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Prediction of weed seedling densities from buried seed reserves

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Summary: Résumé: Zusammenfassung

Bioeconomic models for weed management ultimately require knowledge of weed densities. Weed seedling populations may be predicted by multiplying emergence rates by seedbank densities. However, emergence rates vary according to species, year and management. Furthermore, seedbank estimates may vary with sampling technique, size, number and date. These variables must be quantified before bioeconomic models can be used profitably. Consequently, two experiments were initiated, both in conventionally managed maize. The first experiment documented proportional seedling emergence across years and sites for three taxa: foxtail (*Setaria glauca* [L.] Beauv. and *S. viridis* [L.] Beauv. combined), pigweed (*Amaranthus retroflexus* L.), and lambsquarters (*Chenopodium album* L.). The second experiment was devoted to methodology for estimation of seedbanks: sampling date (autumn or spring), technique (seed extraction or glasshouse germination), and soil sample size for the seed extraction technique. For emergence rates, the following order was observed: foxtail > lambsquarters > pigweed. Emergence rates for each species were related in a parabolic manner to growing degree-days in April. The glasshouse technique appeared to be more reliable than seed extraction for correlation with field seedling densities. For the seed extraction technique, a minimum soil sample size of 100 g was necessary. A spring sampling date appears to be more reliable than an autumn date, probably because many seemingly viable seeds die during winter.

Prevision de la densite de plantules d'adventices a partir des reserves de graines enfouies

Les modèles bioéconomiques en matière de desherbage impliquent la connaissance des densités d'adventices. Les populations de plantules adventices peuvent être prévues à partir des taux de levées multipliés par les densités du stock grainier. Cependant, les taux de levée varient avec les espèces, l'année, et les méthodes culturales; et les estimations du stock grainier peuvent varier avec la technique d'échantillonnage, son nombre, sa taille et sa date. Ces variables doivent être quantifiées avant que les modèles bioéconomiques puissent être utilisés avec profit. En conséquence, deux expérimentations ont été mises en place, les deux en culture de maïs conventionnelle.

La première expérimentation a indiqué le taux de levée des plantules pour les différentes années et sites de 3 taxons: setaires (*Setaria glauca* [L.] *Beauv. et S. viridis* [L.] Beauv., en association), amaranthe réfléchie (*Amaranthus retroflexus* L.) et chenopode blanc (*Chenopodium album* L.). La seconde expérimentation était consacrée à la méthodologie d'estimation du stock grainier: date d'échantillonnage (automne ou printemps); technique (extraction des graines ou germination en serre) et taille de l'échantillon de sol pour la technique dfextraction des graines. Pour les taux de levée: sétaires > chénopode blanc > amaranthe. Les taux de levée pour chaque espèce sont liés de façon parabolique avec les degrés/jour de croissance en Avril — la technique en serre apparaît plus fiable que l'extraction des graines pour la corrélation avec les densités d'adventices au champ.

Pour la technique d'extraction des graines, la taille minimum de l'échantillon nécessaire était de 100 g: un échantillonnage de printemps apparait meilleur qu'un d'automne, probablement parce que de nombreuses semences paraissant viables meurent durant l'hiver.

Prognose der Keimpflanzendichte von Unkräutern nach dem Samenvorrat im Boden

Bioökomische Modelle in der Unkrautbekämpfung setzen die Kenntnis der Unkrautdichte voraus. Die Keimpflanzendichte kann mit dem Produkt aus der Samendichte im Boden mit der Keimrate errechnet werden. Die Keimrate variiert jedoch je nach Pflanzenart, Jahr und Kulturbedingungen, und die Bestimmung der Samenbank hängt von der Probennahmetechnik, -größe, -zahl und -zeit ab. Diese Variablen müssen quantifiziert werden, um brauchbare bioökonomische Modelle zu erhalten. Deshalb wurden in normal angebautem Mais 2 Versuche angelegt, um zum einen die Keimpflanzendichte von 3 Arten(gruppen), Fuchsrote Borstenhirse (*Setaria glauca* (L.) Beauv.)+Grüne B. (*S. viridis* (L.) Beauv.), Zurückgekrümmter Amarant (*Amaranthus retroflexus* L.) und Weißer Gänsefuß (*Chenopodium album* L.), über die Jahre und an verschiedenen Punkten festzustellen und sich zum anderen mit der Methodik der Bestimmung der Samenbank zu befassen: Probennahmezeit (Herbst und Frühjahr), -technik (Samenauswaschung oder Keimung im Gewächshaus) und Bodenprobenumfang. Die Keimraten (im April) waren: Borstenhirse > Gänsefuß > Amarant. Die Keimung im Gewächshaus ergab für die Korrelation mit der Keimpflanzendichte im Feld bessere Werte als die Samenauswaschung. Für die Auswaschung waren mindestens 100 g Boden erforderlich. Probennahmen im Frühjahr erwiesen sich als günstiger als im Herbst, vermutlich wegen des Absterbens vieler keimfähiger Samen über Winter.

