. Seed testing is still based on the agar plate method of detection (Anon., 2009b) and there are recommended limits of seed-borne infection for seed use. In peas, seed-borne infection can effectively be reduced by the use of fungicidal treatments, which include thiabendazole and fludioxonil. However, control of *Ascochyta fabae* in field bean seed is less reliable than in peas.

Peas are also susceptible to infection by pea seed-borne mosaic virus, which is primarily seed-borne and aphid-transmitted. Infection causes severe stunting of the plants, poor pod set, and blemished or undersized seeds. There is little effective control of the virus during crop growth, so it has become important to use only healthy seed stocks in the multiplication process. Vining peas have been the most commonly infected pea crop in the UK over recent years, and a seed test based on ELISA was developed for use on soaked seed by PGRO and Rothamsted Research. This test has been in use for several years, and enables a rapid method of screening seed with potentially damaging levels of virus. An international method for pea seed-borne mosaic virus, also based on ELISA, has recently been published in the ISTA *International Rules for Seed Testing* (Anon., 2009c).

Pea bacterial blight (*Pseudomonas syringae* pv. *pisi*) has been a problem for peas over some years. In the UK, all peas are spring-sown and the risk of losses by this disease is generally of no significance (Roberts *et al*., 1995). However, in countries where autumn sowing is practised the disease can result in widespread yield loss, particularly where frosts occur in late spring when the crops are at the early flowering stage. A seed test has been available for some years to detect the presence or absence of blight in a seed sample.

Vicia beans are very susceptible to infestation by stem nematode (*Ditylenchus dipsaci*). Of the two races observed in the UK, the giant race seems to be the one that is most frequently found in field beans and causes the most damage. Typical symptoms of infestation are seen after emergence when the plants are stunted, stems twisted and swollen and foliage is discoloured and distorted. Nematodes are free-living in soil and in wet conditions move to plants, where they enter the stem tissue and begin to multiply. After moving within the tissues, the nematodes congregate under the testa of developing seed, where they can then dehydrate during seed maturation. When infested seed is planted, the nematodes rehydrate and move to surrounding plants. Residues of nematodes then remain in the soil for up to 10 years in the absence of a host crop.

Farm-saved seed of beans is commonly used in the UK, and this has further increased the risk of damaging nematode populations on farm. Seed testing has now become an essential part of bean growing in the UK. Although the test is not part of the Certification Standards, voluntary testing is the norm and seed laboratories have established a standardised procedure for nematode detection. In the UK, a high proportion of seeds of both winter and spring bean varieties can carry nematodes. Growers are recommended not to plant seed with any nematodes detected in the sample, but despite this the pest remains a major problem for seed production Data from the PGRO seed laboratory for the past 2 years show the proportion of infested seed to be high (Table 1).

Table 1 Proportion of bean samples tested at PGRO infested by stem nematode

Harvest year	Winter beans		Spring beans	
	Total tested	**% infested**	**Total tested**	**% infested**
2007	123	17.3	98	16.3
2008	203	22.2	128	22.7

Seed treatments

Although not seed-borne, downy mildew caused by *Peronospora viciae* is a problem in peas, and in some years also with field beans. There are robust differences in susceptibility of peas and beans to infection, but where susceptible varieties are grown in fields with a history of downy mildew, seedlings are infected from a soil-borne source of inoculum. Oospores of *P. viciae* can survive in soil for many years. The principal means of protection of peas is with fungicidal seed treatments. In the UK, the mixture of cymoxanil, metalaxyl-M and fludioxonil is used extensively, although some seed may be treated with fosetyl aluminium as an alternative. Most vining peas are susceptible to mildew, and seed is treated as a routine. Most combining peas are more tolerant, and only susceptible varieties are treated. Information on varietal susceptibility is published annually in the PGRO *Recommended List of Varieties of Field Peas* (Anon., 2009d).

Choice of seed treatment therefore relies on a number of factors. Firstly, because downy mildew is a difficult disease to control and in peas there is no foliar treatment available, the decision to use the more expensive multipurpose treatment is the primary consideration. Secondly, the level of seed-borne *Ascochyta* is the next consideration, and whether thiabendazole is required. Finally, most peas are treated with a standard protectant such as thiram, but this is only to control *Pythium* infection.

