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REGULAR ARTICLE

Soil type does not affect seed ageing when soil water potential and temperature are controlled

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Abstract To investigate the effects of soil type on seed persistence in a manner that controlled for location and climate variables, three weed species—*Gomphocarpus physocarpus* (swan plant), *Avena sterilis* ssp. *ludoviciana* (wild oat) and *Ligustrum lucidum* (broadleaf privet)—were buried for 21 months in three contrasting soils at a single location. Soil type had a significant effect on seed persistence and seedling vigour, but soil water content and temperature varied between soils due to differences in physical and chemical properties. Warmer, wetter conditions favoured shorter persistence. A laboratory-based test was developed to accelerate the rate of seed ageing within soils, using controlled superoptimal temperature and moisture conditions (the soil-specific accelerated ageing test, SSAAT). The SSAAT demonstrated that soil type per se did not influence seed longevity. Moreover, the order in which seeds aged was the same whether aged in the field or SSAAT, with *L. lucidum* being shortest-lived and *A. sterilis* being longest-lived of the three species.

Keywords Seed longevity · Seed persistence · Soil · Seedling vigour · Accelerated ageing · Weeds · Seed bank · *Avena sterilis* · *Gomphocarpus physocarpus* · *Ligustrum lucidum*

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Introduction

A lack of understanding of seed bank dynamics is a major barrier to effective management of plant populations. For example, seed persistence under field conditions is a key determinant of the required duration of weed eradication programs, yet generally

little is known about the seed persistence of target species (Panetta and Lawes 2005). Efforts to rehabilitate mined lands and to conserve rare and endangered plant species also require knowledge of the seed persistence of populations to maximise the likelihood of successful restoration (Rosef 2008). How long seeds persist in the field depends on factors such as predation, microbial decay, and the inherent longevity of the seeds (Forcella 2003). Thus, it is imperative that the longevity and ageing dynamics of seeds of target species and their populations be understood to enable successful long-term management of soil seed banks.

Traditionally, real-time seed burial experiments have provided estimates of seed persistence based on the viability of seeds recovered from study sites over time. Numerous field studies have tested the seed persistence of a single population of one or more species in a single soil type (Conn et al. 2006; Miller and Nalewaja 1990; Panetta 2000, 2001; Tamado et al. 2002; Taylor et al. 2005; Vivian-Smith and Panetta 2004, 2005). However, few studies report the chemical and physical properties of the soil, and conclusions of such studies may not apply to other populations and locations. Some studies have specifically targeted the influence of soil type and nutrient status on seed persistence (e.g. (Bekker et al. 1998; Benvenuti 2003; Narwal et al. 2008; Wu et al. 2007). However, with the exception of Wu et al. (2007), experiments were conducted under controlled glasshouse conditions, or in soils at different locations, and therefore under unnatural or disparate climates, and the soil water and temperature conditions were not described. Wu et al. (2007) observed differences in the persistence of *Conyza bonariensis* [L.] Conquist seeds in two soils at the same location, however, as with other studies, the moisture and temperature conditions experienced by seeds were not reported. Thus it is not known whether soil type per se can influence seed longevity and therefore persistence, and if so, how and why.

The aim of this study was to investigate whether soil types affect the persistence of seeds. Three species were selected for this study: *Avena sterilis* L. ssp. *ludoviciana* (Dur.) Nyman (wild oat, Poaceae) is a common annual grass weed of crops; *Gomphocarpus physocarpus* E.Mey. (swan plant, Apocynaceae) is an annual–biennial herbaceous weed of pastures and disturbed sites including roadsides; and *Ligustrum lucidum* W.T.Aiton (broadleaf privet, Oleaceae) is a bird-dispersed woody weed of environmental significance. Using these species as models, the study measured the viability and subsequent seedling vigour of seeds aged for up to 21 months in three contrasting soils—a sandy loam, a black silty loam and a red light clay—that were introduced to the same field. A laboratory-based experiment then controlled the water potential and temperature of the same soils to investigate whether soil type per se is a significant factor affecting seed ageing.