Introduction

An important variable in bioeconomic weed management models (King *et al.*, 1986; Schweizer & Lybecker, 1990) is the proportion of a weed's buried seed reserve that germinates and emerges as seedlings. Predictions of emerged seedling densities allow estimations of weed competition, crop yield loss, necessity of control inputs, and financial returns. Unfortunately, data on seedbank emergence proportions are lacking for most species. Even where such information is known (e.g. Roberts & Ricketts, 1979), it exists as static data, i.e. a single value is used to determine the proportion of the seedbank that emerges as seedlings, regardless of variations in weather, soils, tillage, etc. To improve the reliability of seedling emergence estimates in weed management models, the effects of several variables on the proportion of the seedbank that emerges must be explored.

Another important consideration for weed management models is the utility and reliability of the techniques used to measure the seedbank. There are two basic techniques: the glasshouse tray method, and the seed extraction method. Post (1984) has shown that the long-standing, but 'time-consuming' glasshouse tray technique can be completed within 2 weeks if appropriate germination stimulants are employed (e.g. dehydration cycles and potassium nitrate). Malone (1967) described the labour-intensive, but otherwise rapid direct seed extraction method. This latter method has been refined to extract seeds more rapidly from large numbers of very small (<60 g) soil samples simultaneously (Gross & Renner, 1989) and from single large (>1000 g) soil samples (Kovach, Thill & Young, 1988).

Ball & Miller (1989) compared the glasshouse and seed extraction techniques for arable weeds and reached two basic conclusions. First, the two seedbank estimation methods were correlated with one another and, secondly, neither method was reliably related to field seedling populations. Unfortunately, this latter conclusion is highly suspect because Ball & Miller's seedling populations were derived from plots that had been treated with standard rates of one or more preplant-incorporated herbicides. Extensive seedling mortality prior to emergence would almost certainly have occurred in these plots. Brown (1990) estimated seedbanks in vegetation right-of-ways using the two techniques, and concluded that the two methods do not produce similar estimates of the composition and density of the seedbank. Thus the relative reliability of the two methods in terms of predicting weed seedling populations remains unknown.

Consequently, the objectives of this study were as follows: (1) to determine the variability of annual emergence percentages of three weed taxa, namely foxtail (*Setaria glauca* and *S. viridis* combined), lambsquarters (*Chenopodium album*) and pigweed (*Amaranthus retroflexus*); (2) to relate environmental factors and tillage to emergence percentages; (3) to compare the reliability of different seedbank estimation techniques and sampling dates in relation to field populations of weed seedlings; and (4) to determine the effect of sampling date and sample size on the reliability of the seed extraction technique.

Materials and methods

Experiment 1. Buried seed and seedling comparisons

Two sites were chosen at the University of Minnesota's West Central Experimental Station, Morris, MN, USA (45°35′N, 95°53′W). The first site was on a LaPrarie loam soil (Cumulic Udic Haploboroll, fine-loamy, mixed) and the second was on a Nutley clay soil (Udertic Haploboroll, fine, montmorillonitic). At both sites plots were established during early spring of 1988 and 1990. Plots were arranged in four blocks at each site, each block contained 4–6 plots, and plot sizes ranged from 6·1 × 10·7 m to 12·2 × 22·9 m.

