The Effect of Storage Environment on Seed Longevity

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SUMMARY

Seed moisture content, temperature, length of storage and atmospheric gases are the main factors affecting loss of seed viability and the induction of genetic damage during long-term storage of seeds.

Although seeds are evaluated in three categories in terms of their storage behaviour, long-term storage is normally the preferred method of genetic conservation for orthodox seeds. Therefore, this review concerns the effect of storage environment on longevity of orthodox seeds.

Key words: Storage environment, seed longevity, genetic conservation.

ÖZET Tohum Ömrü Üzerine Depolama Ortamının Etkisi

Tohum nem kapsamı, sıcaklık, depolama süresinin uzunluğu ve atmosfer gazları, tohumların uzun süreli depolanmasında canlılık kaybını ve genetik bozulmanın teşvik edilmesini etkileyen başlıca faktörlerdir.

Depolama tavırları ile ilişkili olarak tohumlar üç kategoride değerlendirilmelerine rağmen, uzun süreli depolama normal olarak orthodox tohumların genetik muhafazasında tercih edilen yöntemdir. Bu nedenle, bu inceleme depolama ortamının orthodox tohumların ömrü üzerine etkisi ile ilgilidir.

Anahtar sözcükler: Depolama ortamı, tohum ömrü, genetik muhafaza.

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INTRODUCTION

In most cases, germplasm is stored as seeds, which provide the easiest, safest and most economical method of long-term conservation of genetic resources. The vast majority of economic crop species (arable and horticultural crops) have seeds which can be successfully dried to low moisture contents and stored at low temperatures for long periods without any loss of viability; these are described as orthodox seeds. However, there are exceptions to these generalizations, in particular those seeds which are known as recalcitrant, which cannot be dried without damage. Therefore, their survival is typically limited to a few weeks or months. The seeds of many tropical plantation crops, many tropical fruit crops and a number of temperate and tropical species are recalcitrant (Roberts, 1973).

Recently, Ellis et al. (1990a, 1991a, b) have suggested that there is a third category of seed storage behaviour intermediate between the above categories defined by Roberts. Seeds with intermediate storage behaviour, e.g. coffee and papaya, can be dried safely to about -90 MPa and sometimes to -150 MPa, but further desiccation reduces viability of the surviving seeds. This range is clearly intermediate between the -2 MPa to -3 MPa at which recalcitrant seeds such as cocoa are killed (Roberts and Ellis 1989) and the - 350 MPa or so which is the limit in orthodox seeds can be safely dried to very low moisture contents (Roberts and Ellis 1989, Ellis et al. 1989). In species with intermediate-type seeds of tropical origin, reduction in seed storage temperature from 15°C to 0°C and below may also reduce the longevity of the dry seeds (Ellis et al. 1990a, 1991a, b).

Since long-term refrigerated storage (i.e. - 18° C or less in air-tight containers at a seed moisture content of 5 ± 1 %) is normally the preferred method of genetic conservation for orthodox seeds (IBPGR 1976), the present review concerns the seeds of orthodox type.

It is now well established that several factors (e.g. seed moisture content, temperature, length of storage and atmospheric gases) affect loss of seed viability and the induction of genetic damage in storage. In this review, the effects of these factors are given in detail.

1. SEED MOISTURE CONTENT, TEMPERATURE AND LENGTH OF STORAGE

A great deal of early work has shown that the main factors affecting longevity are temperature and seed moisture content, and a number of attempts were made to quantify their effect (Roberts 1988).

The relationship between seed moisture content, temperature and viability was first described quantitatively by Roberts (1960) in viability equations, developed for wheat, which predicted percentage seed viability under a range of temperatures and moisture content after any period of storage. The same predictions were then shown to apply to other species, e.g. rice (Roberts 1961a), barley, peas and broad beans (Roberts and Abdalla 1968).

