

## Models and sampling for studying weed seed survival with wild mustard (*Sinapis arvensis*) as a case study

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Donald, W. W. 1993. Models and sampling for studying weed seed survival, with wild mustard (*Sinapis arvensis*) as a case study. *Can. J. Plant Sci.* 73: 637–645. Most studies of seed survival over time are not repeated in different years because they are long-term efforts. Methodological research reported in this paper shows that the shape of seed survival curves can differ for the same species for seed produced in different years. Consequently, seed survival of wild mustard could not be described by a single type of seed survivorship curve. Wild mustard seed survival was a negative exponential function of time in one 4-yr-long trial [ $Y = a + b \cdot \exp(-X)$ ], but decreased as a negative linear function of time in a second trial ( $Y = a + b \cdot X$ ), where  $Y$  is percent seed survival,  $X$  is time in years, and  $a$ ,  $b$ , and  $c$  are coefficients. However, both data sets could be adequately described by a mixed negative exponential model [ $Y = a + b \cdot X + c \cdot \exp(-X)$ ]. The negative hyperbolic model [ $Y = a/(X + b)$ ] did not describe both trials as well as did the mixed negative exponential model. Sample sizes of four groups of 100 seed each, harvested each year for four years, provided acceptable nonlinear regression models for seed survival data. It was not advantageous to increase sample size more than this because  $r^2$  was not greatly increased and the residual mean square error (RMSE) was not decreased.

Key words: Model, seed persistence, seed survival, wild mustard, *Sinapis arvensis*

Donald, W. W. 1993. Modèles mathématiques et taille de l'échantillon pour l'étude de la survie des graines de mauvaises herbes, prenant la moutarde des champs (*Sinapis arvensis*) comme exemple type. *Can. J. Plant Sci.* 73: 637–645. La plupart des études sur la survie des graines en fonction du temps ne sont pas répétées dans des années différentes parce que ce sont des études qui prennent beaucoup de temps. La recherche méthodologique rapportée ici montre que la forme des courbes de survie peut différer pour une même espèce selon l'année de production des graines. Par conséquent, il n'a pas été possible de décrire la survie des graines de moutarde par un type seulement de courbe de survie. La survie des graines de cette espèce était une fonction exponentielle négative du temps dans un essai de quatre ans ( $Y = a + b \cdot \exp(-X)$ ), mais elle diminuait en fonction linéaire négative du temps dans un second essai ( $Y = a + b \cdot X$ ), où  $Y$  désigne le pourcentage de survie des graines,  $X$  est le temps en année, et  $a$ ,  $b$ , et  $c$  sont des coefficients. Cependant, les deux jeux de données pourraient être assez adéquatement décrits par un modèle exponentiel négatif mixte ( $Y = a + b \cdot X + c \cdot \exp(-X)$ ). Le modèle hyperbolique négatif ( $Y = a/(X + b)$ ) ne décrivait pas les deux essais aussi bien que le modèle exponentiel négatif mixte. Des échantillons constitués de quatre lots de 100 graines chacun récoltés chaque année pendant quatre ans ont fourni des modèles de régression non linéaire acceptable pour l'analyse des données de survie. Il n'y avait aucun avantage à utiliser des échantillons plus gros: d'une part, la  $r^2$  n'était pas sensiblement plus élevée et de l'autre l'erreur, quadratique moyenne MRSE n'était pas diminuée.

Mots clés: Modèle, longévité, survie des graines, moutarde des champs, *Sinapis arvensis*

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Annual weeds are recurring problems on farmland because seed dormancy allows the buildup of long-lived seed populations in the soil (Roberts 1981). Most often, seed ecologists study weed seed survival in the field by periodically retrieving groups of seed after burying known numbers of seed. Then, seed survival (i.e., the number of intact undamaged seed remaining over time) is determined.

Most commonly, seed has been buried in nylon mesh packets in the field (e.g., Miller and Nalewaja 1990) or in columns of soil either with nylon mesh covering the column ends (e.g., Burnside et al. 1977) or without nylon mesh (Dawson and Bruns 1975). Alternatively, loose seed, either tagged with fluorescent paint (e.g. Naylor 1972) or radioisotopes (Watkinson 1978) or left untagged (Chepil 1946; Ball and Miller 1989), have been introduced into fields which did not previously have the weed. Seed has been left on the soil surface or buried, and the soil has been left undisturbed or periodically stirred to simulate tillage in seed survival research (Roberts 1981). Each approach has advantages and disadvantages and often provides complementary, nonequivalent information on seed survival.