Prior to noticeable weed seedling emergence in spring (March or April), the buried seed reserve was sampled as follows:

(1) soil cores were collected along a diagonal transecting plot;
(2) cores were pooled into one sample for each plant;
(3) cores were 10 cm deep, and when combined they represented a total soil surface area of about 300 cm^2;
(4) samples were spread on to trays, placed in a glasshouse (30/20°C day/night) and kept moist with deionized water;
(5) emerging seedlings were identified and counted;
(6) when emergence ceased, samples were dried, stirred, and rewatered;
(7) steps 5 and 6 were repeated four times;
(8) prior to the last soil stirring, samples were chilled (2°C) for about 30 days;
(9) samples were periodically watered with a nitrate-enriched liquid fertilizer.

Soil core diameter was 5 cm and depth was 10 cm, and 15 cores were collected in each plot except in the clay in 1990. In the latter case, only four cores, each 10 cm in diameter, were collected. This change in procedure was necessary in 1990 because, at the time of sampling, wet clay soil samples could not be removed easily from smaller diameter sample tubes. Nevertheless, the total soil surface area sampled in 1990, about 300 cm^2, should permit relatively reliable estimates of seedbanks. Forcella (1984) observed that for estimation of seedbanks of individual research plots, a cumulatively sampled soil surface area of 250 cm^2 was required, irrespective of the number of cores from which that surface area was derived. This can also be confirmed by reanalysis of the results of Benoit *et al.* (1989; Tables 1 and 2). They found that as soil core diameter (D) increased from 1·9 to 2·7 to 3·3 cm, and the number of samples (N) decreased from 58 to 28 to 20, estimated weed densities and sampling variances remained constant. Extension of this constant D/C relationship through a best-fit ($r^2 = 0{\cdot}99$) reciprocal straight-line function ($n = 1/[-0{\cdot}0273 + 0{\cdot}0234{*}D]$) indicated that for core diameters of 10 cm, 4–5 samples per plot would be required. Naturally, for large fields rather than research plots, the much larger sample numbers suggested by Benoit *et al.* (1989) would be more appropriate.

Each plot was divided into two subplots, one of which received the recommended rate of standard maize herbicides. Maize was subsequently sown at 65 000 seeds ha^{-1} in late April or early May. In autumn, maize grain was harvested in each subplot, weighed, corrected for moisture content, and percentage yield reduction due to weed interference calculated.

Emerged weed seedling densities were determined three times in each plot or subplot. The first seedling count took place immediately prior to disking and harrowing of soils, which had been mouldboard ploughed the previous autumn. Maize was sown soon after the secondary tillage operation, but if sowing was delayed because of adverse weather, seedlings were counted again. The second seedling count took place prior to inter-row cultivation, about 6 weeks after sowing. Inter-rows were cultivated only once. The final seedling count took place about 4 weeks

Table 1. Average percentages of buried seeds emerging as seedlings at three different dates for three weed taxa at two experimental sites

	1988				1990			
Dates	FOX	PIG	LAM	ALL	FOX	PIG	LAM	ALL
North Farm (clay)								
Pre-plant	0	0	0	0	0·4	0	0·2	0·1
Post-plant	23·9	13·7	19·4	14·8	32·9	9·6	1·6	14·7
Post-cultivation	0	0	0	0	2·3	3·1	1·3	2·5
Total	23·9	13·7	19·4	14·8	35·6	12·6	3·1	17·2
Central Farm (loam)								
Pre-plant	0	0	0	0	0·2	0·8	1·5	0·6
Post-plant	21·1	8·8	5·7	15·4	21·8	5·8	6·9	12·3
Post-cultivation	0	0	0	0	5·5	1·8	0·9	3·0
Total	21·1	8·8	5·7	15·4	27·5	8·4	9·3	15·9

FOX = green and yellow foxtail, PIG = redroot pigweed, LAM = common lambsquarters.
Sample numbers for 1988 and 1990 were 32 and 24 (North Farm) and 32 and 16 (Central Farm).

Table 2. Temperature and rainfall in spring for the West Central Experiment Station in 1988 and 1990

	Rainfall (mm)			Minimum temperature (°C)			Maximum temperature (°C)		
Year	April	May	June	April	May	June	April	May	June
1988	15	43	12	−1·8	9·9	15·1	14·7	26·0	31·4
1990	49	42	32	−0·8	5·9	13·2	14·0	18·8	25·2
Mean value*	62	74	99	0·4	7·0	12·8	11·4	19·8	24·8

*Average value over the 30-year period 1951–1980.

after cultivation. All counts were made in six 25 × 40 cm quadrats/plot, with the long axis of the quadrat extending into the inter-row area.