For Vicia beans a similar decision is made, although downy mildew can be controlled effectively by foliar sprays, and seed-borne *A. fabae* is not common. Beans rarely need protection from *Pythium* and therefore most are sown untreated.

Conclusions

Pulse seed is the most expensive input into growing costs, and in order to achieve the optimum plant population for each type, making the most effective use of seed is important. Increasing pressure on growing costs has meant that a large proportion of seed is farm-saved, so it is important for growers to recognise the risks involved if seed is not adequately tested for pests or pathogens and the correct choice of seed treatment made. For seed producers, pests and diseases are important, but so too are the harvesting, handling and processing of seed to ensure the highest seed quality.

Seed treatments remain an important part of successful cropping, and changes in the availability of active ingredients will require continuing development of suitable products for peas and beans.

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Reducing risks in a changing environment for UK potato production

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Introduction

Since the last BCPC seed treatment conference in 2001, pressures on seed potato producers to improve quality and health have continued to increase. Although certification standards for seed tubers have changed little in the intervening period, demands by purchasers for tolerances higher than certification have meant that greater attention to detail is required. However, despite rising input costs, the price of seed potatoes has not risen sufficiently, especially for free market varieties, and profitability of seed production has often been marginal. In consequence, the numbers of seed producers has continued to fall and the area grown reduced (Table 1).

The spectrum of diseases challenging seed production in the UK has not changed, although *Phoma foveata* (gangrene) and *Helminthosporium solani* (silver scurf) appear to have reduced in significance. Conversely, *Colletotrichum coccodes* (black dot) and *Pythium* spp. (watery wound rot) have increased in significance.

Another changing factor has been the range of seed treatment options. Whilst seed tuber treatments for control of *Rhizoctonia solani* (black scurf) have increased, those available for other tuber pathogens have decreased to just two active ingredients, imazalil and thiabendazole. Approval for the use of 2-aminobutane (2AB) ceased in December 2007. As the most effective treatment for the control of *Polyscytalum pustulans* (skin spot) and *P. foveata*, there is potential for a substantial increase in the first of these two diseases. The impact of the loss of 2-aminobutane has yet to be realized. There has been a dearth of new seed tuber treatments for control of tuber diseases and, currently, there are no effective seed treatments for *C. coccodes* or *Pythium* spp.

The only other tuber diseases that remain major threats are dry rot caused by a range of Fusarium spp. (most notably *F. caeruleum*, *F. sambucinum*, *F. culmorum* and *F. avenaceum;* Peters *et al.*, 2008) and bacterial soft rots (*Pectobacterium* spp.), the latter of which cannot be controlled by tuber seed treatment.

Table 1 Numbers of registered producers (seed and ware) and area of seed production in Scotland in 2001 and 2008 (Source: Potato Council Ltd)

	2001	**2008**
No. registered seed producers	673	492
Area of seed production (ha)	12,485	11,145

Table 2 Fungicide use on seed potatoes in Scotland, from Pesticide Usage in Scotland Surveys (tonnes potatoes treated) (Snowdon, 2003; Struthers, 2005, 2007)

Fungicide	2002	2004	2006
imazalil	169,808	119,917	145,886
thiabendazole	–	9,581	800
2-aminobutane*	12,372	3,655	2,353

*Use of 2-aminobutane ceased at the end of 2007.

Whilst seed tuber treatments continue to remain a major plank in seed tuber disease control (Table 2), an increased focus on non-chemical control measures has helped to improve seed tuber health. These measures include earlier harvesting, rapid drying after harvest using positive ventilation and improved store hygiene.

Seed tuber treatment

Apart from dust treatments applied at planting, primarily for the control of *Rhizoctonia solani*, treatment for seed diseases has relied on either hydraulic nozzles or spinning discs to deliver a spray to tubers for more than two decades. Thus, technology for seed tuber treatment has changed little over a period when quality and health demands have increased. Whilst some seed producers treat tubers on the harvester or at loading into store, this early timing of application has not been widely adopted because pickers on a harvester may receive exposure to fungicide treatment, especially in windy weather and most seed is harvested direct into boxes and not subsequently available for treatment when loading into store. Early seed tuber treatment is effective at limiting disease spread in store and to the daughter crop.

