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Author(s): Charles L. Mohler and M. Brett Calloway

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Effects of tillage and mulch on the emergence and survival of weeds in sweet corn

CHARLES L. MOHLER* and M. BRETT CALLOWAY[†][‡]

**Section of Ecology and Systematics, and [†]Department of Plant Breeding and Biometry, Cornell University, Ithaca, New York, USA*

Summary

1. The effects of tillage and non-tillage combined with no mulch and rye (*Secale cereale*) mulch on the emergence and survival of weeds in sweet corn (*Zea mays*) are reported.
2. The four most abundant weed species (*Amaranthus retroflexus*, *Chenopodium album*, *Portulaca oleracea*, and *Digitaria sanguinalis*) showed significantly lower emergence in till than in no-till treatments at one or more census times, probably because of seed burial and greater seed mortality in the till treatments.
3. *Taraxacum officinale* did not show lower emergence rates in till than in no-till, probably because of the short time between seed dispersal and germination.
4. Survival of *Amaranthus* was significantly greater in no-till than in till treatments, with the difference most pronounced late in the growing season.
5. The presence of corn or corn and rye mulch significantly reduced weed emergence for all species at one or more censuses.
6. Rye, killed with herbicide and used as a mulch, slightly decreased emergence and had no effect on survival.
7. A procedure for testing for departure of a survivorship curve from a truncated negative exponential is presented. Survival of annuals and other monocarpic plants should be considered truncated by successful reproduction.
8. In the absence of herbicides, mortality rates for *Amaranthus* and *Chenopodium* declined as the plants grew to maturity.
9. In most treatments, late-emerging plants survived to maturity better than earlier emerging plants, possibly because of shorter exposure to mortality factors. In the absence of herbicides, very dense stands of weeds led to greater mortality of later emerging cohorts.

Key-words: weed survival, tillage, mulching, emergence and survival, sweet corn.

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Introduction

The types and regimes of disturbance induced by management practices largely determine the characteristics of the weedy vegetation in agricultural ecosystems (Bazzaz 1983). To increase production efficiency, agriculturalists would like to be able to predict the outcomes of management options on weed populations in the field. Such predictions require understanding of the response of demographic parameters of weed populations to a range of management practices. This paper reports the effects of tillage, a mulch of rye straw (*Secale cereale*)*, herbicides, and the presence or absence of a crop on the emergence and survival of several spring germinating weeds common in sweet corn (*Zea mays*) cropping systems in the north-eastern United States. This study was unusual relative to most demographic research in that all the abundant species in the community were investigated simultaneously, and their demographic behaviour compared in eight different environmental conditions. Demographic work of this type has great potential for elucidating the dynamics of plant communities. Future papers will deal with fecundity and the seed bank. Agronomic results of this study are reported in Mohler (1991).

[‡] Present address: Department of Plant and Soil Science, Kentucky State University, Frankfort, Kentucky 40601, U.S.A.

* Plant nomenclature follows Gleason 1952.

A change in the abundance and composition of weeds commonly occurs following a switch from primary tillage to no-tillage farming practices (Froud-Williams, Chancellor & Drennan 1981; Koskinen & McWhorter 1986). These changes can be attributed to differences in both tillage and herbicide use. Some controlled experiments comparing different tillage regimes have found more annual weeds in no-till (Jones 1966; Moss 1979; Wilson *et al.* 1986) whereas others have found less (Gallaher 1978; Robinson, Langdale & Stuedmann 1984). Several studies have shown greater numbers of grass weeds in no-till, with either equal or greater numbers of broadleaved weeds in till (Triplett & Little 1972; Cussans 1976; Pollard & Cussans 1976; Wilson *et al.* 1986). Usually, the higher density of grasses in no-till has been attributed to ineffective herbicides.

Much work has been carried out to determine the effect of cultivation on the weed seed bank and subsequent effects on weed populations and the composition of weed communities (Brenchley & Warrington 1933; Wilson, Kerr & Nelson 1985; Van Esso, Ghersa & Soriano 1986; see also references in Roberts 1981). By scarifying seeds and carrying buried seeds up to the surface where they are exposed to light and air, tillage can stimulate germination of weed seeds (Wesson & Wareing 1969; Froud-Williams, Chancellor & Drennan 1984). On the other hand, emergence of most weed species is greatly reduced when the seeds are buried more than a few cm (Chancellor 1964; Peters & Dunn 1971; Froud-Williams, Chancellor & Drennan 1984) and since tillage buries seeds (Moss 1979; Pareja, Staniforth & Pareja 1985; Cousens & Moss 1990), the density of weeds may be lower with tillage. The response of weed seedling density to tillage is thus a product of the interaction among tillage-related germination cues, seed position in the soil and herbicides.