Methods

Plant material

Avena sterilis ssp. *ludoviciana* florets were collected from a chickpea (*Cicer arietinum* L.) crop located between Millmerran and Goondiwindi, Queensland (S 28.19°, E 150.46°) on 20 October 2004. Florets were rubbed coarsely to break off the awns but not to remove the palea and lemma. Collection of *Gomphocarpus physocarpus* seeds from open native pastures on Pepper's Hidden Vale Resort, Grandchester, Queensland (S 27.72°, E 152.43°), occurred on 4 days in June 2004. Mature seeds were taken from pods ('balloons') that had recently dehisced, or that dehisced when lightly squeezed. *Ligustrum lucidum* drupes (fruits) were collected from roadside trees at Mt Tambourine, Queensland (S 27.95°, E 153.18°), on 1 June 2004. Fruits were stored, stems intact, in large plastic-lined paper bags in the laboratory for 7 days before being spread out on shade cloth to dry naturally in a glasshouse. After a further 10 days, fruits were detached from stems. On 25 June 2004, fruits were placed into a 46-L plastic bin and returned to the laboratory. Water contents of collections were determined within 48 h of collection; for testing, fruit tissues from *L. lucidum*, and the palea and lemma from *A. sterilis* were removed. Laboratory storage of fruits and seeds (c. 50% RH at 21±1°C) ranged from 6 weeks to 6 months for different species prior to the start of the experiment so seed water contents were monitored every 2 to 3 months. The field trial started in December 2004; at this time all remaining florets, seeds and fruits were dried to 15% RH at 15°C, and then vacuum-sealed and stored at −20±1°C until required for the laboratory trial. When dried, the 1000

seed weights of seed lots were: 23.7 g (*A. sterilis* florets), 7.6 g (*G. physocarpus* seeds), and 22.5 g (*L. lucidum* seeds, fruit layers removed).

Field trial

A field plot was established at the St Lucia campus of the University of Queensland (27.49569° S, 153.00917° E) to provide an environment for simulating natural seed ageing for 21 months according to a randomised block design of three treatments within each of four blocks. Four 3.75×1.00 m pits (blocks) were dug to a depth of 0.40 m. The vertical edges of the pits were lined and the pits each divided into three sections with 2 mm plastic sheeting. Sections were filled with one of three introduced soils (treatments): a black organic silty loam sourced from a landscape supplier, and a red clay and a sandy loam sourced from coastal Queensland. Pits were filled with soil to approximately 15 cm below the surrounding soil surface, 15 pots (200 mm diameter with the base removed) were arranged within each section, and soil packed around the pots until level with the surrounding soil. Pots were filled with soil to 10 cm below the surrounding soil surface and a layer of nylon mesh (shade cloth) was inserted to limit downward movement of seeds. Within each pot was placed a 1 L soil sample mixed with one of the three test species (c. 700 *A. sterilis* florets, 1,500 *G. physocarpus* seeds, or 1,500 *L. lucidum* fruits); each soil segment thus contained five randomly allocated pots of each species. The pots were then topped with soil until level with the surrounding soil. The burial depth of 10 to 15 cm below the soil surface was used to inhibit germination (Miller and Nalewaja 1990).

Volumetric soil water content and soil temperature were monitored for the 21-month duration of the experiment. An ECH_2O EC-20 probe (Decagon Devices, supplied by Monitor Sensors, Caboolture, Australia) was placed between pots at the centre of each soil segment in one of the four blocks to detect average volumetric soil water content over the range 5 to 25 cm below the soil surface; temperature probes (μSmart, Monitor Sensors) were similarly installed. All sensors were attached to a SL5 200 channel data logger (Monitor Sensors) which recorded estimates of soil water content (in the range 0% to 40% volumetric water content, converted from 0.0 to 1.0 V measurements of capacitance) and temperature at hourly intervals. In the first week following set up, the site and data logging equipment were checked daily, and soils topped up if they had settled. Thereafter, the site was monitored monthly for equipment function and surface weed removal. Water and temperature probes failed intermittently, resulting in some gaps in data.

One pot was recovered for each species from each soil type from each block and placed into a plastic bag at 4.5, 9, 12, 17 and 21 months. A sample of soil was taken from each soil type at each retrieval time and sent for chemical and physical analysis (Incitec Pivot Laboratories, South Werribee, Australia). Bagged samples were stored in a closed 90-L bin for up to 24 h prior to separating seeds and fruits from the soil. Flotation was used to separate seeds; a 9-L bucket was filled with approximately 6 L tap water, the sample added and stirred, and the water poured out through a 1 mm sieve to trap the seeds. A sample of 25 seeds (or as many as were retrieved from the soil if less than 25) were tested for germination.