Most seed tuber treatment occurs at grading and is aimed primarily at reducing disease spread to the daughter crop. However, because treatment is made just prior to bagging or boxing tubers, there is a desire to limit wetting of tubers and thus the risk of bacterial soft rot or blackleg development. This is particularly important when seed tubers are bagged into 1 or 1.25 tonne polypropylene bags in which air movement is limited. A spray application dose of no more than 1.5 l fungicide solution/tonne and preferably two thirds or half this amount is favoured by producers. In addition to the difficulties of spraying tubers evenly, this low water volume can lead to low tuber residues (Figure 1).

In the series of trials shown in Fig. 1, carried out between Agricultural Scientific Services (now SASA) and SAC in the early 1980's, residues were frequently only 25% of target. Although the data is over 20 years old, it remains relevant today as the application systems have not changed.

Spray application of fungicides to seed tubers is made at a time when seed potato growers are at their busiest grading potatoes. There can be frequent changes of seed stock as orders are often made for relatively small quantities of seed. With frequently changing seed stocks, requests for different seed fractions and different speeds of grading (depending on the condition of the

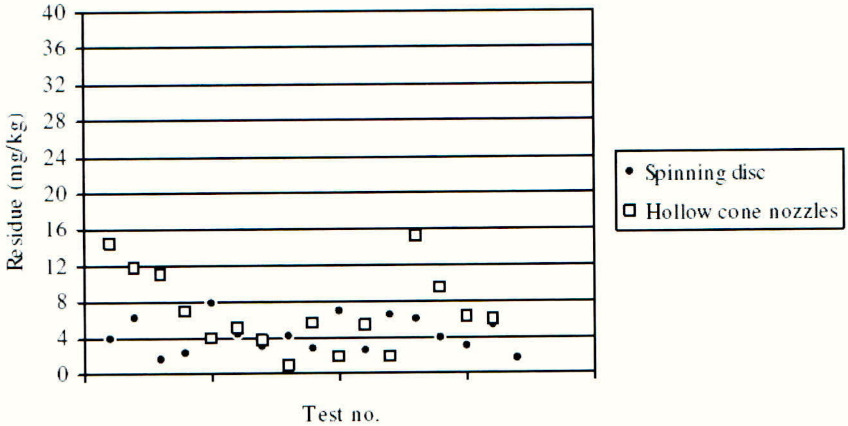

Figure 1 Residues of thiabendazole on seed tubers after application using a spinning disc or hydraulic applicator onto 17 separate tuber lots. Target residue is 40 mg thiabendazole /kg tuber.

stock and the need for more or less picking off), there is a constant requirement to re-calibrate fungicide applications. It is unsurprising that frequent re-calibration does not occur.

In order to achieve optimum control of seed tuber diseases, complete coverage of the tuber surface with fungicide is required. However, even when a water volume of 2 l spray solution per tonne seed is used under good experimental conditions, complete coverage is rarely achieved (Table 3).

Tubers require to be rotating when passing under the spray mist but tubers align themselves along their longest axis on a roller table and, as the data in Table 3 shows, it can be difficult to effectively cover the rose or stolon ends. Tuber dipping would effectively treat all parts of the tuber but the risks of bacterial soft rotting and blackleg are considered so great that this option is not practiced. However, with improved drying methods dipping should be re-examined as an option.

There is an urgent need to identify more consistent ways to apply fungicide spray solutions to tubers.

Table 3 Tuber surface (%) treated with fungicide using hydraulic spray equipment applying 2 l/t spray solution on different parts of potato tubers (SAC data)

	% deposit	**% without deposit**
Middle section	62	38
Rose end	22	78
Average	42	58

Reducing potato disease risks in the changing environment

The conflicting demands of improving tuber health whilst achieving profitability along with the difficulty of applying seed tuber treatments has meant that reliance on seed tuber treatments has lessened (Table 2). Greater attention has been placed by seed companies and seed producers on non-chemical control methods.

In contrast to pre-pack or processing growers, pressure has not been placed on seed producers to limit pesticide use during multiplication. However, a general public pressure to reduce pesticide use has applied further leverage to persuade growers to reduce application of seed treatments.