Less effort has been devoted to the effects of cropping systems on the survival of weeds once they emerge (Sagar & Mortimer 1976; Mortimer 1983). In particular, the effect of tillage on the survival of weed seedlings which emerge later is virtually unexplored. Similarly, although several studies have shown that mulches of small grain residues reduce weed emergence and biomass (Barnes & Putnam 1983; Putnam & DeFrank 1983; Putnam, DeFrank & Barnes 1983; Liebl & Worsham 1983), few investigations have examined the effect of mulches on weed survival.

Demographic studies have been useful in explaining the composition of vegetation found in natural and semi-natural ecosystems (Harper 1977). They may also prove useful in developing models for predicting the weed floras of agricultural ecosystems (Mortimer & Firbank 1983; Cousens *et al.* 1987; Fernandez-Quintanilla 1988).

Methods

The experimental design was a randomized complete block with eight replications. Treatments are summarized in Table 1. Weed seedling emergence and survival were only followed in treatments 1, 2, 6–10 and 12. Accordingly, the other treatments will not be discussed in this paper. 'Jubilee' sweet corn was used in all years.

ESTABLISHMENT OF THE EXPERIMENT

The entire field was ploughed and disced, and on 17 July 1985, planted with corn to establish stubble for the following year. To keep the no-till treatments weed free, atrazine, paraquat and fluazifop-butyl (herbicide names follow Weed Science Society of America 1989) were applied on 30 July, 22 August and 26 August, respectively. Fluazifop-butyl and paraquat were applied as a directed spray between corn rows. Rates of atrazine and fluazifop-butyl (both 0·42 kg ha^{-1}) were sufficiently low to not have affected weed emergence in 1986, and paraquat has no residual activity. Till treatments 2, 7 and 9 were rototilled between rows and hoed. In addition, a string trimmer and glyphosate applied with a wiper were used to keep both till and no-till treatments weed free and insure that input of new weed seeds in 1985 was negligible. No weed control was used in

Table 1. Summary of treatments (treatments 3, 4, 5 and 11 are not discussed in this paper)

Treatment	Tillage	Herbicides	Comments
1. Corn alone	No	G, A, M	
2. Corn alone	Yes	G, A, M	
6. Corn + rye	No	G, A, M	
7. Corn + rye	Yes	G, A, M	
8. No crop	No	G, A, M	Control for treatments 1 & 6
9. No crop	Yes	G, A, M	Control for treatments 2 & 7
10. No crop	Yes	No herbicides	General control
12. Rye alone	No	G, A, M	Control for treatment 7

Herbicide codes: G, glyphosate applied 2–8 days before planting; A, atrazine applied just after corn emergence; M, metolachlor applied just after corn emergence. See text for application rates.

treatment 10. By these means, plots simulating till, no-till and no management fields were established.

PLANTING AND MAINTENANCE

The presence of permanent demography quadrats prevented the use of tractor-powered machinery in the experiment. A rear tine rototiller was used to prepare a seedbed 10–15 cm deep in the tilled treatments, care being taken to keep the demography quadrats in the same position. Corn was hand-planted on 30 May–4 June 1986 and 9–16 June 1987. Five rows 76 cm apart were planted per plot. Kernels were placed in pairs 3·5 cm deep at 20-cm intervals. At the four-leaf stage corn was thinned to a density of 4·9 plants m^{-1} of row (64 300 plants ha^{-1}).

Ammonium nitrate was side-dressed at a rate of 135 kg ha^{-1}, with half applied shortly after crop emergence and the other half applied mid-season. Soil tests showed applications of phosphorus and potassium were unnecessary.

To control perennial weeds and kill the rye, glyphosate with X-77 surfactant was applied 2–8 days before planting at the rate of 1·68 kg active ingredient (a.i.) ha^{-1} to all treatments except treatment 10. One to 5 days following corn emergence, all treatments except treatment 10 were sprayed with a mixture of 0·56 kg a.i. ha^{-1} of atrazine for control of broadleaved weeds and 2·24 kg a.i. ha^{-1} of metolachlor for control of grasses. Atrazine and metolachlor act to prevent seedling emergence and have little effect on growth and survival of plants which manage to emerge after application. All herbicides were applied with a hand-held, constant-pressure boom sprayer.