Models of seed survival have been reviewed and, usually, seed survival is well modeled as a negative exponential function of seed survival over time (Cook 1980; Roberts 1981). Such models take the form:

$$Y = Y_0 \cdot \exp(-a \cdot X) + e$$

where  $Y$  = number of seed at time  $X$ ,  $Y_0$  = number of seed buried initially at time 0,  $a$  = rate of seed loss,  $X$  = time in years from 0 to  $i$ , and  $e$  is an error term. Arithmetic loss models adequately described seed survival for some species (Roberts 1981). Such models take the form

$$Y = Y_0 + a \cdot X + e$$

Recently, Conn (1990) showed that a negative rectangular hyperbola model adequately modeled seed survival for some weed species and accounted for more data variability than

a negative exponential model. Conn's model took the form:

$$Y = a[1/(X + b)] + e$$

$a$  and  $b$  are empirically fitted constants. Because none of these published seed survival models has a satisfactory mechanistic explanation in terms of either weed seed ecology, physiology or biochemistry, they must be considered to be descriptive models. Their value lies in how well they fit the data and whether they adequately describe data variability.

Wild mustard seed survival was chosen as a model system for this methodological research. In the field, 86% of buried undisturbed wild mustard seed survived after 3 yr of burial and 17% survived after 14 yr (Kolk 1962). However, fewer shallow-buried seed survived than more deeply buried seed (Kolk 1962). After 10 yr, 30 and 59% of seed survived at the 8- and 30-cm burial depths, respectively. A seed half-life of 3 yr was reported in untilled burial studies in England (Edwards 1980). Periodic soil disturbance to simulate tillage enhanced the rate of loss of wild mustard from the soil seed bank (Chepil 1946; Warnes and Andersson 1984) probably by stimulating germination (Bibbey 1935; Edwards 1980).

The objectives of this research were: (1) to determine whether seed survival models generated for data collected annually over 4 yr were comparable when experiments were started in different years, using wild mustard seed as a model system, (2) to model the wild mustard seed survival curves by linear and nonlinear least squares regression equations and determine whether a mixed linear-negative exponential model [i.e.,  $Y = a + b \cdot X + c \cdot \exp(-X)$ ] described data variability better than linear, negative exponential, or negative rectangular hyperbola models for data collected annually over 4 yr; and (3) to determine whether increasing sample size was advantageous for improving model fit of a mixed negative exponential model. It was not the intent of this research to prove the general applicability of mixed negative exponential models.

## MATERIALS AND METHODS

The treatments were six sample sizes (1–6 lots of 100 seed each) and five harvest times (0–4 yr). A randomized complete block design with four blocks was employed in a factorial arrangement with six sample sizes and five harvest times as the main factors. Blocking was based on anticipated moisture gradients across the site due to snow accumulation. The experiment was repeated on two adjacent sites as part of another larger experiment (Donald and Tanaka 1993). Trial 1 lasted from the fall of 1983 to 1987 and trial 2 lasted from the fall of 1984 to 1988 on an adjacent site.

Fully mature wild mustard seed was gathered from several hundred plants from one naturally established wild stand near Fargo, North Dakota, on 4 August 1983, for trial 1 and on 3 August 1984 for trial 2. Air-dried seed were stored in darkness at  $-15^{\circ}\text{C}$  before packaging for burial in the field on 13 September 1983, for trial 1 and on 21 September 1984, for trial 2. One hundred seed were packaged in water-permeable nylon (Nitex monofilament nylon 480 micron mesh from Pesco Inc., P.O. Box 24225, Minneapolis, MN 55424) mesh seed packets measuring 5 cm by 12 cm and one packet was buried 1.9 cm deep in each plastic pot (7 cm diam. by 7.5 cm tall) containing Fargo silty clay (fine, montmorillonitic, frigid Vertic Haplaquolls) with 2% sand, 47% silt, 51% clay, 3.9% organic matter, and a pH of 7.7. Then pots were buried in the field flush with the soil surface. Enough seed packets were buried in individual pots so that six packets could be unearthed per block annually for 4 yr. A random number table was used to determine sample selection from each block for each year. The burial site on the North Dakota State University Experimental Farm in Fargo was fenced and individual pots were covered with wide-mesh screening to prevent packet disturbance by rodents or birds without restricting rainfall entry.