Soil-specific accelerated ageing test (SSAAT)

In a variation on the controlled ageing test used in Long et al. (2008), seeds were aged in the laboratory to accelerate ageing within a soil environment. Soils were collected from the field trial site and spread in a 10 to 20 mm layer in shallow plastic dishes that were sealed in boxes above a saturated KNO_3 solution, which created an atmosphere of 94.6% RH at 20°C. Soils were maintained in these conditions for 4 months, and were stirred every 2 to 3 weeks to ensure equilibration. Light was excluded from the boxes by covering them with matt black cloth. The RH of soils was measured using a HygroPalm hygrometer (Rotronic, West Sussex, UK) to establish when equilibrium RH was reached. *A. sterilis* florets, *G. physocarpus* seeds, and *L. lucidum* fruits were equilibrated above saturated KNO_3 at 20°C for 12 days.

Pre-equilibrated seeds were mixed with 20 mL of pre-equilibrated soil and placed in open film canisters (Kodak, Japan) that had their bases replaced with a porous recycled PET bottle fabric (Daison Kaisha, Japan). A 2×3 cm piece of Whatman No. 42 filter paper was embedded in the soil of each canister to permit calculation of soil water potential (WP) (Hamblin 1981). For each treatment and soil type 11 canisters of 50 *A. sterilis* florets, 50 *G. physocarpus*

seeds, and 25 *L. lucidum* fruits were prepared. The SSAAT started when canisters were placed into a sealed box containing a saturated solution of K_2SO_4, providing a relative humidity of 96.7% RH at the ageing temperature of 35°C, which controlled soil hydration to −15.9±0.8 MPa (89.7±0.5% RH), irrespective of the soil type. Nine canisters were removed from the ageing environment intermittently over 24 days. At these times seeds were sifted from the soil, rinsed briefly with H_2O, and tested for germination. Two canisters were retrieved from the ageing environment on the final day of ageing to assess seed water content, which was calculated from the difference in weight before and after drying in aluminium foil pans for 24 h at 105°C.

Seed germination testing

The viability of filled seeds retrieved from the field and laboratory ageing trials was assessed with germination tests. As seeds were mixed freely with soil during burial, it was not possible to be sure that all buried seeds were recovered; therefore the percentage of seeds recovered relative to the number buried was not calculated.

Germination tests used caryopses for *A. sterilis* (glumes were removed from the florets), and seeds for *L. lucidum* (fruit tissue was peeled off) and *G. physocarpus*. Seeds or caryopses were placed on solidified agar (10 g L^{-1} deionised water) in 90-mm Petri dishes that were sealed with Parafilm (Pechiney Plastic Packaging, Menasha, USA). Temperature and light (c. 50 μmol m^{-2} s^{-1} provided by white fluorescent tubes) conditions for germinating each species were optimised during a pilot study (data not shown). Germination of *G. physocarpus* was tested at alternating 25/15°C with a 12-h photoperiod. *L. lucidum* dishes were incubated in light for 48 h and then wrapped in foil to provide complete darkness at 20±1°C. For *A. sterilis*, gibberellic acid (722 μM GA_3) was added to the agar to bypass dormancy, and dishes were incubated at 20±1°C in constant light. Germination was scored every 1 to 2 days for up to 30 days, and a seed was scored as germinated when the radicle protruded ≥ 1 mm. Abnormal germination, recognised when the cotyledon emerged prior to the radicle or when radicle growth was severely stunted, was noted and subtracted from total germination, so that viability data reflect the number of normal germinants arising from filled seeds. Ungerminated seeds were cut open to assess embryo health and check for empty seeds.

Seedling vigour testing

Seedling vigour was measured for seeds aged in the field to look for subtle effects of soil type on seed ageing. At 5 days following germination of the first seed in each dish for *A. sterilis* and *G. physocarpus*, and at 11 days following germination of the first seed in each dish for *L. lucidum*, the root and shoot lengths were measured for each germinated seed in each dish (Matthews and Khajeh-Hosseini 2007; Schaub et al. 2007). Seedling vigour was then expressed as mean root and shoot length, in mm, for each species in each soil at each retrieval time.

Statistical analysis

For each species, data for seed viability and seedling vigour in the field were analysed using a generalised linear model, testing for the effects of time, soil type, blocks and their interactions. Standard errors were calculated as √MSE (mean square error) for a particular factor, and applied to the overall analysis for that factor.

For each treatment in the SSAAT, normal germination (percentage of filled seeds) was plotted against time (days), and simple logistic regression curves were fitted. The times for samples to decline to 50% viability (P_{50}) were compared using two-sample *t*-tests with an overall significance level of 5%. The standard error of the P_{50} term was approximated as √(sum of squared residuals/degrees of freedom error).