Rye was broadcast into the mulch treatments on 10 September 1985 at the rate of 63 kg ha^{-1}. Because of low germination, plots were resown with an additional 60 kg ha^{-1} on 6 October. In 1986, rye was sown on 17 September at the rate of 188 kg ha^{-1}. Rye treatments were mowed with a string trimmer 2–8 days prior to corn planting. Clipping height was approximately 30 cm in 1986. Because working in tall stubble proved difficult, clipping height was reduced to about 6 cm in 1987.

DEMOGRAPHY

In May 1986, four 1 m × 0·5 m demography quadrats were randomly located between rows in each plot and marked with bamboo stakes. Quadrats were censused six times during the growing season. Treatment 10 was censused more frequently in 1986. Censusing began in late May prior to application of glyphosate. The second census occurred between application of glyphosate and tillage, and the third census after tillage and immediately prior to application of atrazine and metolachlor. In 1986, the second census was skipped in the no-till treatments because the third census was only about 1 week later and newly emerging seedlings in these treatments would not be killed by tillage. For simplicity, these first three censuses will be referred to as the pre-disturbance censuses. Because the number of seedlings per quadrat was very large in the pre-disturbance censuses, only two of the four demography quadrats were sampled in each plot. It seemed likely that herbicides and tillage would kill all spring-emerging seedlings. Rather than attempt to mark and follow thousands of seedlings as they died from tillage and herbicide, seedlings emerging in the pre-disturbance censuses were removed during counting. Careful observations at the first post-disturbance census in the two quadrats in each plot from which no seedlings were removed confirmed that no spring-germinating plants survived in any treatment.

Perennials and winter annuals (chiefly *Conyza canadensis*, *Erigeron* spp., *Stellaria media*, *Poa annua* and *Veronica* spp.) which appeared to have emerged the previous autumn were robust enough to survive the disturbances, and so were counted and left in the quadrats. A few of these individuals survived tillage and herbicide but their numbers were so few that analysis of the data was pointless. Some individuals of these species emerging in early spring probably died before the first census, so counts are approximate and will not be discussed in detail. These species are, however, included in the values for total emergence presented below. As cool season germinating species represent less than 20% of the individuals in first census counts for most treatments, the total emergence figures are reasonably accurate.

Atrazine and metolachlor were so effective that additional seedlings did not appear until late July in 1986 and early August in 1987. In both years, the first post-disturbance census (Post 1) was taken shortly after this first flush of seedlings. At this census a coloured toothpick was inserted into the soil on the north side of each seedling and the number of seedlings of each species was recorded. A second post-disturbance census (Post 2) occurred in late August. At this time (i) marked plants which were still alive were counted, (ii) toothpicks corresponding to dead plants were removed, and (iii) all seedlings which had emerged since the previous census were counted and marked with a new colour. Due to a labour shortage, at the late August census in 1987 only the most abundant weed species were marked and counted, namely *Amaranthus retroflexus*, *Chenopodium album*, *Digitaria sanguinalis* and *Portulaca oleracea*. A final census (Post 3) was taken in mid-October 1986 and mid-September 1987 in which dimensions of reproductive individuals were recorded. Data on plant size and seed production will be presented in another paper. Final census data were used to determine the proportion of plants surviving to maturity.

Due to the absence of herbicides in treatment 10, more seedlings emerged, and they emerged earlier. To avoid counting an unnecessarily large number of seedlings in this treatment, only two quadrats were censused per plot. In addition, quadrats were gridded into twenty-five 10 × 20 cm subquadrats, of which five were randomly selected for censusing. Plants were marked during the third census rather than pulled because there was no disturbance after tillage. To record the on-going seedling emergence, two censuses were added to the regular schedule in 1986: one in late June and another in early July. The frequent censusing in 1986 trampled weeds adjacent to the quadrats, and repeated handling caused the dominant species, *Amaranthus* and *Chenopodium*, to grow bent and twisted. To minimize disturbance, censusing frequency was reduced in 1987 and no attempt was made to closely align post-tillage censuses in treatment 10 with those in the other treatments. In 1987, censuses with toothpicks occurred in late June, mid-July and mid-August.