Maintaining seed in as healthy a condition as possible during multiplication by utilising non-chemical methods will limit the need for seed treatment use. However, even where every effort is made to limit disease development using non-chemical methods, there are constant threats of disease ingress from soil and from cross contamination in store. The strategic use of seed treatments is an important element of disease control. Thus the way to cope with potato disease risks in a changing environment is to provide attention to detail and apply seed treatments strategically within a programme of non-chemical control

In targeting seed tuber treatments, seed growers and those who plant seed require to check seed health during multiplication. Even low levels of some pathogens can be important in some circumstances, where they have a potential to increase from low to high levels.

In the future, diagnostic tuber tests using DNA technology may become available to aid detection and pre-symptom development of pathogens. It is potentially possible to quantitatively determine the level of infection by pathogens on a sample of tubers from a stock at low levels and before symptom expression. Such a test is already under development for early detection of *P. pustulans*, a pathogen with a long latent period. Such technology for accurate detection is likely to be adopted for pathogens which are difficult to identify or detect.

The factors that influence decision making on seed treatment are many, and not always based on objectivity. The factors are listed in Table 4.

Normally, justifications for seed tuber treatment are based on variety disease susceptibility and the level of disease present. However, various other factors can influence risk of disease development such as date of harvest, presence of disease on seed from which the crop was grown, an historic problem of disease on the farm, a late harvest, the level of soil contamination, whether previous seed tuber treatments had been applied to either the mother seed or at an earlier stage to the daughter crop and extent of mechanical damage. In addition, there are marketing factors which can influence a decision to apply a seed treatment such as cost, the ultimate market for the crop and the value of the crop.

Apart from these key factors, the decision making process may also take into account other field factors and storage factors (Table 4). Less rational or less objective arguments for using a seed treatment include a desire to guarantee consistency of seed production, a requirement to treat routinely either because of a market or protocol requirement or because of pride or the desire to have reassurance or insurance that losses will not occur.

Integrating these factors into a decision tree is difficult but two sets of guidelines have been published (Wale, 1997; Wale, undated) in which a logical process is attempted.

Table 4 Factors involved with decisions on seed treatment

Factor type	Specific factors
Key factors	Cost Date of harvest Disease presence on seed from which crop was grown Historic disease prevalence Late harvest Level of soil contamination Mechanical damage Previous fungicide applications Ultimate market for variety Value of crop Variety susceptibility/resistance Visible disease on seed
Factors from field in which seed was grown	Known soil contamination by pathogen Level of volunteers Short rotation Weather/soil conditions at harvest
Storage factors	Availability of drying facilities/ventilation after harvest Effectiveness of seed treatment application Environmental issues Grading damage Health and safety issues Length of storage Level of store hygiene Presence of condensation Presence of sprouting
Non-rational factors	Consistency of seed production Market requirement to treat Pride Protocol requirements Reassurance/insurance

Conclusion

Reacting to a changing environment requires a flexible approach. However, such flexibility must fit into a practical context. Whilst striving for control using non-chemical measures represents the most desirable way forward, this requires an attention to detail that may not always be possible. In addition, it is not yet possible to be fully confident about disease risk and even in the best managed units, disease problems can occur. Having facilities such as positive ventilation can reduce disease risk considerably but the flexibility of approach required in a changing environment will mean that seed tuber treatment will always be necessary as a last resort.

Experience in the potato industry in the last two decades has indicated that change will continue to be a feature and pressure on price and quality will continue unabated. Whilst low profit margins in seed potato production detract from investment, there is a need for growers to invest in equipment (such as good quality storage facilities) that will reduce the risk of disease development. Increasing the probability of success by considering all the factors that may impinge on tuber disease forms a major part of disease control. Thus planning ahead is a key requirement for reducing risk: proper prior preparation produces perfect potatoes.

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Seed quality development

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Summary

This paper considers when during seed development and maturation seeds attain their maximum quality – and so the best point at which to harvest seed crops, the effect of environment thereon, and the potential for improving seed quality *ex planta*.

Introduction

High-quality seed are able to 'escape' hostile seed-bed environments by germinating and emerging rapidly and in very good number, and then establishing crop canopies rapidly that capture solar radiation and thereby outcompete weeds.

