Producing quality seed: the problem of seed vigour

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Abstract

While seed vigour is an internationally recognised seed quality parameter, and internationally more than 50 % of seed laboratories conduct vigour tests, vigour testing is yet to become accepted into the rules of the International Seed Testing Association, and the International Seed Trade Federation strongly opposes any such introduction. The major factor fuelling this contentious issue is that so little is known about the current seed production practices reducing seed vigour. This review discusses the concept of seed vigour and how loss of vigour may occur during seed production.

Additional key words: *cell membrane integrity, environment, field and storage performance, genetic effects, germination, heat stress, nutrients, post harvest, seed deterioration, seed position, seed maturity, viability, vigour tests, weathering*

Introduction

The terms 'seed vigour' and 'seed vigour testing' are currently a source of some controversy between seed technologists and the international seed trade. Consider the following:

i seed vigour is an internationally recognised seed quality parameter (McDonald, 1995).
ii vigour differences among high germinating seed lots have been demonstrated for a large number of agricultural, horticultural and tree species (Hampton and TeKrony, 1995)
iii internationally, more than 50 % of seed laboratories (official, company, private) conduct vigour tests (Hampton, 1992a; Spears, 1995)
iv in 1998, US seed laboratories conducted vigour tests on 470,000 seed lots (Spears, 1998)
v vigour testing is yet to be accepted as a chapter for the rules of the International Seed Testing Association (Hampton, 1998a)
vi the International Seed Trade Federation (FIS) opposes the introduction of a vigour testing chapter because (a) recognition of seed vigour may lead to mandatory testing; (b) rules will lead to disputes between buyers and sellers; (c) standards have not been established for trade and production contracts (Dennis TeKrony, pers. comm. 1998)
vii a chronic problem facing the seed industry is the production of low vigour seed (Dornbos, 1995)
viii maximum seed quality (including seed vigour) is reached at or shortly after maximum seed dry weight is attained (although exactly when is under debate (Coolbear, 1995); the important point is that it is well before harvest)
ix there is a need for research to determine which current production practices are responsible for reductions in seed vigour (Hampton, 1995).

These nine points illustrate the fact that seed vigour is a contentious issue for the seed industry, primarily because the question "how do I produce high vigour seed?" can not be answered. In this paper I intend to discuss the concept of seed vigour and how loss of vigour may occur during seed production.

Germination as a Quality Indicator

The seed industry is rather obviously interested in the viability and potential performance of a seed lot. Information is required on the capacity of the seed lot to germinate, to emerge once sown, and to survive during storage. Conventionally this information is obtained via germination testing, where germination is defined as "the emergence and development of the seedling to a stage where the aspect of its essential structures indicates whether or not it is able to develop further into a satisfactory plant under favourable conditions in soil" (ISTA, 1996). The germination test therefore reports the percentage of normal seedlings, abnormal seedlings, and dead/non-germinated seeds in a seed lot.

When maximum seed viability is attained, a seed lot should theoretically have a germination of nearly 100 %, providing dormancy is not a factor. Loss of viability from that point on results from the deterioration processes following physical damage, and seed ageing, both pre- and post-harvest (Powell, 1988). Symptoms of this deterioration include reduced rates of germination and emergence, decreased tolerance to sub-optimal conditions, and inferior seedling growth (Powell *et al.*, 1984). Thus in the absence of dormancy, a germination test result less than an arbitrary high standard (e.g., 90 %) indicates that deterioration has occurred (Hampton and Coolbear, 1990) and performance will be impaired (Table 1). I.e., when the field performance of large numbers of seed lots of the same species/cultivar which range in germination is compared, there is often a highly significant relationship (Castillo *et al.*, 1993) and in such situations the germination test does meet its ultimate objective of providing information with respect to the field planting value of the seed (ISTA, 1996).

Problems arise however when high germinating seed lots of the same cultivar, certification class and chronological age perform differently in the field or after storage (Table 2). It is now well established that seed lots which do not differ in germination may differ substantially in field emergence when sown at the same time in the same field (Dornbos, 1995), and/or may differ in their germination after storage in the same environment or transport to the same destination (Hampton and Hill, 1990). This recognition of performance differences among high germinating seed lots has long been acknowledged, the phenomenon being described by Nobbe (1876) in German as 'Triebkraft' (literally 'driving force'). In English it has been given a variety of names (Perry, 1981) but is now universally recognised as 'seed vigour' (Hampton and TeKrony, 1995).