Altogether, nearly 60 000 seedlings were censused before disturbance and over 10 000 seedlings after disturbance.

ENVIRONMENTAL MEASUREMENTS

Incident sunlight was measured with a Li-Cor Quantum/Radiometer/Photometer® in late June and late July of 1986 and in late July 1987. In 1986, two to eight measurements were made 5 cm above ground level in each demography quadrat, with more measurements in plots which showed greater variability in light level. Above-canopy light level was recorded every few minutes so that the measurements could be converted to per cent of ambient. Measurements were not taken in unshaded quadrats because they received 100% of ambient sunlight by definition. Procedures were similar for the other two recording periods. Measurements were taken only in the first four blocks in July 1986.

Mid-afternoon soil temperature was measured at 2 cm depth during July 1986 using Reotemp® soil thermometers. These measurements approximate maximum soil temperatures during 1986. Two measurements were taken in each of two quadrats. Due to an oversight, block 4 was not sampled.

DATA ANALYSIS

Emergence counts for the pre-disturbance censuses were combined. Differences among treatments were tested using analysis of variance (ANOVA). Treatment 10 was omitted from the analyses because census dates did not correspond to those for the other treatments and emergence rates were obviously higher. Instead, emergence of weed species in treatment 10 was compared to emergence in treatment 9 (tilled control with herbicides).

Survival was determined from post-disturbance census data. Only four species, *Amaranthus retroflexus*, *Chenopodium album*, *Digitaria sanguinalis*, and *Portulaca oleracea*, were sufficiently abundant for analyses. Chi-square tests were used to determine treatment differences among the proportions of seedlings surviving a given interval. For the Post 1 cohort these intervals included: (a) emergence to the Post 2 census; (b) the Post 2 to the Post 3 census; and (c) emergence to the Post 3 census. Note that the proportion surviving over interval (c) is the product of the proportions surviving over intervals (a) and (b). For the Post 2 cohort, the only interval observed was from emergence to the Post 3 census. Data were combined over replications for each treatment to ensure minimum sample size for all cells of contingency tables (Snedecor & Cochran 1967). For the same reason Post 1 and Post 2 cohorts of *Chenopodium* (1987) and *Digitaria* (1986 and 1987) were combined.

Four single degree of freedom orthogonal contrasts were used on the emergence and survivorship data: tillage vs. no-tillage within the corn treatments, rye mulch vs. no rye mulch within the corn treatments, interaction of tillage and mulch within corn treatments, and all corn treatments vs. till and no-till control treatments. Contrasts for survivorship were computed by combining cells of the contingency tables. Duncan's Multiple Range statistics for pairwise comparisons of treatments were computed for the emergence data. When pairwise comparisons are discussed in the text they refer to the Duncan's test.

The larger number of post-disturbance censuses in treatment 10 allowed additional survivorship analyses in that treatment. Departure of treatment 10 survivorship curves from a truncated negative exponential form was tested to determine whether the probability of survival changed as plants matured. The survival of monocarpic plants like the annual species investigated here should be considered truncated by successful reproduction. Senescence following reproduction is fundamentally different from pre-reproduction mortality.

The procedure used a chi-square goodness-of-fit test. E_j, the expected number of deaths in interval j, was computed as

$$E_j = \begin{array}{ll} n\,(1-\mathrm{e}^{-\lambda\, t_j})/(1-\mathrm{e}^{-\lambda T}) & \text{for } j=1 \\ n\,(\mathrm{e}^{-\lambda t_{j-1}}-\mathrm{e}^{-\lambda t_j})/(1-\mathrm{e}^{-\lambda T}) & \text{for } j=2,3,\ \ldots,\ m-1 \\ n\,(\mathrm{e}^{-\lambda t_{m-1}}-\mathrm{e}^{-\lambda T})/(1-\mathrm{e}^{-\lambda T}) & \text{for } j=m, \end{array}$$

where n was the total number of plants dying in all intervals, λ was the decay coefficient of the truncated negative exponential, t_j was the number of days to the end of the jth interval of observation, m was the number of intervals, and T was the number of days until seed set. T was estimated as the time from the first post-disturbance census to the final census, and λ as

$$\lambda = \frac{n}{\sum_{j}^{m} n_j (t_{j-1} - t_j)/2}$$

where n_j was the observed number of deaths in interval j. The test has $m-3$ degrees of freedom, which limits its application to cohorts with at least four intervals of observation.