To relate total annual emergence percentages to weather variables, data from the four site-years described above were combined with those from nearby plots gathered in 1985 and 1986 (Forcella & Lindstrom, 1988; Forcella, 1990). The resulting six site-year data set was compared with regard to monthly rainfall, air temperature, and growing degree-days (base 10°C) alone and in combination for the months of April, May and June. MSUSTAT (Lund, 1988) was used for statistical analyses, and CURVEFIT (Cox, 1989) was used to determine equations for non-linear relationships.

Experiment 2. Sampling techniques for individual plots

The experimental site was the Nutley clay soil and the plots were as described for Experiment 1. In November 1989 and April 1990 soil samples were collected as described above. After the soil had been thoroughly stirred, a 250-ml subsample was withdrawn. The remaining soil was placed in glasshouse trays and treated as described previously; the results derived from these samples will be referred to as glasshouse seedbank estimates.

The 250-ml subsample was divided into 20-g units. Each unit was suspended in 50 ml of a solution to disperse clay particles (Malone, 1967). Suspensions were stirred for 15 min, and subsequently rinsed over a series of screens. The seed material that remained on the screens was washed on to filter paper, sorted into 'dead' and 'viable' categories, and counted by species. The dead category was defined as any non-viable seed or piece of seed coat large enough to be mistaken for a viable seed by an untrained technician. Seeds were considered to be viable if they were firm when pressured by the tip of a dissection needle. The frequencies of first encounter and unit-area densities for each species were determined for cumulative subsample sizes ranging from 20 g to ≥160 g soil. These unit-area estimates were then sequentially regressed against total field seedling densities. MSUSTAT (Lund, 1988) was used for statistical analyses.

Results and discussion

Experiment 1. Buried seed and seedling comparisons

Seedlings emerging after crop sowing were the primary contributors to total emergence from seedbanks of herbicide-free subplots (Table 1). Only minor proportions of the seedbank were represented by emerged seedlings before planting and after cultivation. Ball & Miller (1989) also observed that preplant seedling densities in herbicide-treated plots were of minor importance compared to postplant densities. Virtually no seedlings emerged before planting or after cultivation in 1988. This was probably due to the extremely dry seedbanks because of lack of rain in April (before planting) and June (after cultivation) in that year (Table 2). In 1990, precipitation between April and June was more evenly distributed, thus enabling some emergence to occur before planting and after cultivation (Table 1).

Total cumulative emergence from the buried seed pool of all species combined only ranged from 14·8–17·2% (Table 1). For individual taxa, however, the ranges of site-year emergence values were larger: foxtail, 21·1–35·6%; lambsquarters, 3·1–19·4%; and pigweed, 8·4–13·7%. For a variety of species in the UK, Roberts & Ricketts (1979) reported an emergence range of 2–16%.

To compare the emergence percentages among species, overall average annual emergence percentages were calculated using data collected from nearby plots in 1985 and 1986 (Forcella & Lindstrom, 1988; Forcella, 1990), as well as those in Table 1. The resulting mean values ($n=6$) for foxtail, lambsquarters and pigweed were 26, 15 and 10%, respectively.

In combination with the 1985 and 1986 data, total site-year emergence percentages of each species could be related to growing degree-days (GDD, base 10°C air temperature) in April (Fig. 1). In each case the relationship between percentage emergence and GDD was nonlinear. Best-fit regressions for foxtail, pigweed and lambsquarters were described by a Hoerl function ($r^2=0{\cdot}97$), modified Hoerl function ($r^2=0{\cdot}89$) and parabola ($r^2=0{\cdot}35$), respectively. Correlations between emergence percentages and weather variables of other months or combinations of months were not as strong as those with April GDD.