Seed packets for trial 1 were retrieved from the field at yearly intervals on 14 September 1984, 11 September 1985, 16 September 1986, 14 September 1987, and for trial 2 on 11 September 1985, 16 September 1986, 14 September 1987, and 15 September 1988. Seed were removed from the packets, washed free of soil, air-dried, and the number of intact, firm, undamaged surviving seed were counted and were expressed as a percent of the initial number of seed buried (100).

Seed viability or percent germination was not reported for this paper because it was not of research interest to the author and seed viability is an ambiguous measure of seed survival for buried weed seed bank in field soil. Ambiguity

arises because zero percent seed viability could be reported if either no intact undamaged seed remain or all the seed buried were intact but were dead after time interval  $x$ . Descriptive and mechanistic mathematical models of seed survival as measured by changes in seed viability for commercial crop seed stored under defined environmental conditions were reviewed (Roberts 1986). Crop seed physiologists interested in maintaining seed viability of bulk lots of seed stored under optimum conditions in long-term storage used seed viability to follow seed survival. Crop seed physiologists have not been concerned with studying the total loss of seed from the seed bank under field conditions, as have seed ecologists. Thus, seed ecologists often report seed survival differently (Cook 1980; Roberts 1981; Lonsdale 1988) than do crop seed physiologists (Roberts 1986). The definition presented above and used in this paper is also commonly used by many seed ecologists (Cook 1980; Roberts 1981; Lonsdale 1988).

Either linear or nonlinear least squares regression analysis was used to model percent seed survival versus time for each trial using Tablecurve version 3.0 software (Jandel Scientific, 65 Koch Rd., Corte Madera, CA 94925). In the nonlinear regression performed by this software, the Levenburg-Marquardt algorithm iteratively fitted nonlinear equations by adjusting the equation parameters to minimize the goodness of fit  $\chi^2$  parameter. The algorithm identified convergence when the coefficient of determination ( $R^2$ ) remained unchanged for five consecutive iterations. The  $R^2$  represents the proportion of variability due to the independent variable in the regression equation. The magnitude of the ANOVA  $F$  value, residual mean square error (RMSE) and  $R^2$ , and inspection of plots of residuals versus the independent variable were used to evaluate the adequacy of regression models. The slopes and intercepts of selected regression models are presented  $\pm$  standard errors in Fig. 1. All slopes and intercepts were significantly different from zero at  $P \leq 0.01$ .

## RESULTS

### Regression Modeling of Seed Survival Curves

Seed survival studies are not generally repeated over time. In the current research, wild mustard seed survival curves differed between trials and, consequently, could not be modeled by a simple mathematical function (Fig. 1). In initial exploratory regression

