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Abstract

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Keywords

question, just, than, dormancy, germinate, not, more

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RESEARCH OPINION

To germinate or not to germinate: more than just a question of dormancy

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Keywords: dormancy, germination, light, nitrate, restoration, smoke, temperature

Consider the following four quotations concerning the distinction between breaking dormancy and stimulating germination.

To many people, seed dormancy simply means that a seed has not germinated, but we will soon see that this definition is inadequate. Unfavourable environmental conditions are one reason for lack of seed germination. That is, seeds could be in a paper bag on the laboratory shelf (i.e. lack of water), buried in mud at the bottom of a lake (i.e. insufficient oxygen and/or light), or exposed to temperatures that are above or below those suitable for plant growth. These obviously unfavourable conditions for germination are examples of how the environment rather than some factor associated with the seed *per se* prevents germination. A second reason why seeds may not germinate is that some property of the seed (or dispersal unit) prevents it. Thus, the lack of germination is a seed rather than an environmental problem. Dormancy that results from some characteristic of the seed is called organic dormancy, and this type of dormancy usually is of most interest to seed biologists and ecologists. (Baskin and Baskin, 1998)

The switch to germination represents a transition to or from one stable non-germinating state to another germinating state. As such, germination control can be viewed as a classical bifurcating system with two stable attracting states: non-germination and germination (Tyson *et al.*, 2003). In-between lies a critical unstable transition that is passed as the system flips from the unstable state that provides the borderline (and thus quantifies the critical point for transition) between the two stable ones. The role of

dormancy is to modify the sensitivity of seeds to signals that flip the switch. (Penfield and King, 2009).

... the distinction between the agents responsible for dormancy alleviation (time, temperature and moisture) and those germination agents such as smoke (butenolide), nitrates and light whose roles are more appropriately defined as germination stimulants that act only once dormancy has been alleviated. (Merritt *et al.*, 2007)

If one equates dormancy with failure of germination, Vegis' theory would imply that, except for seeds that are fully dormant, the dormancy of seeds kept at a temperature outside the range required for germination can be relieved by transferring them to a temperature inside this range. This view is shared by Bewley & Black (1982), who stated that dormancy may vary with external conditions, usually of temperature. On the other hand, dormancy is supposed to be an adaptive trait (e.g. Simpson, 1990). This implies that dormancy should not be a measure of the external conditions a seed is currently exposed to, but be a characteristic of the seed. We believe that these inconsistencies result from an inaccurate definition of dormancy. Firstly, dormancy should be able to have any value between all and nothing, and, secondly, it should be a seed trait (cf. Gordon, 1973).

Karssen (1982) emphasized that seasonal periodicity in the field-emergence of annuals is the combined result of seasonal periodicity in the field temperature and seasonal periodicity in the width of the range of temperatures suited for germination. Germination in the field is restricted to the period when the field temperature and the temperature range over which germination can proceed overlap. Dormancy is only related to the width of the temperature range for germination, not to the question whether or not the current temperature is inside this range. Derkx & Karssen (1993a) showed that in *Sisymbrium officinale* changes in dormancy not only comprise changes in temperature requirements for germination, but also in its requirements for nitrate and light. Sensitivity to light and nitrate, both necessary

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stimuli for the germination of this species, increased when dormancy was broken and decreased when dormancy was induced. Generalizing the concept of Karssen (1982), which is solely based on one factor, temperature, one may say that germination occurs when internal requirements and external factors meet. Dormancy is only related to the requirements for germination, not to the question whether or not these requirements are met in a particular environment. This is the reason why we oppose Harper's (1959) concept of dormancy. Standstill of plant growth, which he calls dormancy, only indicates that the requirements for growth are not met. We propose a different definition of seed dormancy: *dormancy is a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate*. The wider the range of conditions at which a seed is able to germinate, the smaller its degree of dormancy (cf. Hilhorst, 1993). One could regard dormancy as the seed's fastidiousness about the germination conditions it requires, whereas germination is the seed's response to an overlap of the environmental conditions and the germination requirements, defined by the degree of dormancy. (Vleeshouwers *et al.*, 1995)

That all seems quite clear, doesn't it? In fact, Vleeshouwers *et al.* (1995) make the point with such elegance that it can scarcely be improved upon. Despite the serious harm inflicted on our understanding of seed dormancy by Harper (1959, 1977), we had always been happy in the belief that the damage had been repaired long ago, and that all seed biologists now appreciate the simple, yet crucial, distinction between germination and dormancy. Therefore you can imagine the surprise and dismay we felt, at the recent ISSS Seed Ecology Conference in Utah, that the opinion from several speakers was that (physiological) dormancy is broken by light, smoke, nitrate or diurnal temperature alternations.

