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RESEARCH OPINION

Are seed dormancy and persistence in soil related?

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Abstract

There is confusion in the ecological literature between seed dormancy and persistence in soil. Some ecologists seem to assume that dormancy is necessary for persistence, while others imply that dormancy and persistence are virtually synonymous. Here, we show that there is no close relationship between dormancy and persistence and, incidentally, that conventional methods of investigating soil seed banks underestimate the persistence of species with dormant seeds. The confusion appears to arise from the concept of 'enforced dormancy', which is not genuinely dormancy at all, and would be eliminated if ecologists adopted the definition of dormancy employed by physiologists. Dormancy is a characteristic of the seed, not of the environment, the degree of which defines the conditions required to make the seed germinate.

Keywords: seed bank, seed dormancy, seed longevity, seed persistence

Introduction

In the ecological literature, it is widely assumed (although rarely stated explicitly) that seeds require some form of dormancy if they are to accumulate a persistent soil seed bank. Indeed, it is clear that many ecologists regard dormancy and persistence as essentially indistinguishable. For example: 'Seeds in a dormant state in the seed bank can be regarded as a "deposit account". In addition it is convenient to recognize and distinguish a "current account", a temporary stage in which the only hindrance to immediate germination is a shortage of water and a favourable temperature.' (Harper, 1977). For Harper, dormancy was clearly the normal state of seeds in the soil, with non-dormancy merely a transient stage between dormancy breaking and germination. Similarly, many theoretical treatments of the evolution of 'dormancy' are in fact concerned with persistence, not dormancy (e.g. Venable and Brown, 1988; Rees, 1997). Later, we consider how this confusion between dormancy and persistence has arisen, but first we briefly examine the relationship (if any) between these two states.

Data sources and methods

From Thompson *et al*. (1997) we were able to calculate an index of seed longevity in soil according to the method described in Thompson *et al*. (1998). The index can take any value from 0 (all records transient) to 1 (all records persistent). To include the largest possible number of species, we calculated the index for all species with at least five valid records, or four if these were unanimous, i.e. all transient or all persistent. Thus, we had longevity indices for 599 species. From Baskin and Baskin (1998) we were able to allocate 252 species to one of four dormancy states: physiological dormancy, morphophysiological dormancy, physical dormancy or non-dormant. Too few species had simple morphological dormancy for analysis. We assumed a further 61 species were non-dormant if freshly collected seeds germinated to ⩾70% in Grime *et al*. (1981), while the additional eight *Carex* spp. in Schütz (2000) were physiologically dormant. Finally, all remaining members of the *Convolvulaceae*, *Cistaceae*, *Leguminosae*, *Geraniaceae* and *Malvaceae* were assumed to have physical dormancy (Baskin and Baskin, 1998). In total, we were able to characterize the dormancy status of 339 of the 599 species for which a longevity index was known.

There is, however, a potentially serious problem in

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analysing the relationship between dormancy and persistence in this way. The majority of the data in Thompson *et al*. (1997) were derived from studies in which the composition of the seed bank was determined by germinating the seeds in soil samples. If dormancy reduces the probability of germination, dormant seeds in the seed bank may often remain undetected and persistence may be underestimated. To test for this possibility, we extracted from Thompson *et al*. (1997) those data based on (a) artificial burial experiments, and (b) studies in which seeds were physically extracted from soil samples. In neither of these methods does detection of seeds in the soil depend on germination; so these data should provide a less biased estimate of persistence. Because only a minority of studies employed these methods, data were available for fewer species. An index of persistence could be calculated for only 216 species, of which 147 could be allocated to one of the four dormancy types. To improve normality and homogeneity of variances, we arcsine transformed the square root indices before analysis.