Results

Field trial

The red, sandy and black soils used in this study differed in their physical and chemical properties (Table 1) and in their volumetric water content and temperature (Fig. 1) during the 21-month field study. The black silty loam soil was moister, warmer and contained higher levels of organic carbon and several other nutrients, including sulphate, phosphorus, potassium, calcium and magnesium compared to the red light clay and sandy loam soils. Chemically there was less

Table 1 Chemical and physical properties of the three soils monitored for up to 21 months: a black silty loam, a sandy loam and a red clay

Chemical or physical property	Black				Sandy						Red					
	Time (months)				Time (months)						Time (months)					
	0	4.5	9	12	0	4.5	9	12	17	21	0	4.5	9	12	17	21
Texture	Silty loam				Sandy loam						Light clay					
pH (1:5 water)	7.7	7.4	8.0	7.6	7.1	6.9	6.7	7.0	7.2	7.0	6.0	6.1	5.8	5.8	5.8	5.6
Organic carbon (%)	4.9	5.4	4.6	4.4	0.45	0.39	0.47	0.40	0.45	0.31	0.79	0.98	1.1	1.0	0.96	0.90
NO_3^- (mg kg^{-1})	5.4	2.8	1.3	11	<1.0	15	4.4	2.9	5.6	3.6	<1.0	11	6.8	11	9.0	25
NH_4^+ (mg kg^{-1})	7.6	3.2	2.6	2.9	1.0	<0.60	<0.60	0.80	0.89	0.63	2.7	0.77	13	0.91	<0.60	2.9
SO_4^{-2} (mg kg^{-1})	590	200	43	19	3.5	2.5	1.5	<1.0	1.5	1.9	82	67	72	74	74	75
Phosphorus (mg kg^{-1})	390	350	410	440	18	13	11	13	18	14	7.2	7.3	7.1	9.6	8.7	6.7
Potassium (mEq 100 g^{-1})	4.5	1.6	2.1	1.3	0.12	0.23	0.19	0.15	0.15	0.15	0.12	0.28	0.18	0.17	0.32	0.28
Calcium (mEq 100 g^{-1})	21	16	17	19	4.1	3.7	4.6	3.9	3.7	4.2	2.4	2.6	2.9	3.0	2.8	2.8
Magnesium (mEq 100 g^{-1})	5.8	3.3	3.8	2.9	1.6	1.5	1.8	1.6	1.5	1.6	3.6	3.8	4.0	4.0	3.6	3.7
Aluminium (mEq 100 g^{-1})	–	–	–	–	–	–	–	–	–	–	0.11	–	0.11	0.17	0.10	0.10
Sodium (mEq 100 g^{-1})	21	0.34	0.26	0.11	<0.20	0.048	0.043	0.038	0.10	0.087	0.33	0.30	0.20	0.13	0.21	0.24
Chloride (mEq 100 g^{-1})	1400	52	<10	12	19	<10	<10	<10	18	13	20	<10	<10	12	23	31
EC (dS m^{-1})	1.49	0.38	0.15	0.16	0.03	0.05	0.02	0.02	0.03	0.03	0.04	0.06	0.05	0.05	0.07	0.09
Copper (mg kg^{-1})	9.9	5.5	6.1	6.5	0.34	0.43	0.30	0.34	0.33	0.34	0.12	0.13	0.087	0.10	0.089	0.094
Zinc (mg kg^{-1})	68	45	55	53	0.51	0.59	0.42	0.46	0.51	0.41	0.40	0.40	0.30	0.35	0.34	0.32
Manganese (mg kg^{-1})	21	11	1.7	3.7	9.8	8.6	7.5	9.5	7.7	9.4	2.6	3.0	1.9	2.4	2.0	2.6
Iron (mg kg^{-1})	100	59	52	75	25	22	21	22	20	19	7.2	6.1	4.3	6.9	5.6	6.1
Boron (mg kg^{-1})	11	2.8	4.2	2.9	0.21	0.20	0.24	0.16	0.19	0.18	0.97	0.58	0.76	0.78	0.69	0.75
CEC (mEq 100 g^{-1})	33.4	21.2	23.2	23.3	6.02	5.48	6.63	5.69	5.45	6.04	6.56	6.98	7.39	7.47	7.03	7.12
Sodium % of cations	6.3	1.6	1.1	0.47	–	0.88	0.65	0.67	1.8	1.4	5	4.3	2.7	1.7	3.0	3.4
Dispersion index	0	0	0	2	6	0	2	0	4	8	0	0	0	0	0	0
Slaking	−	−	+	−	+++	+	+++	+	+++	+++	++	+	+++	+++	++	++