But, these equations had two faults: they were only accurate within limited ranges of temperature and moisture content and, more important, they failed to take into account the initial quality of the seeds which also has a considerable effect on their longevity. Consequently, the original equations have been modified by Ellis and Roberts (1980a, b), for barley, to produce a single improved viability equation which overcomes these problems, and is applicable over a very wide range of storage environments: from 3°C to 90°C and 5 % to 25 % moisture content (f.wt). This equation has, then, been shown to be applicable to all species to which it has been applied, e.g. onion (Ellis and Roberts 1981), soybean, chickpea and cowpea (Ellis et al. 1982) and lettuce (Kraak and Vos, 1987). Recently, Dickie et al. (1990) have proved that this viability equation is applicable over a wider range of storage environments: from -20°C to 90°C and 1.8 % to 25 % (f.wt), in the cereal barley, the grain legumes chickpea, cowpea and soybean, the leaf vegetable lettuce and the timber trees elm, mahogany and terb.

The improved viability equation is based on the proposition that in a constant storage environment, the distribution of individual seed life-spans within a population (seed lot) is normal, so that survival curves are cumulative normal distribution of negative slope. Transformation of percentage viability to probits (or normal equivalent deviates) results in linear survival curves and can be described as (Ellis and Roberts, 1980a):

$$v = K_i - p / \sigma \tag{1}$$

where

v - is probit of percentage viability after storage,

p - is storage period,

σ - is the standard deviation of individual seed life-spans, and

 K_i - is the seed lot constant and is the intercept value at zero storage time of the probit survival curve.

The value of K_i indicates the quality and potential longevity of the seed lot and consequently its value varies between seed lots. It depends on both genotype and pre-storage environment. The pre-storage environment includes the conditions experienced around the time of harvest (Roberts 1983). In addition, the pre-storage environment includes the seed drying process which can also affect the K_i value (Nellist 1981).

However, the K_i value is not affected by the storage environment which can only affect the slope $(1/\sigma)$ of the survival curve: the better the storage conditions, the larger the value of σ . Ellis and Roberts (1980a, b, 1981) showed that σ is affected by seed moisture content and storage temperature as follows:

$$\sigma = 10^{K_E - C_w \log m - C_H t - C_Q t^2}$$
 (2)

where

m - is moisture content (percent wet weight basis),

t - is temperature (°C), and

 $K_{\text{E}},\ C_{\text{W}},\ C_{\text{H}}$ and C_{Q} - are constants within a species but which differ between species.

Substituting the right side of equation (2) for σ in equation (1) gives:

$$v = K_i - p / 10^{K_E - C_w \log m - C_H t - C_0 t^2}$$
 (3)

which can be used to predict percentage viability (since v is probit of percentage viability) after any storage period, p, at moisture content, m, and storage temperature, t. K_i has to be determined separately for each seed lot; but within a given species, the four constants (i.e. K_E , C_W , C_H and C_Q) in the exponent of equation 3, which together determined the slope of the survival curve, do not vary. They are not affected by either genotype or pre-storage conditions, i.e. they are not affected by seed quality (Roberts 1983).

2. SEED MOISTURE CONTENT

We already know that there is a negative logarithmic relationship between seed longevity and moisture content (Ellis and Roberts 1980b, 1981, Ellis et al.

1982, 1986, 1988, 1989, 1990b, c, Kraak and Vos 1987). A lower limit of this relationship has been shown for many diverse species (Ellis et al. 1988, Roberts and Ellis 1989). The value of this lower limit varies considerably among species, e.g. from 2 % in groundnut (Ellis et al. 1990d) to 6.2 % moisture content in pea (Ellis et al. 1989). This lower limit to the otherwise negative logarithmic relations between longevity and moisture thus provides a practical limit to seed desiccation for storage (Ellis 1991).

However, seed longevity in many crops examined responds identically to differences in equilibrium relative humidity and, thus, water potential. This relationship extends to about 10-11% equilibrium relative humidity, or water potentials close to -350 MPa, below which further desiccation begins to remove the strongly bound water fraction (Ellis et al. 1989, 1990b, c). The partial removal of this fraction has little or no further influence on seed longevity, presumably because it has little chemical potential. It is suggested that most orthodox seeds could be stored at this water potential for long term storage. More importantly, for many oily seeds, it corresponds to values significantly lower than the current recommended seed moisture content of 5 % (i.e. between about 2 % and 4 %, depending on the critical moisture content for the particular species) (Ellis et al. 1990d).