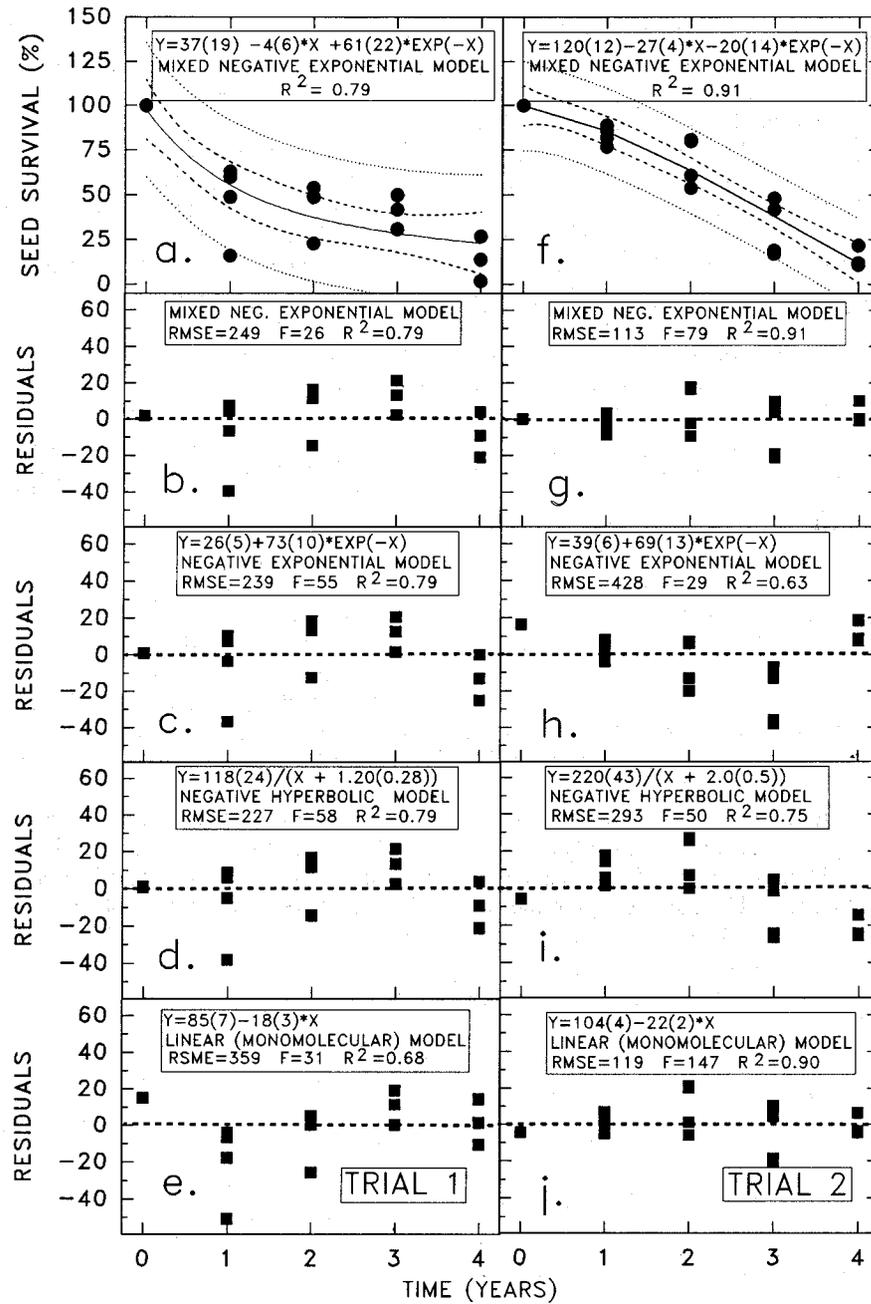


Fig. 1. Wild mustard seed survival over time in trials 1 and 2. Means  $\pm$  standard errors in parentheses are presented for linear and nonlinear least squares regression equations, as well as 95% confidence intervals (dashed lines) and 95% prediction intervals (dotted lines) (a and f). Residuals over time are presented for a mixed negative exponential model (b and g), negative exponential model (c and h), negative hyperbolic model (d and c) and negative linear model (e and j). RMSE = residual mean square error, F = F probability value for the regression ANOVA (F = MSE due to regression/MSE due to residuals), and  $R^2$  = coefficient of variation.

analyses, seed survival over time was best modeled as a negative exponential function of time in trial 1 (Fig. 1c), but decreased as a negative linear model in trial 2 (Fig. 1j). The greatest absolute difference in seed survival curves between trials 1 and 2 occurred during the first year after burial, and more seed in trial 1 were lost by year 1 than in trial 2. A model taking the form of a mixed linear-negative exponential model was flexible enough to describe both data sets. A negative hyperbolic model described data variability as well as the mixed linear-negative exponential model in trial 1 (Fig. d) but not in trial 2 (Fig. 1i).

#### Sample Sizes for Seed Survival Modeling Research

In designing seed survival studies, one must balance the sample size needed to detect real differences between treatments and the cost of such sampling (Gomez and Gomez 1984). The effect of increasing sample size from 1 to 6 on a mixed negative exponential model for a randomized complete block design with four blocks is summarized in Table 1. There was no advantage to taking more than one sample for a randomized complete block design with four blocks for a mixed negative exponential model for seed survival of wild mustard; RMSEs were not decreased and  $R^2$  were not increased by increasing sample size from 1 to 6 ( $N=4-24$ ) for such designs.

As expected, the SEs for estimates of individual model coefficients decreased as sample size increased.