Slaking: − water stable, + minimal, ++ partial, +++ considerable

distinction between the red and sandy soils, but the red soil exhibited higher water levels and lower temperatures than the sandy soil. Soil volumetric water content varied intermittently in response to rain events, and temperature varied daily and seasonally, becoming cooler towards the winter months. Daily fluctuations of approximately 7°C were common for each soil (hourly data not shown), with seasonal variation ranging up to approximately 20°C between summer and winter. Overall, the soils provided three contrasting environments for the comparison of seed ageing in response to soil types introduced to the same location.

During burial in soil there was a gradual reduction in the number of filled seeds retrieved, but it was not possible to quantify this. Visual inspection of soil samples indicated that seeds decomposed or germinated fatally. For the black soil, no filled seeds were recovered at 12 months and subsequent retrieval times. Seeds were recovered throughout the 21 months for the red and sandy soils for two species. Seeds of *L. lucidum* were only recovered at 4.5 months from the black and sandy soils, and up to 9 months in the red soil. Similarly, *A. sterilis* and *G. physocarpus* seeds aged in the black soil could be recovered only for the first 9 months. Thus for field ageing, germination and vigour tests reflect those seeds that had not already germinated or decomposed prior to sample retrieval.

Soil type clearly had an effect on the health of seeds recovered during the 21-month burial period ($P<0.05$). Most obvious was the effect of the black soil: germination of all species recovered from the black soil at 4.5 and 9 months was lower than for seeds recovered from the red and sandy soils (Fig. 2), *A. sterilis* seedling growth was slower after retrieval

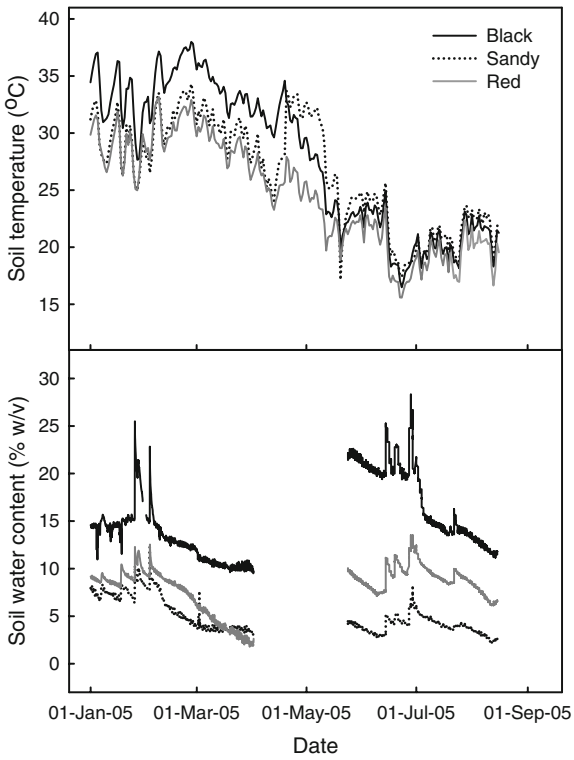

Fig. 1 Mean daily soil temperature (°C) and hourly soil volumetric water content (% w/v) of three contrasting soils at the same site as recorded from January to August 2005 at 10 cm below the soil surface. Black soil (*solid black line*), sandy soil (*dotted black line*) and red soil (*solid grey line*). Breaks in soil water content data are due to equipment failure

from black soil than the other soils (Fig. 3a, b), and no seeds of any species were recovered after 9 months. Decline in seed health was much slower in the red and sandy soil types, with only *L. lucidum* exhibiting a decline in viability; seeds of *G. physocarpus* and *A. sterilis* persisted for 21 months and filled seeds retrieved from the soils retained >90% germination (Fig. 2a, b). Seeds that were retrieved from the soil but failed to germinate during viability-testing were generally not viable upon cut-testing; *G. physocarpus* and *L. lucidum* seeds exhibited discoloured embryos and *A. sterilis* seeds bloated when not viable.

