CORRESPONDENCE

Seed dormancy

Introduction

This letter is not as much an expression of disagreement as an, in my view, very essential extension of Marc Cohn's opinion paper on seed dormancy research (Cohn, 1996). I will not dispute the several definitions of dormancy and germination discussed in his paper. Recent discussions on the Seed Biology Internet have clearly shown that it is virtually impossible to reach some kind of consensus that could be used in a meaningful way in seed research. Here I will mainly focus on the differences and transitions between the dormant and non-dormant states as depicted in Figure 2 of Cohn's article.

Dormant, non-dormant, slow-germinating or dead seeds?

The 4 states mentioned in this heading all have in common that they are characterized by the absence of germination. Yet, a distinction between these states is a major pre-requisite for meaningful research.

In many species there is no problem in assessing whether seeds are dead or viable. However, as pointed out by Cohn there may be a major problem when dealing with wild species. A recent survey in our laboratory of *circa* 30 species from the French Pyrenees for dormancy yielded several batches of seeds that were not germinating under any of the conditions applied. Neither removal of the embryo, nor application of gibberellins resulted in signs of growth. Tetrazolium tests were negative and, thus, we were inclined to declare these seeds dead. However, extended cold treatments resulted in very slow but normal germination of up to 30% (N. Overmars and N. Smits, personal communication).

A major constraint to studying dormancy, according to Cohn is the continuum between dormancy and germination. This makes it awkward to attribute observed events to either process. This is true for many crop species. Most crop seeds lack dormancy as a result of extensive breeding. Although dormancy in crop seeds may occur, especially under stress conditions, or as a result of certain growing conditions, it is not a general characteristic. This feature makes crop species not particularly suitable for dormancy studies. For this purpose wild species are the obvious choice, since in the natural environment dormancy plays a quintessential ecological role in the survival of species.

Many weedy annuals of the temperate zone show seasonal dormancy cycling (e.g. Karssen, 1982; Baskin and Baskin, 1985). Most of them have an absolute requirement for light and often also for nitrate. It has been shown that during the periods of dormancy the seeds may be completely insensitive to light and nitrate (e.g. Bouwmeester and Karssen, 1993). In my opinion, this feature makes these wild species the preferred and maybe only objects in which dormancy can be successfully studied. Because of their absolute dependency on germination stimulants, they provide us with the tools to separate the state of non-dormancy from germination. Thus, a comparison between dormancy and non-dormancy can be made.

Sisymbrium officinale, a model species for dormancy research?

The cruciferous species *Sisymbrium officinale* has been utilized for dormancy and germination studies in the Dept. of Plant Physiology since the early seventies. Important reasons for choosing this species at the time were: abundance, ease of harvesting, absolute dependency on light and nitrate for germination, easily manipulatable dormancy levels, and high stability during dry storage. For example, a recently tested seed batch from 1987, stored dry at 4°C in a sealed plastic container, did not differ significantly in performance compared to the tests executed in 1988 and later years. Thus, in contrast to *Arabidopsis thaliana* seeds (Derkx and Karssen, 1993), dormancy levels in *Sisymbrium officinale* do not show fluctuations during storage and do not exhibit detectable ageing during 10 years of dry storage.