#### DISCUSSION

Lonsdale (1988) suggested that seed survival over time is best described by families of curves, rather than one class of simple functional relationships (i.e., negative exponential), although he did not present data to support his assertion. The mixed negative exponential model (i.e.  $Y = a + b*X + c*\exp(-X)$ ) used here is a good candidate for this role in that it described the data variability for seed survival curves of wild mustard well for both trials (Fig. 1a and f), as indicated by plots of residuals and other statistics (Fig. 1b and g). A mixed negative exponential model is a good compromise for modeling seed survival curves which could be either negative exponential or linear functions of time.

Some authors of seed survival studies have tacitly assumed that the shape of seed survival curves is a characteristic of a species. For example, the seed ecologists Thompson and Grime (1979) have classified four types of seed bank dynamic behavior, as weed species' characteristics. In their classification system, there is no discussion of the possibility that a species could have several different types of seed survival curves, probably because seed ecologists do not generally repeat seed

Table 1. Impact of increasing sample size on  $R^2$  and residual mean square for mixed negative exponential models in Fig. 1 describing seed survival curves for wild mustard

Trial	Groups harvested per block	Samples per harvest	$R^2$	RMSE	Standard error of model coefficients		
					a SE	b SE	c SE
1	1	4	0.79	249	18.5	5.9	22.2
	2	8	0.71	309	14.1	4.4	16.9
	3	12	0.68	367	12.4	3.9	14.9
	4	16	0.72	314	9.9	3.1	11.9
	5	20	0.74	288	8.4	2.6	10.2
	6	24	0.76	265	7.4	2.3	8.9
2	1	4	0.91	113	12.0	3.9	14.4
	2	8	0.90	110	8.4	2.6	10.1
	3	12	0.89	116	7.1	2.3	8.6
	4	16	0.86	159	7.1	2.3	8.6
	5	20	0.82	188	6.9	2.2	8.3
	6	24	0.84	177	6.0	1.9	7.3

survival studies in time. The shapes of the seed survival curves for wild mustard (Fig. 1a and f) are probably not a genetically determined species' characteristic alone, but likely reflect the interaction of a species seed phenotype and environment.

One of the unique aspects of this research is that the experiment was repeated in time. Also, each trial of the experiment lasted 4 yr and had five annual observations for the independent variable time, including time zero. This allowed nonlinear seed survival curves to be distinguished from linear relationships. I was able to find only three examples of seed survival studies which were repeated in time in the published literature (i.e., for common crupina (*Crupina vulgaris*) (Thill et al. 1985), subterranean clover (*Trifolium subterraneum* L.) (Bolland and Collins 1987), and wild oat (*Avena fatua* L.) (Zorner et al. 1984). Several other published seed survival studies have been repeated over time, but the authors reported seed emergence to measure seed survival over time rather than the number of intact undamaged seed remaining (e.g. Roberts and Boddrell 1983). None of the authors of these studies published mathematical models for their seed survival data.

While the biological causes for differences in wild mustard seed survival curves between trials cannot be determined from this research, there are several possible explanations:

(1) Seed collected for each trial in different years could differ in genotype leading to different seed survival curves. However, it is likely that the seed mixtures used were genetically diverse because this is a wild species, rather than a genetically uniform crop variety, and seed for each trial was collected from several hundred plants at the same site. Genotypic differences in wild mustard seed dormancy have been demonstrated (Garbutt and Witcombe 1986), although the impact of seed dormancy on seed persistence in the field was not reported in this latter research.

(2) Lonsdale (1988) suggested that year-to-year differences in the shapes of seed survival curves may be due to differences in the frequency distribution of different seed phenotypes initially buried, rather than genotypic differences. The environment under which seed matured may have influenced the seed survival curves through effects on seed phenotype rather than on genotype. Wild mustard