Results

Mean longevity indices of the four groups, based on all data, did not differ (one-way ANOVA, $F_{3,335} = 2.00$, $P = 0.11$) and are shown in Fig. 1 (black bars). Mean indices, based on artificial burial and physical extraction data only, are also shown in Fig. 1 (white bars). Statistical analysis of these data was inconclusive: a one-way ANOVA revealed a marginally significant effect of dormancy type on persistence ($F_{3,143} = 2.97$, $P = 0.034$), with a tendency for non-dormant seeds to be less persistent. A Tukey HSD test was unable to separate the dormancy types into significantly different groups. However, for each of the three types of dormancy (although not for non-dormant seeds), a *t*-test revealed a significant difference between the mean longevity index based on all data and that based on data from burial and extraction data only (Fig. 1).

Discussion

We can draw two clear conclusions from these results. First, the seed longevity data in Thompson *et al*. (1997) have a significant tendency to underestimate longevity in soil of species with dormant seeds. This underestimation does not affect non-dormant seeds. Nevertheless, it is not quite clear which is the 'correct' estimate of longevity. Extraction of naturally buried seeds from soil, followed by determination of viability, is probably the least ambiguous means of estimating longevity. On the other hand, as pointed out by Thompson *et al*. (1997), artificial burial circumvents the natural processes of seed burial, and therefore, carries an inherent risk of overestimating longevity. In any case, since relatively few studies used either of these two methods, the quantity of data available for analysis is much reduced. There is some evidence that the usual germination methods can be improved. For example, Ter Heerdt *et al*. (1996) found that concentrating soil samples by washing and sieving improved the germination of most species, although it is not clear whether this reflects dormancy breaking or merely improved germination of non-dormant seeds. However, few studies have used this method, and not everyone is convinced that it can always be employed without losing seeds (Traba *et al*., 1998).

The second conclusion is that there is no close relationship between seed dormancy and persistence in the soil. Although non-dormant seeds have a slight tendency to be less persistent, dormancy is neither a necessary nor a sufficient condition for the accumulation of a persistent seed bank, and there is no realistic prospect of predicting persistence from dormancy; almost all combinations of persistence and dormancy exist.

How did this confusion between persistence and dormancy arise, and does it matter? The problem can almost certainly be traced to Harper's (1959, 1977) definition of three types of dormancy: innate, induced and enforced. Innate and induced, now more usually known as primary and secondary (Baskin and Baskin, 1998), are genuinely types of dormancy, but enforced is not. As Baskin and Baskin (1998) point out, 'Enforced dormancy is … the arrested growth of *non-dormant* seeds … due to unfavorable environmental conditions' (our italics). So-called enforced dormancy, therefore, includes all seeds other than those that are truly dormant and those actually germinating. Murdoch and Ellis (2000) recommended that a seed that remains ungerminated, because the minimum requirements for germination are lacking, is better described as *quiescent*, although whether a word is actually needed for such an ill-defined state is questionable. Many ecologists, taking their cue from Harper, still make rather little distinction between innate and enforced dormancy. 'The formation of a persistent seed bank as a selected life history trait depends on innate or enforced dormancy' (Cavieres and Arroyo, 2001) is a typical recent quote.

Does it matter that plant ecologists and physiologists use such an important word to mean quite different things? Most of the time, probably not, because ecologists and physiologists normally inhabit different worlds, read different journals and do not exchange data. Occasionally, however, wires can become seriously crossed. For example, Rees (1994) described a model that predicts a negative correlation