In the wild, the survival of a plant species is often based on the production of a very large number of seeds to ensure the subsequent development to maturity of comparatively few plants: within-population variability, for example in the degree of seed dormancy, is often a major factor in wild species' survival strategies. In agriculture, horticulture and forestry, however, the objective of commercial growers when sowing every single seed is to produce a seedling that will emerge and subsequently establish as a healthy plant that will subsequently contribute to a uniform, high-yielding crop that can be harvested in a timely manner. This paper considers the development of seed quality within seed populations rather than just the individual seed. My starting point is a quote from William Shakespeare: '*Be not afraid of greatness: some are born great, some achieve greatness and some have greatness thrust upon them.*' (*Twelfth Night*, Act II, Scene V). My principal focus is 'when' within seed development and maturation do seeds '*have greatness thrust upon them*', the effect of environment thereon, and the extent to which seed producers can manipulate aspects of what otherwise might be deemed a natural process in order to produce consistently high quality seed lots.

Seed weight and moisture content

After pollination, a period of histo-differentiation within the developing seeds is followed by reserve accumulation. Visually, fruit enlargement is followed by seed enlargement, whereby a high proportion of the early mass (and bulk) of the seed is water. Much of this water is then progressively replaced by assimilates, typically from current photosynthesis combined with the remobilisation of reserves to the seed. At the end of reserve accumulation, vascular detachment occurs. In agronomic terms, the factors that can influence the potential yield of a seed crop have no further influence beyond this point – because no more assimilates can be deposited within the seeds. For this reason, the end of seed filling was termed physiological maturity by agronomists (Shaw & Loomis, 1951). In some species, such as the cereals, legumes and brassicas, seed moisture contents then decline substantially thereafter until they approach

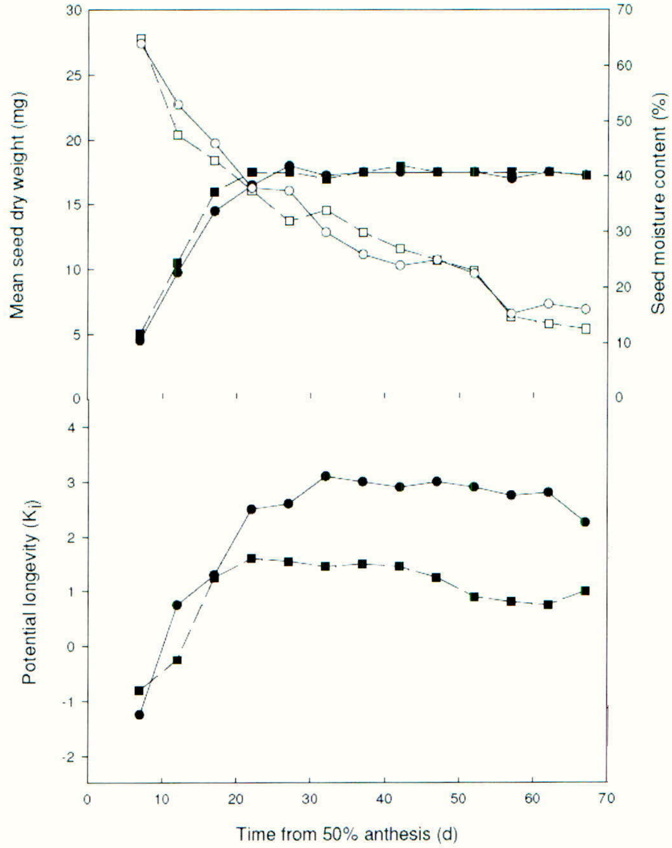

Figure 1 Changes in mean seed dry weight (solid symbols, upper figure), moisture content (open symbols, upper figure), and potential longevity in air-dry seed storage (solid symbols, lower figure; constant K_i of the seed viability equation) during the development and maturation of seeds of the *japonica* rice cultivar Taipei 309 in controlled environments of 28/20°C (circles) or 32/24°C (squares). (Redrawn from Ellis *et al.*, 1993.)

equilibrium with ambient relative humidity, whereas in species with fleshy fruits the fruit structure delays seed moisture content decline appreciably.