To return briefly to germination testing. The major limitation of the standard laboratory germination test as an assessment of seed lot potential performance is its inability to detect quality differences among high germinating seed lots (Roberts, 1984). Because of the nature of the normal distribution on which the seed survival curve is based, a small difference in percentage germination represents a large difference in the process of deterioration (Ellis and Roberts, 1980). It is in these circumstances (Fig. 1) that a more sensitive differentiation of potential performance (seed vigour testing) is necessary (Hampton and Coolbear, 1990).

Table 1. Comparison of laboratory germination and field emergence of 94 soybean (*Glycine max* L. Merr.) seed lots which had a minimum germination of 80%[1].

Laboratory germination (%)	No. of lots	Percentage of lots with field emergence >80%	>70%
90-94	29	48	83
85-89	47	25	55
80-84	18	0	33

[1] Calculated from the data of Delouche (1973).

Table 2. Field, post-storage and post-transport performance of seed lots which germination data indicate are of similar quality.

	Seed lot 1	2	3	4
Field - *Pisum sativum* L.[1]				
germination (%)	93	92	95	97
field emergence (%)	84	71	68	82
Storage - *Trifolium pratense* L[2]				
pre-storage germination (%)	90	90	90	90
post-storage (12 months) germination (%)	71	90	66	89
Transport - *Bromus willdenowii* Kunth[3]				
pre-transport germination (%)	94	96	93	90
post overseas-transport germination(%)	87	19	74	53

[1] adapted from Castillo *et al.* (1993)
[2] adapted from Wang and Hampton (1991)
[3] from Hampton and TeKrony (1995)

What is Seed Vigour?

This is not an easy question to answer as the term refers to a concept, not a single measurable property such as germination (Perry, 1981). The Vigour Test Committee of the International Seed Testing Association has recently defined seed vigour as "an index of the extent of the physiological deterioration and/or mechanical integrity of a high germinating seed lot which governs its ability to perform in a wide range of environments (Hampton, 1998b). The aspects of performance associated with seed vigour include:

i the rate and uniformity of seed germination and seedling growth
ii field performance, including the extent, rate and uniformity of seedling emergence
iii performance after storage, particularly the retention of germination capacity.

Seeds which perform well are termed 'high vigour' seeds (Perry, 1978). Early seed vigour research concentrated on the effects that the physical characteristics of seed had on vigour (Perry, 1980), but more recent investigations have concentrated on the physiological causes of vigour differences, particularly the role of seed deterioration (Coolbear, 1995). Ellis and Roberts (1980) regarded low vigour seed as the result of seed deterioration processes, and Powell (1988) suggested that cell membrane integrity, as determined by deteriorative biochemical changes (and/or physical disruption) could be considered to be a fundamental cause of differences in seed vigour. However, seed deterioration also involves genetic damage, changes in respiratory activity, enzyme and protein changes, hormonal changes, and the accumulation of toxic metabolites (Priestley, 1986); it is a matrix of interrelated events (Coolbear, 1995). As Coolbear (1995) concluded "no one aspect of seed metabolism is likely to provide a clear universal index of seed deterioration, for there are too many events going on at the same time".

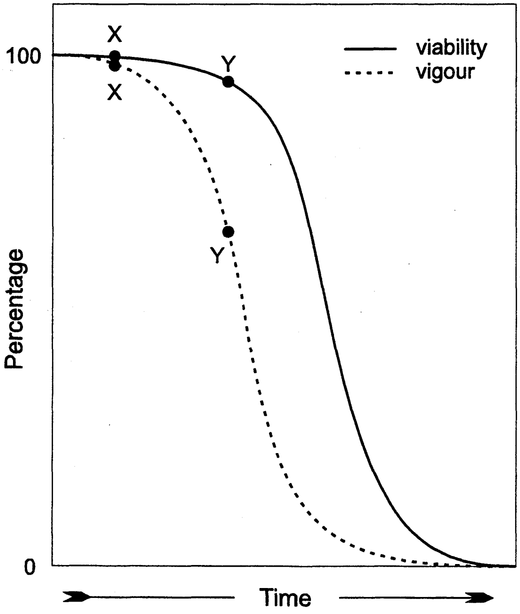

Figure 1. Relationship between seed viability and vigour over time. The X and Y points on the viability and vigour curves illustrate the increasing difference between viability and vigour as seed lot deterioration increases over time. (Adapted from Delouche and Caldwell, 1960).