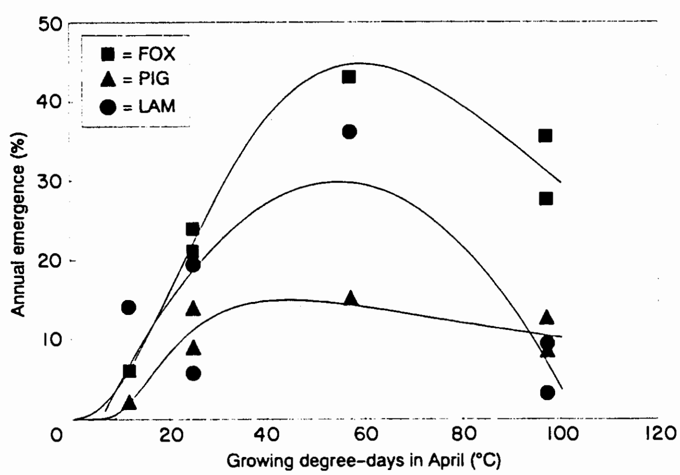

Fig. 1. Total emergence of three weed species in relation to growing degree-days in April. Equations defining the relationships are as follows: foxtail, $Y=0{\cdot}0205*0{\cdot}9587^{X}*X^{2{\cdot}4958}$; pigweed, $Y=16766{\cdot}9*7{\cdot}68E\text{-}29^{(1/X)}*X^{-1{\cdot}4679}$; lambsquarters, $Y=-8{\cdot}1326+1{\cdot}3876*X-0{\cdot}0127*X^2$, where Y = percentage emergence, and X = growing degree-days.

A possible explanation for the 'parabolic' relationship between eventual total seasonal emergence and GDD in April is as follows. April is the first month of the year in Minnesota, during which the upper 10 cm of soil (the soil depth from which weeds may emerge) are not consistently frozen, thereby allowing biological activity. Extremely high temperatures in April may induce secondary dormancy in seeds (Baskin & Baskin, 1985), particularly as was the case in 1990 when the soil was too dry to support germination. The greater depression in emergence of lambsquarters than of other species with high April GDD probably reflects this taxon's greater sensitivity to high temperature, and the ease with which secondary dormancy is induced (e.g. Williams & Harper, 1965; Karssen 1980/1981). In contrast, very low April temperatures (e.g. 1986) physically inhibit germination, which typically commences in the latter part of this month.

The preceding emergence data were averaged over all plots within sites and years. Naturally, emergence values among individual plots were more variable. To emphasize this variability, buried seed and total seedling emergence data

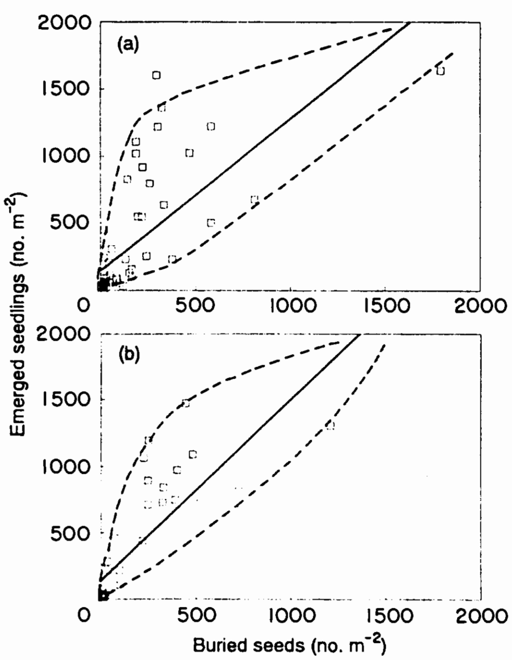

Fig. 2. Total numbers of seedlings arising from seedbanks of varying density for foxtail (a) in 1988 and (b) in 1990. Data from two sites, Central Farm (CF) and North Farm (NF), have been combined.

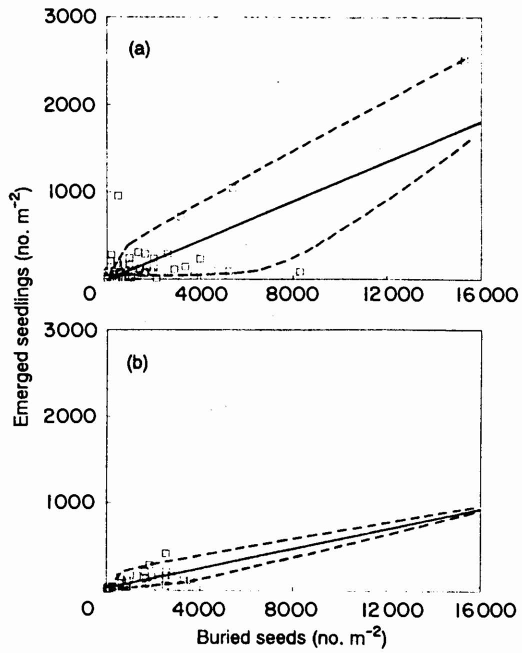

Fig. 3. Total numbers of seedlings arising from seedbanks of varying density for pigweed (a) in 1988 and (b) in 1990. Data from two sites, Central Farm (CF) and North Farm (NF), have been combined.