Soil-specific accelerated ageing test

In contrast to the field trial, soil type had no effect on the persistence of seeds in the SSAAT (Fig. 4); *A. sterilis* P=0.968, *G. physocarpus* P=0.706, *L. lucidum* P=0.716. Although the RH experienced by seeds in the SSAAT was consistent across soils, seed water content varied between species. Seed water content for *A. sterilis* in the ageing environment was 19.4%, and for *G. physocarpus* was slightly higher at 23% (Table 2). *L. lucidum* fruits had the highest water content at an average of 25.5%, with minor variation between soils. The order of relative seed persistence in the SSAAT was the same as in the field trial: seeds of *L. lucidum* were the shortest-lived (P_{50}=5.9±1.9 days, n=18), followed by those of *G. physocarpus* (P_{50}=10.0±3.3 days, n=22) and *A. sterilis* (P_{50}=14.6±2.0 days, n=20).

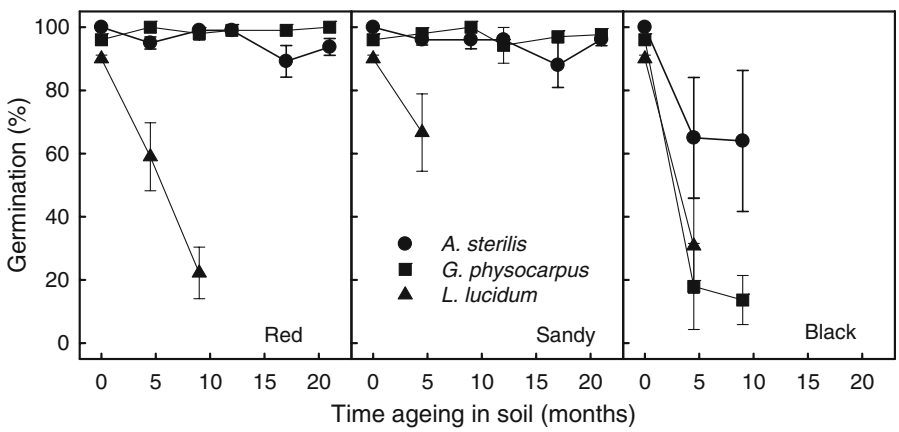

Fig. 2 Viability (as % germination of filled seeds) of *A. sterilis* caryopses (*circle*), *G. physocarpus* seeds (*square*), and *L. lucidum* seeds (*triangle*) following ageing in red, sandy and black soils for up to 21 months. After 4.5 months, no filled *L. lucidum* seed samples were recovered from the sandy and black soils, and none were recovered after 9 months in the red soil. No seeds were recovered from the black soil after 9 months. *Vertical bars* represent ±1 SE