Although not yet fully understood, seed deterioration has come to be recognised as the major cause of reduced seed vigour (Hampton and TeKrony, 1995) and vigour tests which can measure either some direct aspect of the deterioration processes (e.g., cell membrane integrity/-conductivity test), or a consequence of the deterioration process (e.g., reduced tolerance to environmental stresses/cold test; accelerated ageing test) have been successfully used internationally (Hampton and TeKrony, 1995).

Why is Seed Vigour a Problem for Seed Production?

Most seed producers grow their crops under contract to a seed company. That contract will include quality specifications, particularly for germination and analytical purity. Failure to attain the quality standards specified may mean that the seed produced will not be accepted by the company, or may mean that the seed is accepted but at a price substantially less than that originally contracted. Most growers either have the skills required, or the access to technology transfer personnel, to enable them to meet the quality standards presently required. However a major problem would arise if seed vigour was to be included as part of the quality requirement for a contract simply because so little is as yet known about the factors responsible for the loss of seed vigour during seed production (see the next section of this paper). Given the present knowledge of the subject, producing seed lots which could meet a seed vigour quality standard would be more a matter of good luck, rather than good management.

Another factor to consider is that, in the absence of any seed vigour information, high germinating seed lots are of similar trading value. Sections of the seed industry are perhaps understandably reluctant to press for vigour information, let alone support research which addresses how to produce high vigour seed.

How is Vigour Lost During Seed Production?

Seed deterioration is considered to begin at physiological maturity (i.e., pre-harvest) and continues during harvesting, processing and storage at a rate greatly influenced by genetic, production and environmental factors (Hampton and TeKrony, 1995). Its time course ranges from a few days (Table 3) to many years. Thus high germinating seed lots which are chronologically the same age may have deteriorated at different rates, and therefore differ markedly in seed vigour (Fig. 1).

Environmental factors

"The degree of seed ageing that occurs in the field clearly cannot be controlled" (Matthews and Powell, 1986), but this is not necessarily correct. If a crop can be managed to avoid prolonged exposure to adverse environmental conditions during seed maturation, higher vigour seed may be produced.

The importance of the climatic components of the environment are well recognised for seed production (Delouche, 1980) but not always for seed quality. Yet in garden peas in New Zealand, season and region of production (Table 4), location of the crop within a district, position of the plant within the field and position of the pod within the crop have all been shown to affect seed vigour as determined by the incidence of hollow heart and the conductivity of seed lots (Hampton and Scott, 1982; Hampton, 1985; Castillo *et al.*, 1993). Adam *et al.* (1989) showed that delaying sowing of soybean in Ohio from 30 April to 30 May significantly increased seed quality (as determined by conductivity and accelerated ageing testing), and explained this result by suggesting that the later sowing avoided seed maturing in hotter and more humid conditions (TeKrony, *et al.*, 1980). Castillo *et al.* (1994) also found that delaying sowing produced higher vigour garden pea seed (Table 5), and also suggested this response was explained

Table 3. Trends in soybean seed germination and vigour following different harvest times[1]

	Germination (%) before and after accelerated ageing when seed was hand harvested at:							
	physiological maturity		harvest maturity (HM)		14d after HM		28d after HM	
Year	before	after	before	after	before	after	before	after
1973	98	94	98	88	94	58	93	65
1974	94	85	91	83	92	85	90	41
1975	84	89	94	85	96	66	91	57
1976	91	96	82	58	87	65	82	52
1977	79	79	82	69	77	66	79	50

[1]Modified from TeKrony *et al.* (1980)

Table 4. Effect of region of production and season on seed vigour parameters in garden pea cv. Small Sieve Freezer[1]