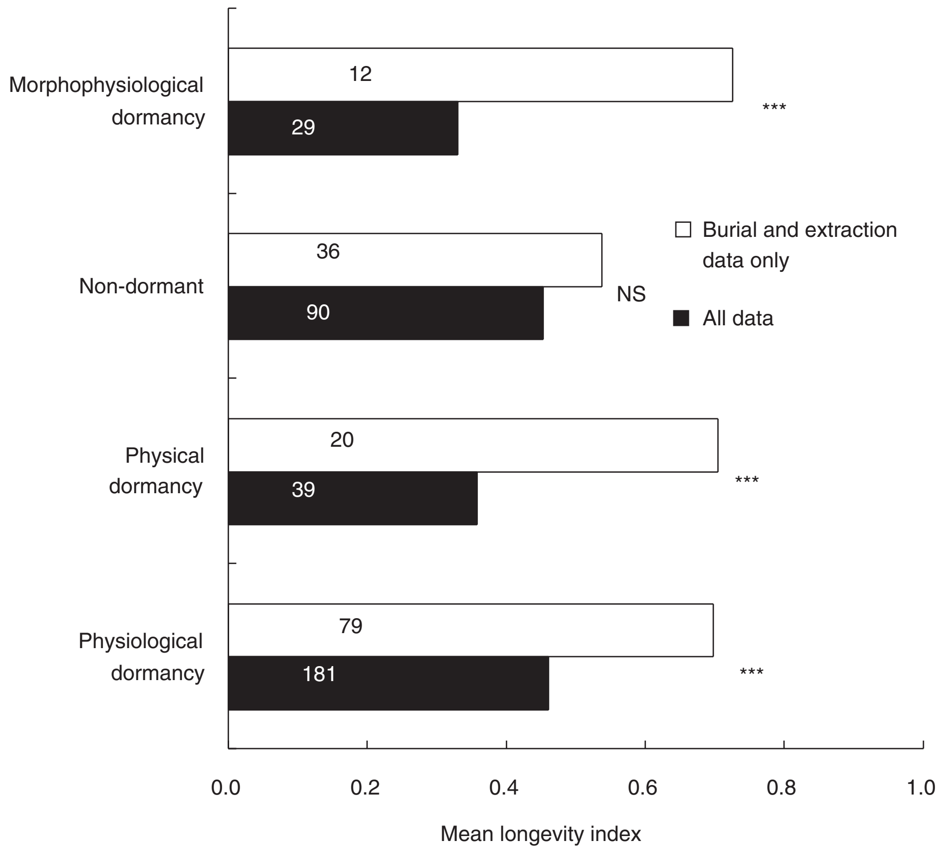

Figure 1. Mean longevity index of species in four dormancy classes in the north-western European flora. *** ($P < 0.001$) and NS (not significant) apply to the differences between data sources within dormancy types, and are based on one-tailed *t*-tests. Numbers on bars are sample sizes. See text for significance of differences between longevity indices of dormancy types and for sources of dormancy data. Seed longevity data are from Thompson *et al.* (1997). Original data are plotted, but all statistical analyses were performed on arcsine square root data.

between adult longevity and seed persistence. Rees suggested this prediction was supported by the data of Baskin and Baskin (1988), which showed that seeds of annuals are generally more *dormant* than those of perennials. In fact, as we have seen, the correlation between dormancy and persistence is extremely weak (Fig. 1), so the Baskin and Baskin data are not relevant. As it happens, annuals can have both more dormant and more persistent seeds than perennials (e.g. Thompson *et al.*, 1998), but this need not necessarily be true. For example, temperate shrubs nearly all have deep dormancy (Baskin and Baskin, 1998), but there is very little evidence for seed persistence among such plants (Thompson *et al.*, 1997). Seed dormancy and persistence are quite distinct phenomena, and confusing them may divert attention from seed traits that are crucial to the evolution of persistence, e.g. burial (Peart, 1984; Thompson *et al.*, 1993, 2001) and chemical defence against pathogens (Hendry *et al.*, 1994; Blaney and Kotanen, 2001).

Clearly, ecologists and physiologists need to start using dormancy to mean the same thing. Although it is ecologists who need to change, it would be helpful if physiologists were also completely consistent in their use of the term and avoided, for example, confusing dormancy and vigour (Grappin *et al.*, 2000). Largely owing to the efforts of Carol and Jerry Baskin, there are now consistent and unambiguous definitions of the various types of dormancy, and it is time ecologists learned to use them. How optimistic are we that ecologists will do this? Not very. Eight years ago, Leo Vleeshouwers proposed that dormancy be defined as 'a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate' (Vleeshouwers *et al.*, 1995). Dormancy is thus the seed's fastidiousness about the germination conditions it requires, while germination is what happens when these requirements overlap with the environmental conditions. Others have made the same point more recently (Eira and Caldas, 2000), while Baskin and Baskin (1998) are crystal clear on the subject, but so far we detect very little evidence of change.