There is also an upper limit to the negative logarithmic relations between longevity and moisture. Previously, Villiers (1973, 1975) and Villiers and Edgcumbe (1975) showed in lettuce that seeds stored fully hydrated can survive for long periods without significant loss of viability. However, Ibrahim and Roberts (1983) and Ibrahim et al. (1983) concluded that, under anaerobic conditions the trend of decrease in longevity with increase in hydration continues up to about 27 % moisture content, but above this value there is no further change in longevity. In contrast, under aerobic conditions (if oxygen is freely available) longevity increases exponentially up to 44 % moisture content, this increase starting at about 15 % moisture content at 20°C and at about 24 % at 35°C. Therefore, the upper limit occurs whether or not oxygen is available, but there is no improvement to longevity at higher moisture contents without the free availability of oxygen. An upper limit to the negative logarithmic relations between longevity and moisture has also been determined in other species, e.g. in onion (Ward and Powell 1983), in wheat (Petruzzelli 1986), in niger and tef (Zewdie and Ellis 1991). According to Roberts (1988) and Zewdie and Ellis (1991), the value of this upper limit (a common minimum water potential) is probably between -14 and - 15 MPa.

3. TEMPERATURE

Previously, it was thought that relations between the logarithm of seed viability period and temperature at one moisture content were linear and negative (Roberts 1961a, 1972, Roberts and Abdalla 1968), and the temperature coefficient, Q₁₀ (for change in rate of loss in viability per 10°C rise in temperature), was not expected to vary with temperature (Roberts 1972). However, later, it was found in barley seeds that Q₁₀ was not stable but increased quite dramatically with increasing temperature. To quantify this variation, the basic semi-logarithmic relationship was modified by the addition of a quadratic term (Ellis and Roberts 1980a, b).

It is now well established that this model describing the relative effect of temperature and the longevity of barley seed between -20°C and 90°C also explains all previous, divergent reports of the value of Q₁₀ for a wide range of species, including cereals, legumes, vegetables, grasses and ornamentals (Ellis and Roberts, 1981). Furthermore, this basic model can be applied to other species (Ellis and Roberts 1981, Ellis et al. 1982a, Kraak and Vos 1987, Dickie et al. 1990).

4. GASES

For many years, research has been conducted on the effects of a partial vacuum and also gases such as carbon dioxide, oxygen, nitrogen, helium and argon on the longevity of various kinds of seeds (Roberts 1961b, Bass et al. 1963a, b, Harrison, 1966, Rao and Roberts 1990). However, the results were complex and some of them were conflicting.

Under most conditions, storage in nitrogen resulted in a longer period of viability than storage in air under similar conditions of temperature and moisture. Increases in the concentration of oxygen during storage decreased the viability period most rapidly (Roberts 1961b, Harrison 1966). Roberts (1961b) concluded that carbon dioxide was certainly not markedly deleterious to viability. However, Bass et al. (1963a, b) indicated little or no special advantage of using a vacuum, air, carbon dioxide, nitrogen, helium or argon in terms of seed viability.

In a further study, Ibrahim et al. (1983) proposed that above the critical moisture content, which varies between species, repair mechanisms are activated and are sustained by respiration in the presence of oxygen. Therefore, seed moisture content is an important factor in a gaseous environment during storage (i.e. at the low moisture content oxygen is deleterious to seed survival but at the high moisture content it has a beneficial effect in improving longevity).

Recently, Rao and Roberts (1990) concluded that the beneficial effect on longevity observed in the nitrogenous atmosphere at low moisture content is only marginal and also, replacing air with nitrogen would not reduce the amount of genetic damage accumulating for any given loss of seed viability. They also concluded that with the additional technical complications associated with replacing the air in the storage atmosphere, the use of inert gases or a vacuum in controlling genetic deterioration and improving longevity in seed storage seems unwarranted.

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