for individual plots from both the Central Farm and North Farm experiments were combined and plotted in Figs 2–5. Coefficients from linear regressions that best fit these data tend to coincide with the average total emergence values shown in Table 1. However, high variability surrounding linear regression equations may preclude their use in bioeconomic models. For such modelling purposes emergence 'boundaries' may be a practical alternative to regression 'lines'. Standard statistical boundaries, i.e. confidence limits, can be easily calculated for linear regressions, but the resulting double-concave or hourglass shape of such confidence limits does not conform to the data distributions shown in Fig. 2. The data more often appear to be distributed as ellipses (double-convex).

For bioeconomic models, the upper boundary of an ellipse would describe the maximum possible number of seedlings to emerge from a seedbank. This would represent a 'low-risk' equation for decisions regarding weed management. The lower boundary would describe the minimum possible number of seedlings to emerge from a seedbank, and its use in a

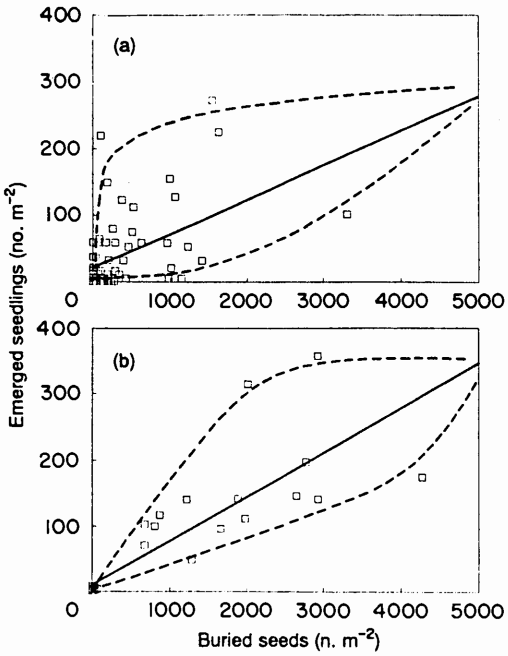

Fig. 4. Total numbers of seedlings arising from seedbanks of varying density for lambsquarters (a) in 1988 and (b) in 1990. Data from two sites, Central Farm (CF) and North Farm (NF), have been combined.

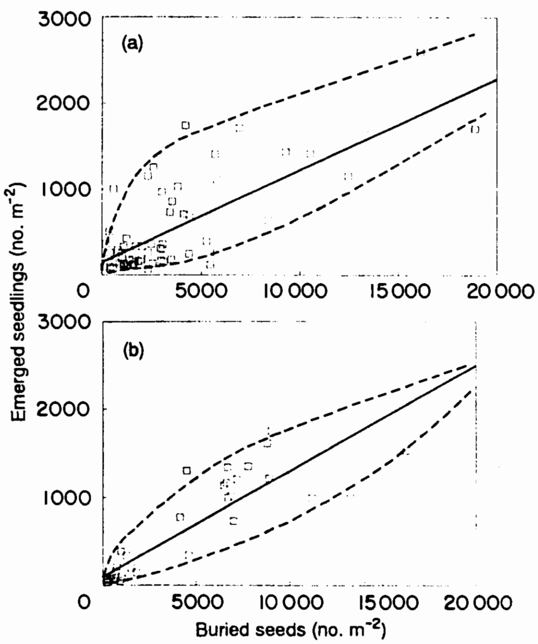

Fig. 5. Total numbers of seedlings arising from seedbanks of varying density for three taxa combined (foxtail, pigweed and lambsquarters) (a) in 1988 and (b) in 1990. Data from two sites, Central Farm (CF) and North Farm (NF), have been combined.

bioeconomic model would represent a 'high-risk' management option.