	Percentage of seed lots with :	
Region/Season	hollow heart <10%	conductivity <20TScm/g
Wirarapa		
1981	71	16
1982	65	7
1983	76	8
Canterbury		
1981	93	14
1982	61	20
1983	95	34

[1]data adapted from Hampton (1985)

Table 5. Effect of time of sowing on the quality of garden pea seed harvested at 15% seed moisture content[1]

		Quality parameters of harvested seed		
Time of sowing	Harvest date[2]	germination (%)	conductivity (µs/cm/g)	hollow heart (%)
1988/89				
Nov	27 Jan	90a	15.28b	11.8b
Dec	24 Feb	96a	11.86a	2.8a
1989/90				
Nov	24 Jan	92a	13.25b	12.2b
Dec	20 Feb	93a	7.94a	6.3a

[1]data adapted from Castillo *et al.* (1994)
[2]hand harvested

by differing environments during seed development, as both humidity and rainfall were lower in February (when the December sown crop matured) than January (when the November sown crop matured). Importantly, results such as these suggest that the optimum sowing time for producing high quality seed is not necessarily the same as that for grain production. For example early May is the sowing date for maximum soybean yield in Ohio (Adam *et al.*, 1989) while in peas, yield is reduced as spring sowing is delayed (Gane *et al.*, 1984).

At least three environmental factors can contribute to seed vigour loss after physiological maturity (Dornbos, 1995).

i alternate drying and wetting (weathering): Woodstock *et al.* (1985) found that in cotton, weathering caused disruption to cell membranes, while there was also evidence of changes in both lipid and protein bodies as well as loss of ribosomes and impaired respiratory capacity (Coolbear, 1995).

ii hot, dry weather: Dornbos *et al.* (1989) reported that larger quantities of total phospholipids were isolated from soybean seeds that developed under high temperature and drought stress, and postulated that this may negatively influence membrane integrity (see Dornbos, 1995). Increased electrolyte leakage was associated with high temperature in garden peas (Castillo, 1992) and soybean (Spears *et al.*, 1997), and heat stress during durum wheat seed development resulted in metabolic changes (reduced ATP levels and embryonic mitochondrial activities) and the degeneration of mitochondria. Germination *per se* was not affected but seed vigour was significantly reduced (Grass, 1995).

iii Warm, humid weather: such conditions prolong the desiccation period (i.e., the decline in seed moisture from ca. 50 % to ca. 14 %), and the continual respiration and consumption of readily metabolised cell contents such as sugars can reduce vigour (TeKrony *et al.*, 1980). In addition, these environmental conditions favour pathogen attack which may also contribute to seed deterioration through physical damage and biochemical degradation (Coolbear, 1995).

Nutrition of the mother plant

It is a long held belief that when soil fertility becomes limiting, plants respond by producing less seed rather than reducing seed quality *per se*. Is this assumption correct?

Elemental deficiencies and imbalances during seed development may affect seed vigour, particularly if they influence cell membrane integrity (Padrit *et al.*, 1996). Calcium deficiency, for example, plays an important role in loss of membrane integrity (Hecht-Buchholz, 1979; Powell, 1986). However, most of the limited information available refers to the effects of nitrogen (N) and phosphorus (P), the hypothesis being that because both these elements are major constituents of proteins and phospholipids, the 'building blocks' of cell membranes, deficiencies or imbalances may affect seed vigour (Hadavizedeh and George, 1988). These authors reported that lower garden pea seed protein concentration and reduced amounts of protein per seed were associated with higher conductivity from hand harvested seeds, which by implication suggests poorer cell membrane integrity. Padrit *et al.* (1996) showed that increasing N application significantly increased garden pea seed vigour as conductivity and hollow heart were reduced (Table 6), while P application had no effect on conductivity but did reduce hollow heart (Table 7). In the herbage grasses browntop (*Agrostis capillaris* L.) and perennial ryegrass (*Lolium perenne* L.) Bennett *et al.* (1998) have shown that as seed N concentration increased seed vigour increased, thus supporting the earlier work of Ene and Bean (1975) who reported that increasing maternal N increased seed vigour.