Light readings were converted to percentage of ambient and averaged within a quadrat. Quadrat means were then averaged for each plot and subjected to ANOVA. Similarly, soil temperatures for each quadrat were averaged and the mean temperature for each plot computed from quadrat means. Plot means were then subjected to ANOVA.

Results

SEEDLING EMERGENCE

Six species had sufficient emergence to warrant statistical analysis: *Amaranthus retroflexus*, *Chenopodium album*, *Portulaca oleracea*, *Digitaria sanguinalis*, *Galinsoga ciliata* and *Taraxacum officinale*. The only significant difference among treatments for *Galinsoga* was a higher emergence in uncropped controls at one census (1986 Post 2), so it is not discussed further.

Effects of tillage

The most striking result of this study was the substantial difference in seedling emergence between till and no-till treatments in the presence of a corn crop. *Amaranthus*, *Chenopodium*, *Portulaca* and *Digitaria* all showed significantly lower emergence in till treatments than in no-till treatments at one or more census times (Table 2). Where differences were not statistically significant, the tendency for tilled treatments to have less seedling emergence was consistent across census dates and species. Emergence combined over all species showed the same pattern for most census dates, due to the large contribution of the four species just mentioned (Table 2). However, at the Post 2 census in 1986, autumn-germinating species contributed to a non-significant trend toward greater total emergence in the tilled treatments.

Comparison of the till and no-till controls (treatments 9 and 8, respectively) showed inconsistencies between species (Table 2). *Digitaria* tended to have greater emergence in the no-till control, but due to high variability among plots the difference was only significant at the 1987 Post 1 census. In contrast, *Amaranthus* and total seedlings had consistently greater emergence in the tilled control. The differences were significant for the 1986 pre-disturbance census and Post 2 censuses in both years. The other species also tended to have greater emergence in the tilled control, but none of the comparisons were statistically significant.

Emergence of *Taraxacum* was unaffected by tillage.

Effects of rye mulch

In treatments with corn, emergence was generally either unaffected or lowered by the presence of a rye mulch (Table 2). This difference was particularly great at the pre-disturbance censuses (Table 2). A significant interaction between mulch and tillage existed only for *Taraxacum* at the Post 1 census of 1986. This was a sparse data set, and the apparent interaction was probably not biologically meaningful.

Comparison of emergence in treatment 8 (no-till control without rye) with treatment 12 (no-till control with rye) also showed that a rye mulch had an effect on the weeds (Table 2, particularly, *Chenopodium*, *Portulaca* and *Digitaria*). *Portulaca* seemed to be especially sensitive to rye mulch in these treatments. Only *Taraxacum* had statistically greater emergence in the control with rye.

Effects of the corn crop

In most cases, emergence was substantially greater in control treatments (treatments 8 & 9) than in corresponding treatments with corn or corn plus rye (Table 2). The principal exception to this trend was that in 1986 emergence in treatment 8 was less than in the corn treatments for some species. *Taraxacum* emergence again differed from other species, being lower in both of the unmulched controls than in the corn treatments at the pre-disturbance censuses in 1986.

Treatment 10

As expected, weed emergence was much greater in treatment 10 (tilled control without herbicides) than in treatment 9 (tilled control with herbicides) (Table 3). *Amaranthus* and *Chenopodium* were the only species which emerged in large numbers throughout the growing season in treatment 10. Both had consistently lower emergence at succeeding censuses following tillage (Figs 1 & 2).

SEEDLING SURVIVAL

Because emergence was generally low for most species after herbicides were applied, analysis of seedling survivorship was necessarily limited. Only *Amaranthus* had sufficient post-disturbance emergence to allow comparison of all treatments in both years.

Overall, a high percentage of *Amaranthus* emerging after disturbance survived to maturity. Survival of *Chenopodium* and *Portulaca* in the corn treatments was low in 1986 but was similar to *Amaranthus*

Table 2. Emergence of seedlings (number m^{-2}) summed for preplanting censuses (ΣPre), and at first and second post-disturbance censuses