Crop losses due to weed interference ranged from 0% to about 80% in both 1988 and 1990 (Fig. 6). The magnitude of yield reduction was related to total (combined species) weed seedling density. With densities of less than 250 seedlings m^{-2}, an approximately linear relationship existed between seedling density and maize yield reduction. In the very dry year of 1988, the slope of this linear relationship appeared to be greater than that for 1990. Above 250–500 seedlings m^{-2}, an asymptote was reached for maize yield reduction. At these high densities the asymptote ranged from about 40–80% yield reduction, but averaged 61% in 1988 and 67% in 1990. In both years yield loss (Y%) and seedling density (SD) data appeared to fit second-order hyperbola functions: in 1988, Y% = 61 −(3785/SD) + (86067/SD^2) ($r^2=0{\cdot}20$), and in 1990, Y% = 67−(4199/SD) + (76235/SD^2) ($r^2=0{\cdot}70$). However, as shown in Fig. 6, boundaries may more appropriately describe crop yield loss than simple curvilinear equations.

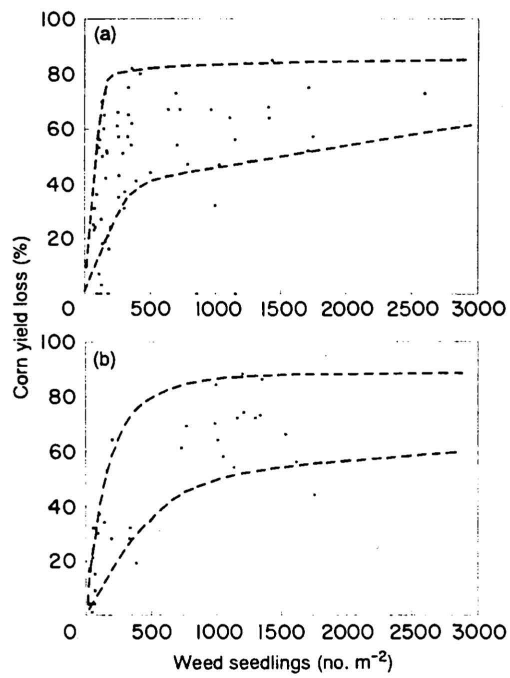

Fig. 6. Percentage corn yield reduction for two sites (combined) (a) in 1988 and (b) in 1990, in relation to total weed seedling density.

Experiment 2. Sampling techniques for individual plots

The minimum quantity of soil required to detect a single seed of each weed species was determined for each soil sample. These quantities are presented as frequencies of first encounter (EF) (Fig. 7) for both autumn and spring sampling dates. EF values for foxtail were very similar in autumn and spring, ranging from 15% in 20-g samples to 45% in 160-g samples. EF values for foxtail were consistently lower than those for pigweed and lambsquarters. EF values for the latter species were similar to one another, but the autumn values were much lower than those for spring samples. Autumn EF values ranged from 20–60% for pigweed and from 10–60% for lambsquarters along the 20–160 g soil sample gradient. In contrast, spring EF values ranged from 55–80% for pigweed and from 35–85% for lambsquarters, with an asymptote being reached at about 80 g of soil for both species. These results indicate (1) that spring is a better sampling date than autumn for the two broadleaf species, and (2) that if sample sizes of <100 g are used, important species may not be detected.

Unit-area seedbank densities calculated from different soil sample sizes, as well as from glasshouse samples, were variably correlated with field seedling densities (Fig. 8). Foxtail seedling density was only weakly correlated with autumn seedbank estimates regardless of soil sample size, but all spring seedbank estimates were relatively strongly correlated with seedling density. Pigweed seedling density was only weakly correlated with seedbank estimates derived from small soil sample sizes, but was relatively strongly correlated with all soil sample sizes of >80 g, regardless of the sampling date. Correlations of glasshouse seedbank estimates with field seedling densities for foxtail and pigweed were consistently relatively high. These results again suggest that spring seedbank