The upper diagram in Figure 1 provides an example of the trends for both the moisture content and the dry weight of developing and maturing seeds of a cereal. In both seed production environments in this particular case, seed-filling ended around 20 days after anthesis.

Ability to germinate, to tolerate desiccation, and to survive *ex planta*

In the context of harvesting seeds that can then be stored to subsequently establish a crop, the following phasing occurs: developing seeds first develop the ability to germinate (provided investigators are able to break their dormancy); they then become desiccation tolerant (in those species that are desiccation tolerant); and their quality (in particular their potential to survive subsequent air-dry conditions, see below) then improves further. These three phases are rather more spread out across seed development and maturation in the temperate cereals than is the case in the grain legumes, in which all three phases tend to occur comparatively close to each other and quite late on.

A belief had developed that improvement in seed quality terminated at the end of the seed-filing period, that seeds then began to age and so deteriorate thereafter, and consequently maximum seed quality coincides with physiological maturity (Harrington, 1972). However, detailed research across a wide range of cultivated (agriculture, horticulture and forestry) and wild species in normal production environments has now shown that view to be largely incorrect. Rather, seed quality continues to improve for a considerable period beyond the end of the seed-filling phase (e.g. Demir & Ellis, 1992a, 1992b, 1993; Ellis & Pieta-Filho, 1992; Ellis *et al.*, 1993; Hay & Probert, 1995; Hong & Ellis, 1992; Hong *et al.*, 1993; Kameswara Rao *et al.*, 1991; Pieta Filho & Ellis, 1991a; Zanakis *et al.*, 1994). In crops such as the cereals and grain legumes, maximum quality tends to occur in most environments close to the stage that farmers would recognise as harvest maturity. Accordingly, while the term physiological maturity may be an appropriate term for agronomists, it is a misleading and so an unhelpful term in seed production. The end of the seed-filling period is now described more simply as mass maturity (Ellis & Pieta Filho, 1992).

The solid circles in the lower diagram in Figure 1 provide an example in a *japonica* rice, whereby one estimate of seed quality (an estimate of the potential longevity of the seed in subsequent air dry storage) continued to improve until 32 days after anthesis, some 12 days after mass maturity, when seed moisture content had declined to about 35%, and then remained stable for a further 20–30 days or so.

Some will question the estimate of subsequent seed storage life as an indicator of seed quality. Since there is often a long period between seed harvest and sowing, often considerable in the case of vegetable seeds, potential seed longevity is one seed quality characteristic of direct concern to both seedsmen and growers. Potential seed longevity is also an accurate, and quite sensitive, indicator of other aspects of seed quality, including emergence ability. Hence, when other sensitive measures of seed quality have also been used, similar conclusions have been drawn that maximum quality is obtained some considerable time after mass maturity: for example, emergence ability and subsequent seedling size (Pieta Filho & Ellis, 1991b) or growth (Demir & Ellis, 1993).

Environment

The field environment can affect seed quality through its effect on seed quality development. We are especially aware in the UK of good and poor seed production years, whereby (for quality but not necessarily yield) warmer drier summers tend to be superior to cooler wetter ones. Sanhewe *et al.* (1996) provided good evidence of just such a progressive benefit to wheat seed quality from small increases in temperature (means from 14.3 to 18.4°C) from a systematic investigation in temperature-gradient tunnels.

However, at some value a further increase in the temperature of the seed production environment can become a problem rather than a benefit. The solid squares in the lower diagram in Figure 1 provide an example of the progress of seed quality development in a seed production environment that was too warm for high seed quality (but not for seed filling and so seed weight, upper diagram). Comparison of the warmer (solid squares) with the cooler environment (solid circles) shows that seed quality development was similar during the majority of the seed-filling phase, but ended around 18–22 days after anthesis and so some 10–14 or so days earlier than was the case in the cooler regime. This was a characteristic of the type of variety (a *japonica*): other types of rice showed no differences in the progress of seed quality development between the temperature regimes (Ellis *et al.*, 1993). In the warmer regime, maximum seed quality in the *japonica* was therefore first attained close to the end of the seed–filling phase. Contrary to Harrington (1972), however, no dramatic decline in seed quality was detected over the subsequent 20 days or so.