		Corn crop				Control			Statistics			
Rye tillage treatment		NT 1	T 2	R NT 6	R T 7	NT 8	T 9	R NT 12	ANOVA	T vs. NT	R vs. NR	Corn vs. Cont.
Amaranthus retroflexus												
1986	ΣPre	43·3	36·6	40·0	29·1	9·3	68·1	4·2	***	NS	NS	NS
	Post 1	6·2	0·7	7·2	1·1	0·3	0·4	0·6	***	***	NS	***
	Post 2	3·9	0·7	1·5	0·4	1·1	3·7	1·0	***	***	*	+
1987	ΣPre	20·4	5·7	9·3	1·3	66·3	91·4	190·0	***	**	*	***
	Post 1	5·2	0·8	1·6	0·5	5·6	8·7	6·8	***	**	+	***
	Post 2	0·4	0·1	0·3	0·1	1·0	2·3	1·8	***	NS	NS	***
Chenopodium album												
1986	ΣPre	72·2	57·1	25·7	37·9	38·0	67·8	10·3	*	NS	+	NS
	Post 1	4·2	0·8	2·6	1·4	2·1	1·3	1·2	NS	**	NS	NS
	Post 2	0·8	0·1	0·5	0·4	1·9	2·1	2·3	**	NS	NS	***
1987	ΣPre	17·4	10·0	9·8	4·9	30·9	27·6	19·1	**	+	+	***
	Post 1	0·7	0·4	0·1	0·5	0·6	0·8	0·6	NS	NS	NS	NS
	Post 2	0·1	0·5	0·0	0·2	0·3	1·0	0·1	*	+	NS	*
Portulaca oleracea												
1986	ΣPre	29·2	11·8	17·7	7·1	29·7	46·1	3·2	***	*	NS	*
	Post 1	1·4	0·3	0·8	0·7	0·9	0·3	0·6	NS	NS	NS	NS
	Post 2	1·1	0·5	0·4	0·1	3·5	4·4	3·4	***	NS	NS	***
1987	ΣPre	4·1	0·8	0·4	0·1	201	211	1·6	***	NS	*	***
	Post 1	1·3	0·1	0·1	0·1	7·6	3·2	1·7	***	NS	NS	***
	Post 2	0·2	0·0	0·0	0·0	2·1	2·2	0·9	***	NS	NS	***
Digitaria sanguinalis												
1986	ΣPre	5·9	1·0	6·3	1·4	2·2	1·0	0·6	NS	*	NS	NS
	Post 1	0·6	0·0	1·1	0·1	0·1	0·1	0·0	***	***	NS	+
	Post 2	0·1	0·0	0·2	0·1	0·0	0·0	0·1	NS	*	NS	+
1987	ΣPre	22·8	2·5	15·4	4·2	30·8	6·5	6·4	*	**	NS	NS
	Post 1	1·3	0·0	0·8	0·0	1·3	0·0	0·3	**	***	NS	NS
	Post 2	0·2	0·0	0·1	0·0	0·1	0·1	0·2	NS	+	NS	NS
Taraxacum officinale												
1986	ΣPre	10·5	13·4	10·5	11·1	2·0	3·6	20·6	***	NS	NS	***
	Post 1	0·1	0·3	0·2	0·0	0·1	0·0	0·1	NS	NS	NS	NS
	Post 2	0·1	0·1	0·1	0·1	0·1	0·0	0·1	NS	NS	NS	NS
1987	ΣPre	142	98·5	70·0	56·2	28·6	49·8	116	+	NS	+	*
	Post 1	0·6	0·5	0·5	0·4	0·1	0·1	0·6	NS	NS	NS	**
Total seedlings												
1986	ΣPre	277	240	213	202	125	349	99·7	**	NS	NS	NS
	Post 1	18·1	8·2	16·4	12·0	3·3	4·8	3·6	***	+	NS	***
	Post 2	15·5	16·7	6·3	12·8	6·6	27·5	11·5	NS	NS	NS	NS
1987	ΣPre	425	251	206	185	796	1112	572	***	NS	+	***
	Post 1	25·8	9·1	19·1	7·9	17·3	19·7	19·4	NS	+	NS	NS

Numbers are the geometric means of eight replications. Significance levels are shown for the ANOVA on log-transformed values and for three predefined orthogonal contrasts: T against (vs.) NT, till vs. no-till within corn treatments; R vs. NR, rye vs. no-rye within corn treatments; Corn vs. Cont., all four corn treatments vs. treatments 8 and 9. A fourth orthogonal contrast of mulch by tillage interaction within corn treatments was significant only for *Taraxacum* at the first post-disturbance census in 1986. Significance levels: NS, not significant; + $P < 0{\cdot}1$; * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$. Total seedlings includes species additional to the five listed in the table.

in 1987. Overall survival of *Digitaria* was high in all treatments, with no significant differences in survival among treatments (Table 4).