At the risk of repeating what has already been said *ad nauseam* by others, let us explain several serious problems with this approach. First, if *anything* that makes a seed germinate can be said to break dormancy, then several things follow: any seed whose current requirements for germination are not met by its environment is dormant by definition; thus *all* seeds not actually germinating are dormant; dormancy breaking and germination stimulation become synonymous; and dormancy ceases to have any independent meaning. In response to this difficulty, we have heard the feeble excuse that, of course, seeds that are just dry aren't dormant, because water is essential for germination, whereas the other cues mentioned above are somehow 'optional'. But this requires a highly arbitrary definition of 'essential'. For example, is oxygen 'essential' for seed germination? Before you answer, consider that anoxia is essential for germination in

some species (Probert and Brenchley, 1999). And try telling a small seed buried beneath 10 cm of soil that light is 'optional'.

Second, whatever the underlying molecular events, there is a very clear ecological distinction between dormancy breaking and germination. Dormancy is essentially a calendar that enables a seed to keep track of the changing seasons. Thus in the tropics, a seed's prior experience of temperature and moisture tells it whether it is at the start of the dry season (probably bad for germination) or at the end (probably good). In temperate climates, previous experience tells the seed whether it's spring or autumn, and depending on local climate, either season may be the best for germination; sometimes this varies even in the same species (Skordilis and Thanos, 1995). In both cases dormancy breaking and/or acquisition involve slow changes to the seed itself that gradually change its willingness to germinate. But these changes do not in themselves guarantee that germination will take place; in fact in species with persistent soil seed-banks, dormancy may wax and wane for years or even decades without germination occurring. Only if the seed experiences an appropriate cue that informs it of a favourable current environment while (relatively) non-dormant will germination occur. Light confirms there has been some disturbance that has brought a buried seed to the surface, smoke that there has been a fire, alternating temperatures and/or increased nitrate concentration that covering vegetation has been removed.

Third, distinguishing between dormancy and germination is not purely a theoretical exercise. Problems can just as easily be created in the more applied fields of research and conservation management. Take, for example, the rehabilitation of plant communities after disturbances such as mining. A lack of understanding of the difference between conditions required to reduce dormancy and cues that promote germination, can (and often does) lead to the misapplication of germination cues, like smoke, to dormant seeds. At best, this may promote germination of a proportion of the seed lot that may not be dormant at the time. At worst, it can result in a waste of effort, precious funding and expensive seed collecting work. Numerous germination studies take the same approach and, faced with no resulting germination, conclude erroneously that the cue tested does not affect germination. However, perhaps it could, if only the seed wasn't dormant. Without a distinction between dormancy and germination, results from experimental treatments on dormant seeds are often not clear and this can hinder subsequent research, by diverting attention away from developing the right questions in these applied areas: 'What factors control dormancy?' and 'Which cues promote germination once seeds are non-dormant?'

Thus a germination cue is a change in the *environment* that aligns that environment with the germination requirements of the seed; dormancy breaking is a change in the *seed* that determines what those requirements are. How could anything so simple be misunderstood, sometimes by people who ought to know better? Especially when problems that this misunderstanding causes can hinder restoration and waste money. Frankly, we don't know. Maybe the seeds of doubt are sown by undergraduate lectures, long overdue for revision, that still report the eccentric ideas of Harper (1959), who clearly couldn't resist a Shakespearean sound-bite. Perhaps others are confused by the complexity of the molecular events that underlie both germination and dormancy. Maybe some have trouble grasping that temperature can both break dormancy and stimulate germination, sometimes at the same time; that dormancy is a continuous variable; and that even non-dormant seeds can still require many cues to persuade them to germinate.

As the great Daniel Côme once remarked, there are only two questions in seed biology: 'What is germination?' and 'What is dormancy?' It's a pity that, at a very basic level, some of us are still getting the answer to at least one of those questions wrong.

Note from the Editor

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the SSR home page, or, in case of a substantial response, by means of an Opinion Paper.

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