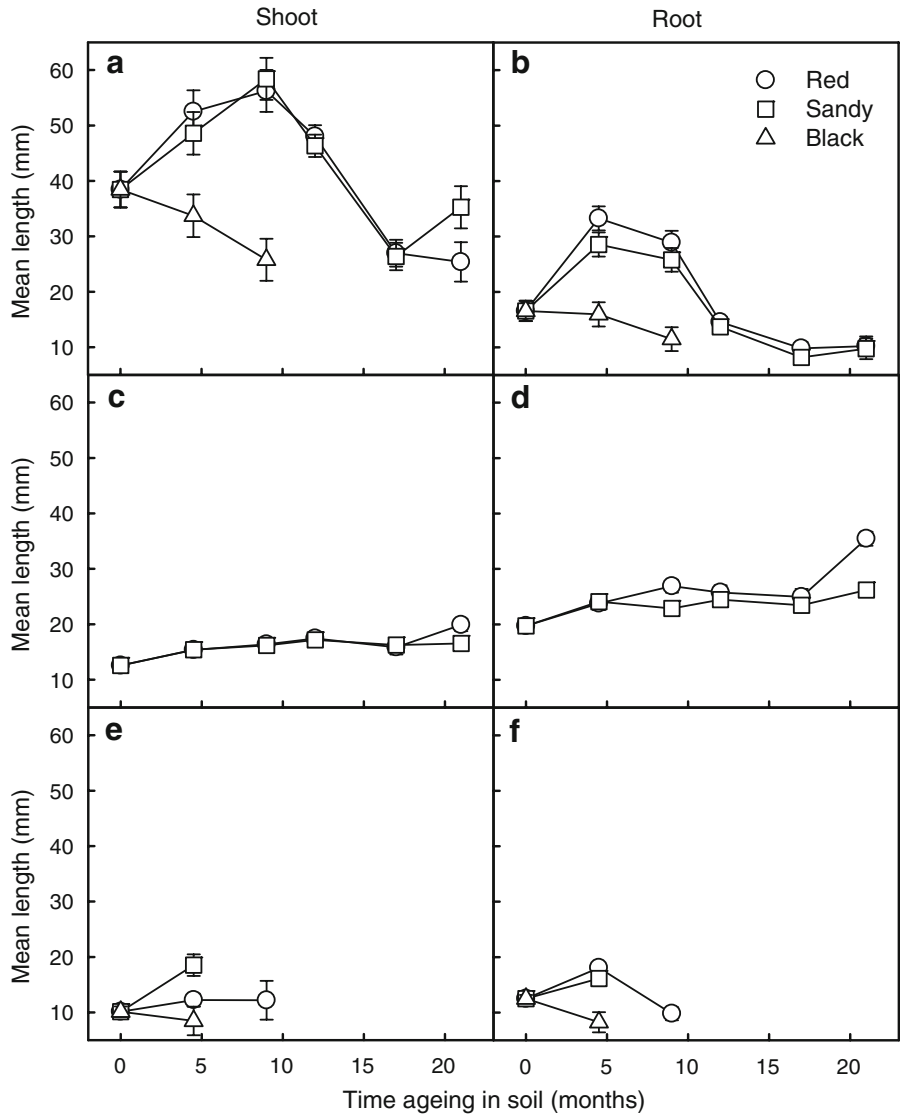

Fig. 3 Mean shoot length (mm) and root length (mm) of *A. sterilis* seedlings at 5 days after the first seed germinated (5 DAG, **a** and **b**), *G. physocarpus* at 5 DAG (**c** and **d**), and *L. lucidum* at 11 DAG (**e** and **f**). Seeds were aged in three soils for up to 21 months: red soil (*circle*), sandy soil (*square*), black soil (*triangle*). *Vertical bars* represent ±1 SE where larger than the symbol. *G. physocarpus* seeds were recovered in sufficient numbers for vigour testing only from the red and sandy soil types

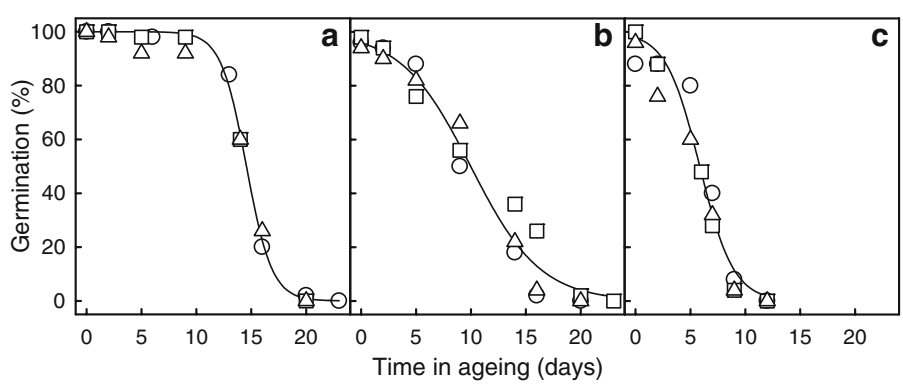

Fig. 4 Germination of *A. sterilis* caryopses (**a**), *G. physocarpus* seeds (**b**), and *L. lucidum* seeds (**c**) following ageing in three soils at 35±0.5°C; red soil (*circle*), sandy soil (*square*), black soil (*triangle*) in the soil-specific accelerated ageing test (SSAAT). A logistic regression is fitted to the germination data of each species across all soils

Table 2 Seed water contents (mean±1 SE of two samples) measured on a fresh weight basis for treatments in the soil-specific accelerated ageing test (SSAAT)

Species	Unit	Soil type	Seed water content (%)
A. sterilis	Floret	Red	19.1±0.2
		Sandy	19.8±0.2
		Black	19.2±0.3
G. physocarpus	Seed	Red	21.8±0.5
		Sandy	23.9±0.4
		Black	23.5±0.6
L. lucidum	Fruit	Red	28.6±2.7
		Sandy	26.6±1.7
		Black	21.6±1.3

Water contents of the tested dispersal units were assessed on the final day of ageing at 96.7% RH and 35°C for each species and soil type

Discussion

Soil type had a marked influence on the persistence of seeds in the field study, with seeds of all three species dying more quickly in black than in red and sandy soils (Fig. 2). Several earlier studies have investigated the role of soil type in determining seed persistence but their results are not conclusive (Bekker et al. 1998; Narwal et al. 2008; Van et al. 2005; Wu et al. 2007). Each of these studies identified differences in seed persistence between soils, but it is difficult to distinguish the degree of influence imparted by soil types as distinct from temperature and hydrological conditions, which may also have varied between sites or potted soils, but were not reported.