In general, plants in the Post 2 cohort survived better than those in the Post 1 cohort (Table 4). The trend was statistically significant for *Chenopodium* in most treatments in 1986 and for *Amaranthus* in several treatments in 1987.

Effects of tillage

Amaranthus survival was significantly greater in no-till. The tillage effect on Post 1 cohort survival developed late in the growing season, after the Post 2 census (Table 4). Differences in *Chenopodium* survival among treatments were mostly non-existent or uninterpretable, except that the Post 2 cohort in

Table 3. Emergence of seedlings (number m^{-2}) for the most abundant species in treatment 10, the tilled control without herbicide

	No herbicide 10	Herbicide 9
Amaranthus retroflexus		
1986 ΣPre	1916	68·1
1st Post	251	0·4
1987 ΣPre	788	91·4
1st Post	296	8·7
Chenopodium album		
1986 ΣPre	3704	67·8
1st Post	645	1·3
1987 ΣPre	546	27·6
1st Post	157	0·8
Portulaca oleracea		
1986 ΣPre	20·3	46·1
1st Post	9·9	0·3
1987 ΣPre*	(>1·9)	211·0
1st Post*	(>8·7)	3·2
Digitaria sanguinalis		
1986 ΣPre	26·3	1·0
1st Post	1·4	0·1
1987 ΣPre	55·0	6·5
1st Post	1·8	0·0

ΣPre is the sum of the first three (i.e. pre-disturbance) censuses for treatment 9, and is the sum of first two censuses for treatment 10. 1st Post is the first post-tillage census for both treatments. For treatment 9 it occurred in late July in 1986 and early August in 1987. For treatment 10 it occurred in late June in 1986 and early July in 1987. Numbers are geometric means of eight replications.

* Due to recording errors the exact number of *Portulaca* emerging in treatment 10 in 1987 was not determined.

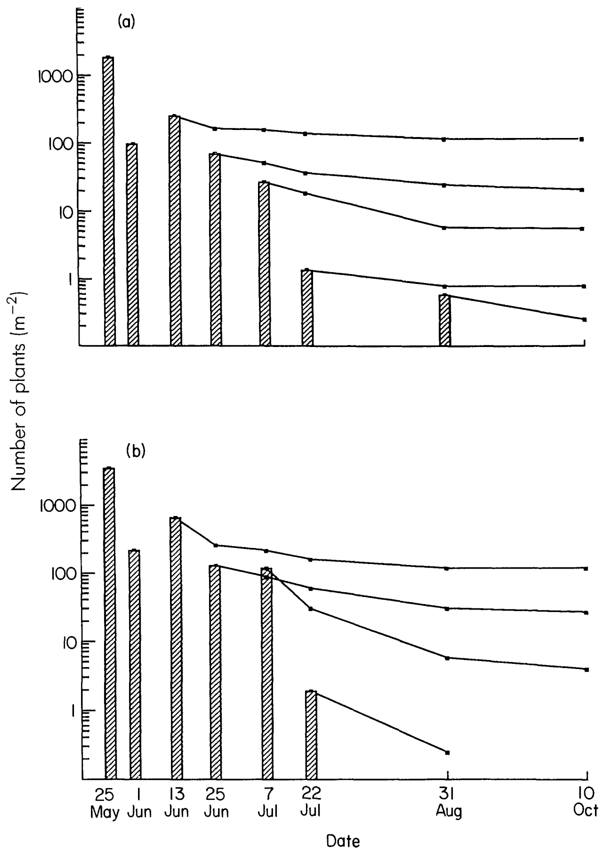

Fig. 1. Emergence and survival of (a) *Amaranthus retroflexus* and (b) *Chenopodium album* in the tilled control without herbicides (treatments 10) in 1986 (number m^{-2}). Bars show emergence of cohorts. Lines show subsequent survival of cohorts. Most censuses took several days; the dates shown were the midpoints of the census intervals.

1986 survived significantly better in no-till than in till. The 1987 Post 1 *Portulaca* cohort survived better in the tilled control than in the no-till control.

Effects of rye mulch

In general, rye had little effect on survival. The presence of rye did seem to improve *Portulaca* survival in open conditions: survival was significantly higher in treatment 12 than in 8 for the Post 1 cohort's second interval in 1986 and for both intervals in 1987.