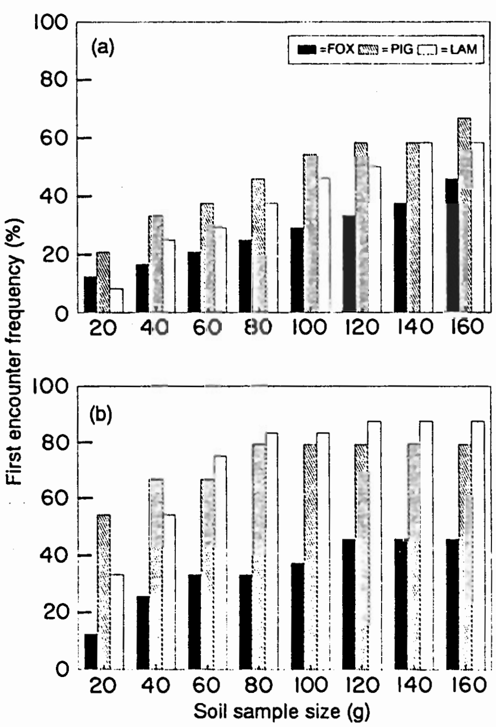

Fig. 7. Frequency of encounter of one or more seeds of foxtail, pigweed and lambsquarters in soil samples of different size. Soil samples were collected twice, (a) in autumn and (b) in spring, at the same site in the same plots.

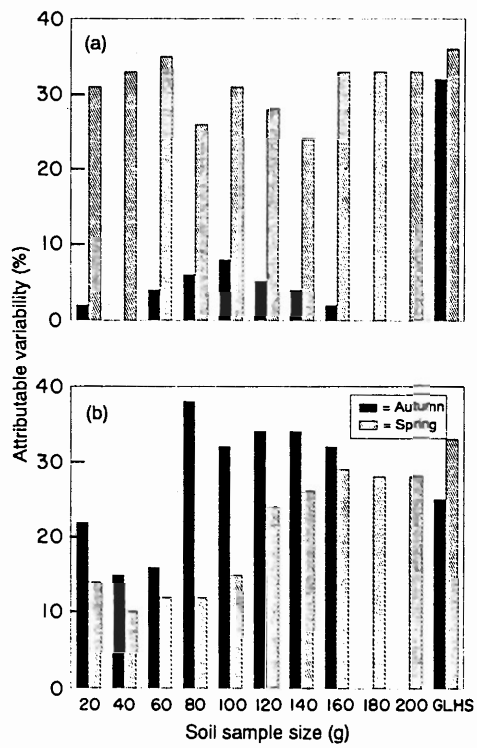

Fig. 8. Attributable variability (r^2*100) of regressions of seedbank density estimates on field seedling densities for (a) foxtail and (b) pigweed. Seedbank densities were estimated by two methods: the seed extraction technique from soil samples ranging from 20–200 g in weight, and the glasshouse technique (GLHS). Soil samples were collected from the field in both autumn and spring.

sampling dates are more reliable than autumn dates for prediction of foxtail seedling densities. This is probably due to the fact that many of the firm foxtail seeds identified in the autumn samples may have been non-viable; over winter these non-viable seeds would have passed into the 'dead' category. In contrast, autumn and spring seedbank sampling dates appear to be equally reliable in prediction of pigweed seedling densities. However, with this species, as indicated earlier, sample sizes of < 80 g are unreliable for prediction of pigweed seedling density.

For each species an overwhelming majority of the seedbank was composed of 'dead' seeds. Dead seeds consistently represented >80% of the seedbank and, as might be expected, the proportion of dead seeds was higher in spring than in autumn. The autumn and spring percentages of dead seeds for foxtail, pigweed and lambsquarters were 92 and 84%, 96 and 83%, and 92 and 85%, respectively. The overall least significant difference among these values, based on analysis of variance, was 6% ($P = 0{\cdot}05$).

Conclusions

Several conclusions can be drawn from these results with regard to seedbanks and bioeconomic models.

(1) Annual emergence rates differ between species, in the following order: foxtail > lambsquarters > pigweed.
(2) Rates of emergence vary between years, with April growing degree-days apparently being a controlling environmental variable.
(3) A single line may not adequately describe the relationship between seedbank size and subsequent densities of emerged seedlings. Instead, boundaries circumscribing the variation of the seedbank/seedling relationship may be more useful.
(4) Seedbanks are largely composed of dead seeds, the proportions of which are higher in spring than in autumn.
(5) The frequency with which apparently viable seeds in the seedbank are encountered increases with soil sample size. A minimum sample size of 100 g is suggested for direct seed extraction techniques.
(6) Spring sampling dates are apparently more consistently reliable than autumn sampling dates for prediction of final seedling densities.
(7) Glasshouse sampling techniques are more consistently reliable than seed extraction techniques, the latter being more dependent on sample size and sampling date.

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