Despite these reports, a direct link between soil fertility, fertiliser application rate, seed protein and phospholipid content, cell membrane integrity, and the ability of the developing seed to withstand environmental stress still remains to be established (Padrit *et al.*, 1996; Rowarth *et al.*, 1998) mainly because in New Zealand, the detailed experimental work required has failed to attract funding.

Position on the mother plant

The influence of seed position on seed quality has been investigated in many species, and components such as seed size, embryo size, germination and vigour are known to vary, depending on such factors as assimilate supply, photosynthetic activity, plant morphology, maturity and the micro-environment. Adam *et al.* (1989) reported that soybean seed from the upper part of the canopy exhibited higher vigour as compared to seeds from the bottom portion, and suggested that assimilate supply and environmental stress factors could account for these differences. In contrast Castillo *et al.* (1993) and Padrit *et al.* (1996) reported that garden pea seeds from the top pods in the canopy had greater hollow heart and higher conductivity (i.e., lower vigour) than did seeds from lower positions, although this response was influenced by cultivar and plant population, and nitrogen application (Table 8). Hollow heart incidence is known to increase with length of exposure to temperature >25°C (Halligan, 1986), possibly because seed protein synthesis is disrupted. It is also possible that top pods do not receive the same allocation of assimilates as received by older lower pods, and that this competition results in weaker seed membranes and greater susceptibility to hollow heart (Flinn and Pate, 1968).

Stage of maturity at harvest.

Seeds attain physiological maturity at seed moisture contents (SMC) ranging from 40-60 % depending on the species, and then continue to lose moisture until 'harvest maturity' is reached. When seed is harvested will obviously impact on seed vigour. In attempts to prevent yield loss through seed shedding, some vegetable seed crops are combine harvested at physiological maturity (Gray, 1987) and the physical disruption to cell contents following this mechanical impaction will accelerate seed deterioration. Other seed crops such as the herbage grasses may be direct harvested at 35-42 % SMC, or swathed at ca 40 % SMC and left to reach 'harvest maturity' (ca 14 % SMC) in the swath.

However, do 'traditional' harvest methods necessarily produce the highest vigour seed? In garden pea, Gane *et al.* (1984) found that harvesting at around 25 % SMC minimised harvest damage and produced higher quality seed than when harvest was at 15 % SMC, a result confirmed by Castillo *et al.* (1992) (Table 9). At 25 % SMC, seeds were better able to withstand the shocks of mechanical harvesting (less physical damage), and also had a reduced exposure to high temperatures and humidity (Castillo *et al.*, 1992). However for safe storage, seeds harvested at these moisture contents must then be dried, and this process may also affect seed vigour (Hampton, 1992b).

Table 6. Effect of nitrogen application on seed quality parameters in garden pea cv. Pania following hand harvesting at 15% seed moisture content.[1]

N (kg/ha)	Germination (%) before AA[2]	Germination (%) after AA	Conductivity (μS cm/g)	Hollow Heart (%)
0	96	57	16.6	17.3
100	96	61	15.4	9.3
200	98	67	13.2	4.1
LSD $_{P<0.05}$	NS	3.5	2.21	3.91

[1] adapted from Padrit *et al.* (1996)
[2] accelerated ageing vigour test

Table 7. Effect of phosphorus application on seed quality parameters in garden pea cv. Pania following hand harvesting at 15% seed moisture content.[1]

P[2] (kg/ha)	Germination (%) before AA[3]	Germination (%) after AA	Conductivity (μS cm/g)	Hollow Heart (%)
0	95	61	15.8	12.1
22.5	95	66	15.3	7.3
LSD $_{P<0.05}$	NS	4.0	NS	2.16

[1] adapted from Padrit *et al.* (1996)
[2] prior to application the site had an Olsen P of 13 μg/g
[3] accelerated ageing vigour test

Table 8. Interaction between nitrogen application rate and pod position for the incidence of hollow heart in garden pea cv. Pania hand harvested at 15% seed moisture content. (LSD$_{P<0.05}$ = 3.10.) [1]

N (kg/ha)	Hollow heart (%) in seeds from: bottom pods	middle pods	top pods
0	13.8	15.7	24.3
100	6.8	8.8	11.3
200	2.5	3.0	2.8

[1] adapted from Padrit *et al.* (1996).