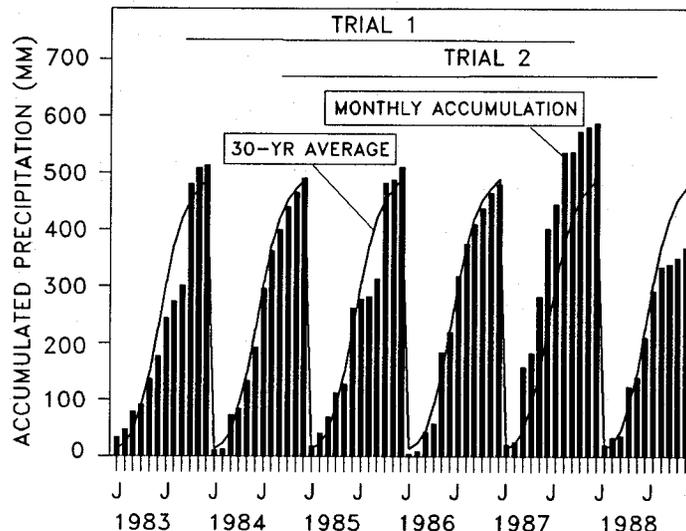


Fig. 2. Monthly accumulated precipitation (solid vertical bars) for trials 1 and 2 and the 30-yr average accumulated precipitation (line). Weather data were gathered at Hector International Airport approximately 1 km north of the experimental site. The period over which trials 1 and 2 were conducted is indicated by horizontal lines.

seed matured under drought conditions in trial 1, but not in trial 2 (Fig. 2). Plant water stress and seed moisture content during maturation reportedly influenced subsequent seed germination (Adams and Rinne 1980). Maternal and/or environmental conditions during seed maturation also have been shown to influence weed seed germination in the subsequent growing season (Gray and Thomas 1982; Naylor 1983; Schaal 1984; Shaanker et al. 1988). Thus, maternal effects or differences in maternal environmental may have led to differences in seed survival curves, but I was unable to find published reports demonstrating such effects on weed seed persistence over several years in the field.

(3) Seed germination is thought to be the major cause for seed loss from the buried seed bank (Cook 1980; Roberts 1981). Fluctuations in year-to-year rainfall in fall (Fig. 2) favoring greater fall germination during the first growing season after initial burial may also account for differences in the shapes of wild mustard seed survival curves between trials (Fig. 1), although percent germination and emergence were not measured in this research. Seed in trial 1 experienced normal fall rainfall 1 year after burial, whereas seed in trial 2 experienced late summer and fall drought (Fig. 2). Cumulative rainfall throughout year 1 was similar to the 30-yr average and likely did not limit seed germination throughout the first year after seed burial in trial 1 (Fig. 2). Rainfall, however, was severely limited throughout the summer and fall of the first growing season after initial seed burial in trial 2 and probably limited germination throughout summer and fall leading to greater seed survival in trial 2 in year 2 compared with trial 1.

The latter explanation for differences between trials is consistent with reports concerning wild mustard germination and emergence from the scientific literature. Although wild mustard is a summer annual in most temperate climates (Fogg 1950; Edwards 1980; Roberts and Boddrell 1983) with most emergence occurring in spring and early summer, some seedlings emerge in fall (Edwards 1980).

There is one caveat for this research that also applies to most published research modeling weed seed survival. Almost all published models of seed persistence are based on data collected annually at the same time over several years. Lonsdale (1988) suggested that the shape of seed survival curves may be an artifact of infrequent seed sampling over time (i.e., annual sampling). Sampling only once per year may mask more complex seed survival curves that cannot be adequately described by any published models or the mixed negative exponential model suggested in this paper. For example, complex seed survival curves were observed for jointed goatgrass (*Aegilops cylindrica* L.) seed survival when sampled at biweekly intervals over 2 yr (Donald 1991) compared to less frequent yearly sampling (Donald and Zimdahl 1987). Jointed goatgrass seed survival curves in the former study (Donald 1991) could not be adequately modeled by simple mathematical functions, such as the negative exponential function. In jointed goatgrass, periods of greatest seed loss corresponded to periods of greatest seed emergence in fall, which were related, in turn, to fall rainfall.

This methodological study contributes to research on seed survival by demonstrating that the shape of seed survival curves can change from year to year for the same species. Families of functional relationships may be useful for modeling seed survival curves of one species, as Lonsdale (1988) suggested. This possibility should be examined on other data sets for other species to examine its general applicability, although the number of published seed survival studies repeated in time is limited. The mixed negative exponential model used here is suggested as a flexible alternative to simpler functions for descriptively modeling data variability of seed survival curves. Sample sizes of four lots of 100 seed each harvested per year provided acceptable estimates of slopes and intercepts of seed survival curves using a mixed negative exponential model in a randomized complete block design with four blocks.

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