References

Baskin, C.C. and Baskin, J.M. (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* **75**, 286–305.

Baskin, C.C. and Baskin, J.M. (1998) *Seeds; Ecology, biogeography and evolution of dormancy and germination*. San Diego, Academic Press.

Blaney, C.S. and Kotanen, P.M. (2001) Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. *Journal of Applied Ecology* **38**, 1104–1113.

Cavieres, L.A. and Arroyo, M.T.K. (2001) Persistent soil seed banks in *Phacelia secunda* (Hydrophyllaceae): experimental detection of variation along an altitudinal gradient in the Andes of central Chile (33 degrees S). *Journal of Ecology* **89**, 31–39.

Eira, M.T.S. and Caldas, L.S. (2000) Seed dormancy and germination as concurrent processes. *Revista Brasileira de Fisiologia Vegetal* **12**, 85–104.

Grappin, P., Bouinot, D., Sotta, B., Miginiac, E. and Jullien, M. (2000) Control of seed dormancy in *Nicotiana plumbaginifolia*: post-imbibition abscisic acid synthesis imposes dormancy maintenance. *Planta* **210**, 279–285.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. and Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059.

Harper, J.L. (1959) The ecological significance of dormancy. pp. 415–420 *in Proceedings of the IV international congress of crop protection*. Braunschweig, Internationalen Pflanzenschutz-Kongresses.

Harper, J.L. (1977) *Population biology of plants*. London, Academic Press.

Hendry, G.A.F., Thompson, K., Moss, C.J., Edwards, E. and Thorpe, P.C. (1994) Seed persistence: a correlation between seed longevity in the soil and ortho-dihydroxyphenol concentration. *Functional Ecology* **8**, 658–664.

Murdoch, A.J. and Ellis, R.H. (2000) Dormancy, viability and longevity. pp. 183–214 *in* Fenner, M. (Ed.) *Seeds: The ecology of regeneration in plant communities* (2nd edition). Wallingford, UK, CABI Publishing.

Peart, M.H. (1984) The effects of morphology, orientation and position of grass diaspores on seedling survival. *Journal of Ecology* **72**, 437–453.

Rees, M. (1994) Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* **144**, 43–64.

Rees, M. (1997) Seed dormancy. pp. 214–238 *in* Crawley, M.J. (Ed.) *Plant ecology* (2nd edition). Oxford, Blackwell.

Schütz, W. (2000) Ecology of seed dormancy and germination in sedges (*Carex*). *Perspectives in Plant Ecology, Evolution and Systematics* **3**, 67–89.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. and Bakker, J.P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10**, 144–151.

Thompson, K., Band, S.R. and Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology* **7**, 236–241.

Thompson, K., Bakker, J.P. and Bekker, R.M. (1997) *The soil seed banks of north west Europe: Methodology, density and longevity*. Cambridge, Cambridge University Press.

Thompson, K., Bakker, J.P., Bekker, R.M. and Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* **86**, 163–169.

Thompson, K., Jalili, A., Hodgson, J.G., Hamzeh'ee, B., Asri, Y., Shaw, S., Shirvany, A., Yazdani, S., Khoshnevis, M., Zarrinkamar, F., Ghahramani, M.-A. and Safavi, R. (2001) Seed size, shape and persistence in the soil in an Iranian flora. *Seed Science Research* **11**, 345–355.

Traba, J., Levassor, C. and Peco, B. (1998) Concentrating samples can lead to seed losses in soil bank estimations. *Functional Ecology* **12**, 975–976.

Venable, D.L. and Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* **131**, 360–384.

Vleeshouwers, L.M., Bouwmeester, H.J. and Karssen, C.M. (1995) Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* **83**, 1031–1037.

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