For the present study, three soils were brought to a single location and so experienced the same climatic conditions. The soils were specifically chosen for their contrasting chemical and physical properties, and consequently temperature and water-holding capacity differed between them. The black soil, which was the warmest and wettest, aged seeds of all three species more quickly than the cooler and drier red and sandy soils. These results are supported by other field studies that found higher soil water and temperature conditions to increase seed mortality (Davis et al. 2005; Mickelson and Grey 2006; Van et al. 2005). Indeed, raising temperature and water content reduces seed longevity in ex situ storage (Walters 1998).

Seed viability for *L. lucidum* declined more rapidly than for the other two species, with a noticeable reduction in germination by the first retrieval at 4.5 months in all three soils (Fig. 2). Furthermore, *L. lucidum* fruits were recovered only until 4.5 months in the sandy soil and 9 months in the red soil, whereas the other two species were recovered and retained high viability in these two soils throughout the 21-month study. The difference in seed ageing between *G. physocarpus* and *A. sterilis* was more difficult to distinguish, as these species performed similarly in the red and sandy soils except that *A. sterilis* exhibited an initial increase in the rate of seedling growth followed by a decline after 12 months in the soil, while *G. physocarpus* retained vigorous seedling growth throughout the experiment. However, differences in seed viability between these species were evident in the black soil, where the viability of retrieved filled seeds was higher for *A. sterilis* at both 4.5 and 9 months. Thus, overall, *L. lucidum* was the shortest-lived species, followed by *G. physocarpus* and *A. sterilis*.

Seedling vigour varied as a consequence of burial in the different soils. Most noticeably, *A. sterilis* and *L. lucidum* grew more slowly when retrieved from the black soil than the red and sandy soils (Fig. 3). For *A. sterilis* seeds in the red and sandy soils, after-ripening most likely caused the improved seedling vigour by 9 months of burial, before ageing or secondary dormancy forced its decline. The steady rise of *G. physocarpus* vigour in the red and sandy soils may be due to a priming effect resulting from hydration–dehydration cycles in response to rainfall (Gonzalez-Zertuche et al. 2001), or may indicate that seeds with greater longevity tended also to be more vigorous. Therefore it is clear that a seed that has been buried in soil for months or years prior to germination is unlikely to have an equivalent capability of producing a healthy plant as a fresh seed. This has an impact on emergence modelling, for which every seed in the soil is commonly considered to be equivalent to every other seed (e.g. Pannell et al. 2004), and accurate modelling will require a greater understanding of the way in which seedling vigour changes in response to ageing in soils.

The finding that seed persistence and seedling vigour are dependent on soil type highlights the importance of careful selection of field conditions used in seed persistence studies. Pertinently, the results of field studies conducted in soil types different to where the species or population occurs

(or may potentially occur) may afford inaccurate estimates of persistence. For example, had the persistence of the three species used in this study been assessed in the black soil only, they would all have been categorised as having a transient seed bank because no seeds could be found after 9 months. However, *A. sterilis* seed survival has been estimated at 27 to 43 months and this species has been classified therefore as developing a persistent seed bank (Sanchez Del Arco et al. 1995).

Following the observed differences in seed persistence in the field, apparently owing to soil type, the SSAAT was designed to separate the effects of soil type from climatic effects. While soil type is commonly viewed as an significant factor affecting seed persistence (Albrecht and Auerswald 2003; Bekker et al. 1998), we have shown that when soil WP and temperature are controlled, soil type per se appears to have no influence on seed longevity (Fig. 4). Soils in situ vary in their temperature and WP due to an interaction of rainfall and temperature with soil physical and chemical properties such as colour, particle size and organic matter content. For example, the dark colour, silty loam texture and relatively high organic-matter content of the black soil caused it to retain more warmth and water than the red and sandy soils in the field trial. Thus, just as temperature and water content are the key factors affecting seed ageing in ex situ storage (Walters 1998), seed ageing in the field is predominantly affected by the temperature and water content that results from an interaction between soils and climate.

In summary, by controlling for variation in soil WP and temperature, the SSAAT showed that soil type per se may not significantly influence seed longevity in unsaturated soils; soil physical and chemical properties interact with the prevailing climate to influence the microclimate experienced by seeds and therefore seed ageing. Thus water and temperature are the confirmed as the two main factors affecting seed longevity, even under field conditions.

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