Studies with *S. officinale* over the past decade have led to a model for regulating dormancy by temperature through changes in availability of receptors for phytochrome and nitrate (Hilhorst *et al.*, 1996). The basic assumption was that the sensitivity to naturally occurring environmental factors was the principal regulatory principle. These studies were possible because the seeds only germinated in the presence of light and nitrate. In other words, the transition from the non-dormant state to the germination phase could be effectively blocked by depriving the seeds of light and nitrate (Fig. 1). There may be ecological arguments that light and nitrate are the signals that initiate the germination process of perceptive (non-dormant) seeds. It seems inopportune for seeds to start germination before the perception of these signals. The progress of germination requires energy. However, those seeds in the soil seed bank that will not be exposed to light and nitrate will have 'wasted' energy, as they will enter (secondary) dormancy after prolonged periods of non-dormancy. We know that seasonal dormancy cycling may continue for very
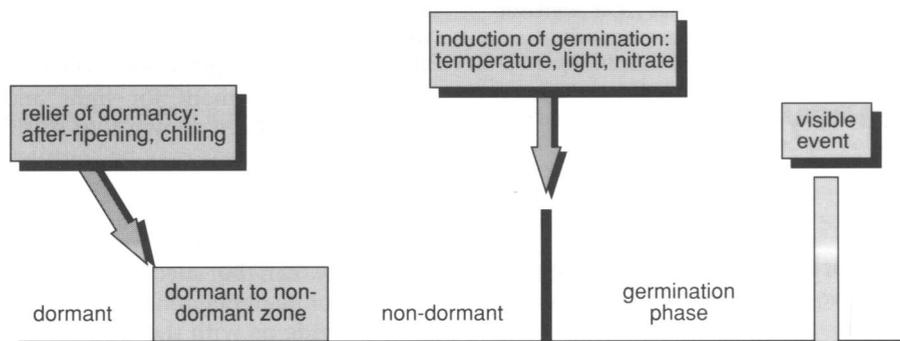
Figure 1. Scheme of dormancy-breaking and germination processes. Modified from Cohn (1996).

long periods and, thus, it seems plausible to assume that utilization of energy is very economical.

When breaking dormancy of *S. officinale* seeds by e.g. chilling, sensitivity to light and nitrate increases. There are indications that sensitivity of all the seeds in the population is maximized to approximately similar levels. For example, fluence-response curves after dormancy relief are often unusually steep: the whole seed population germinates within a very narrow range of fluence values (Hilhorst and Karssen, 1988).

A very clear example of a block to the transition from non-dormancy to the germination phase comes from studies by Derkx *et al.* (1993). Respiratory activity was measured during imbibition of *S. officinale* seeds that were either dormant or non-dormant, before and after exposure to light and nitrate (Fig. 2). Oxygen uptake rate only increased after exposure of non-dormant seeds to light and nitrate. In the absence of these factors, both dormant and non-dormant seeds showed similar low levels of oxygen uptake. The experiments also showed that increased oxygen uptake occurred within 5 h after exposure to light and nitrate whereas visible germination could not be detected until after 24 h. Thus, measurable changes in metabolic activity may occur at relatively early stages of germination and give rise to confusion with dormancy relief.

Conclusion

In a group of weedy species the non-dormant state can be separated from the germination phase by the characteristic feature of these species that light and/or nitrate are absolute requirements for the initiation of germination. The well studied species *Sisymbrium officinale* seems very promising as a model for in-depth molecular studies. The great advantage of this species is that, by easy manipulation, populations
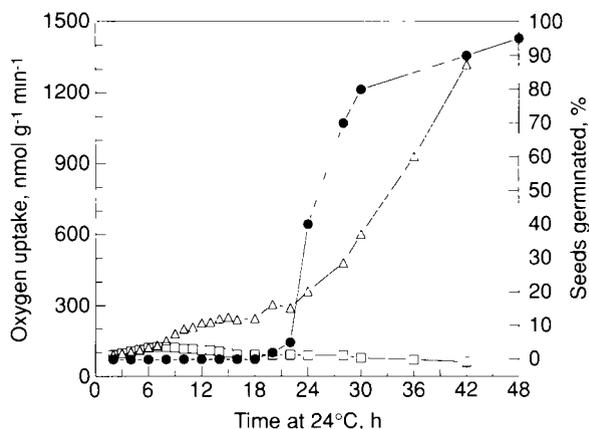
Figure 2. Rates of O_2-uptake of non-dormant, non-germinating (□) and of non-dormant, germinating seeds (△) of *Sisymbrium officinale*. Seeds were kept at 24°C in 25 mM KNO_3 in the dark (□) or were irradiated with a 15-min red light pulse after 105 min and returned to darkness (△). Germination of the red irradiated seeds was scored at various times after the red light pulse (●). O_2-uptake was measured at 24°C under dim green light. Note that seeds are largely dormant after 48 h of dark incubation. Redrawn from Derkx and Karssen (1993).

can be made dormant or non-dormant, and, may be synchronized in the non-dormant state.

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