Table 9. Effect of seed moisture content at harvest on the conductivity and hollow heart of hand harvested seeds of two garden pea cultivars.[1]

Seed moisture (%)	cv.Pania conductivity (μ/cm/g)	cv.Pania hollow heart (%)	cv. Princess conductivity (μ/cm/g)	cv. Princess hollow heart (%)
40	27.1	8.7	11.3	3.1
25	16.3	11.8	12.2	14.8
15	19.5	21.5	13.3	14.5
LSD $_{P<0.05}$	2.33	1.64	0.94	1.69

[1] data from Castillo *et al.* (1992)

Post-harvest treatments

After harvest, seed will often need to be dried to reduce SMC to a level considered safe for storage (from 8-14 % SMC depending on the species). This may be achieved by using either cool or heated air, and the risk of completely killing seed during this process is high, particularly for inexperienced operators (Hampton, 1992b). However while experienced growers can dry seed and maintain germination, little is known of the effects of this process on seed vigour. Hampton and Hill (1990) reported that prairie grass (*Bromus willdenowii* Kunth) seed which was left to air dry, rather than dried with heated air, had similar germination but greater vigour (Table 10). Thuy *et al.* (1999) reported that maize seed germination and vigour could be maintained following high temperature (60°C) drying followed by tempering for 45 minutes at 21°C, providing the drying time did not exceed 10 minutes per cycle. Increasing the drying time to 15 minutes per cycle significantly reduced seed vigour, but not germination.

Post-harvest seed treatment also includes cleaning and transport, and Hampton (1991) suggested that the first step in evaluating the effects of production practices on seed vigour should be with the mechanised processes. Physical damage is regularly detected (Scott and Hampton, 1985) and damage at the cellular level must therefore also be occurring.

Genetic effects

Genetic differences exist among cultivars for the ability to acquire and maintain good seed quality in stressful environments, but these differences appear to be small in comparison with the effect of stress itself (Dornbos, 1995). Nevertheless, it is possible to select for seed properties which would reduce/delay seed vigour loss. For example Kuo (1989) found that a small number of soybean cultivars had seed coats which were 'delayed permeable', i.e., seeds were not hard, but imbibition did not begin until at least one hour after soaking began. Selection for this character would allow better maintenance of vigour, because seeds would be less susceptible to cycles of wetting and drying prior to harvest (Kuo, 1989). Plant breeders have often inadvertently selected for increased seed vigour (Copeland and McDonald, 1995), but there is a need for more specific selection where enhanced seed vigour is a primary objective.

Table 10. Effect of harvest method and drying method on germination and vigour of seed of Prairie grass cv. Grassland Matua sampled during the drying process.[1]

	Moisture content	% germination	
Treatment	of sample	initial	after AA[2]
1. Direct combine 45% SMC, then hot air dried at 30°C.	20%	93	66
	12%	93	66
2. Direct combine 45% SMC, cool air dried to 39% SMC then hot air dried at 30°C.	39%	91	90
	12%	92	85
3. Swath 45% SMC, combine 30% SMC, then hot air dried at 30°C.	15%	92	56
	11%	95	53
4. Swath 45% SMC, combined 22% SMC, then unheated forced air dried.	22%	98	91
	13%	98	89
	11%	97	83

[1] data from Hampton and Hill (1990)

[2] accelerated ageing test for vigour

Conclusion

Nearly 20 years after TeKrony *et al.* (1980) concluded that "a chronic problem facing the seed industry is the production of seeds that possess low vigour" we still know little about how seed production processes and the environment interact to affect the physiological processes that determine seed vigour. There are some sections of the seed industry who would not agree that this is a chronic problem, and are content to ignore seed vigour and all its implications. Yet seed vigour is important to many growers, traders and users of seed, and the demand for seed vigour information is increasing (Hampton and TeKrony, 1995).

The subject of seed vigour is complex, and one that presents many challenges for seed technology and seed physiology. There is a need for a much greater understanding at the physiological and biochemical level of the factors which limit seed performance; there is probably a need to modify production systems to consistently produce high vigour seed, and to recognise that conditions for maximising yield may not be the same as for maximising quality. The opportunities for quality research are many, but little will be achieved if seed industry support is not forthcoming.

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