The example of the effect of environment shown in Figure 1 is extreme, in the sense that the warmer regime is beyond those that *japonica* rices normally experience. Nevertheless, it can be seen that a temperature regime that was not at all stressful for seed yield was considerably so for seed quality (solid symbols in upper and lower diagrams, respectively). In the context of anticipated climate change in summer temperatures in the UK, increases in mean temperature of 2 to 4°C during wheat seed development and maturation can be shown to improve the rate of progress of seed quality development and, despite the reduction in the overall duration of seed development and maturation also resulting from the increase in temperature, an overall benefit to seed quality at harvest (Sanhewe *et al.*, 1996). As might be expected, substantial increase in CO_2 concentration did result in heavier seeds but there was no effect on seed quality (Sanhewe *et al.*, 1996).

Economy of nature versus adaptation to different ecologies

From the above, it might be suggested that seed quality is more or less maximal at shedding in the case of wild species. This may well be true in many such species: good examples of contrasting species in which this is the case include Norway maple (Hong & Ellis, 1992) and foxglove (Hay & Probert, 1995). But of course there are examples in some ecologies where seed development continues after shedding (e.g. certain winter-flowering annuals) or at the other extreme where viviparous germination occurs prior to shedding (e.g. mangrove), or where seeds do not shed until some considerable time after seed maturity (e.g. ash).

Moreover, despite considerable selection for uniformity in crops, we may have the problem of a lack of uniformity in the progress of the development and maturation within the seed crop, such as occurs in carrot, for example.

Ex planta seed treatment

Despite these caveats, it is clear from the research to date that there is a great deal of evidence for the economy of nature in seed quality development. To what extent then is it possible for particular treatments to seeds to complement natural seed quality development? There are indeed numerous ways in which the quality of the seed lot can be improved after harvest. For example, seed cleaning can not only remove weed seeds, but can also remove broken and/or poorly filled seeds. And from the point of view of mechanical sowing, seed size can be more tightly limited to narrow bands to ensure smooth flowing through drills and precision drilling in the seed bed.

Here, I wish to mention briefly the scope of procedures which in effect mimic, extend, or resume the seed maturation process after harvest. First, there is good evidence that prematurely harvested seeds can mature *ex planta* if the subsequent environment enables the slow loss in moisture, as would have occurred on the mother plant (e.g. Hong & Ellis, 1997).

Seed priming is an interesting technique because, depending upon the circumstances, it has the potential to improve seed quality in a variety of somewhat different ways. The origin of the use of the term priming was in the context of advancing the process of germination directly and indirectly (by breaking dormancy), simply to reduce the subsequent period from sowing to seedling emergence, but in many of those reports there were sometimes problems with the subsequent desiccation tolerance of the primed seeds and/or their survival during subsequent air dry storage (Heydecker & Gibbins, 1978). The point I wish to emphasise here, however, is the potential for priming (or indeed just a moist atmosphere) and subsequent slow desiccation to enable immature seeds to resume components of the maturation process and thereby improve in quality (Butler *et al.*, 2009). Similarly, there is good evidence that some of the deterioration that aged (that is, stored for some time in poor environments) seeds have accumulated can be repaired by priming (Powell *et al.*, 2000). The ability of high moisture content conditions, provided sufficient oxygen is available and germination can be prevented, to enable the 'repair' of ageing damage is well known (Villiers & Edgcumbe, 1975; Ibrahim & Roberts, 1983).

In this context, seed quality development in fleshy-fruited species is also interesting and highly relevant. Developing and maturing tomato seeds first attained maximum seed quality at 23 days after mass maturity, and then maintained this high quality for at least a further 30–40 days while they remained within fruits on the mother plant at around 50% moisture content (Demir & Ellis 1992a). That is, they tolerated a very considerable delay to harvest without any decline in seed quality.

In conclusion, it is possible to improve seeds by treating them physically (e.g. by pelleting) as well as chemically (whether as a means of improving emergence and establishment or as a method of delivering crop protection chemicals systemically to the subsequent crop). My ambition in this communication has been to emphasise that there is much that can be done to ensure that the inherent quality of seeds, prior to any such physical or chemical treatment, can be maximised.

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