Effects of the corn crop

Reduced light levels in corn treatments caused *Amaranthus* to become etiolated, fall over, and grow prostrate on the ground. Nevertheless, *Amaranthus* emerging under corn had an overall probability of 0·43 of reaching maturity, and the presence of corn had an inconsistent, and generally minor effect on *Amaranthus* survival (Table 4).

Portulaca survived much better in the open control plots in 1986 (Table 4). Comparison of *Portulaca* survival in corn and controls in 1987 was hindered by extremely low emergence in three of the four corn treatments. However, the contrast of no-till corn (treatment 1) with the no-till control (treatment 8) in 1987 indicated that open conditions did not favour *Portulaca* survival in that year.

Treatment 10

All cohorts of both *Amaranthus* and *Chenopodium* in treatment 10 showed Deevey's type III survivorship curves (Figs 1 & 2; Deevey 1947). The first and second *Amaranthus* and *Chenopodium* cohorts in 1986 were censused a sufficient number of times to test for departure from a truncated negative exponential survivorship function. Of these, all but the second cohort of *Amaranthus* showed significant departure at the $P < 0·05$ level. Thus, mortality was higher early in life and declined as the plants matured. In contrast to the other treatments, early emerging cohorts generally had higher survival to seed set than later cohorts (Table 5), the only exception being the second cohort of *Chenopodium* in 1986.

Table 4. Proportion of seedlings surviving between censuses

		Corn crop				Controls			Statistics				
	Rye tillage treatment	NT 1	T 2	R NT 6	R T 7	NT 8	T 9	R NT 12	Treatment effects	T vs. NT	R vs. NR	Corn vs. Cont.	Notes
Amaranthus retroflexus													
1986	P1: P1 to P2	0·56	0·53	0·57	0·46	0·50	0·71	0·45	NS	NS	NS	NS	
	P1: P2 to P3	0·78	0·50	0·81	0·55	1·00	0·60	1·00	+	**	NS	NS	
	P1: P1 to P3	0·44	0·27	0·46	0·25	0·50	0·43	0·45	NS	*	NS	NS	
	P2: P2 to P3	0·35$^{\mathrm{NS}}$	0·08$^{\mathrm{NS}}$	0·54$^{\mathrm{NS}}$	0·22$^{\mathrm{NS}}$	0·59$^{\mathrm{NS}}$	0·31$^{\mathrm{NS}}$	0·55$^{\mathrm{NS}}$	**	*	NS	NS	
1987	P1: P1 to P2	0·77	0·67	0·82	0·70	0·55	0·64	0·85	***	NS	NS	***	
	P1: P2 to P3	0·71	0·50	0·68	0·29	0·77	0·72	0·65	*	*	NS	+	
	P1: P1 to P3	0·55	0·33	0·55	0·20	0·43	0·46	0·56	*	*	NS	NS	
	P2: P2 to P3	0·71$^{\mathrm{NS}}$	0·33$^{\mathrm{NS}}$	0·83$^{\mathrm{NS}}$	1·00*	0·62*	0·57$^{\mathrm{NS}}$	0·94***	**	NS	NS	NS	(1)
Chenopodium album													
1986	P1: P1 to P2	0·07	0·00	0·01	0·30	0·03	0·11	0·07	***	**	NS	NS	(3)
	P1: P2 to P3	0·00	----	0·00	0·50	1·00	1·00	1·00					(4, 5)
	P1: P1 to P3	0·00	0·00	0·00	0·15	0·03	0·11	0·07	+	--	*	NS	(2)
	P2: P2 to P3	0·53***	0·00^{--}	0·23***	0·00$^{\mathrm{NS}}$	0·36***	0·44**	0·31**	+	*	*	NS	(2)
1987	P1 + P2 to P3	0·41	0·61	0·33	0·43	0·52	0·36	0·32	NS	NS	NS	NS	(9)
Portulaca oleracea													
1986	P1: P1 to P2	0·20	0·67	0·46	0·35	0·55	0·20	0·56	*	NS	NS	+	(3)
	P1: P2 to P3	0·20	0·00	0·00	0·00	0·47	1·00	0·89	***	--	--	***	(2, 6)
	P1: P1 to P3	0·04	0·00	0·00	0·00	0·26	0·20	0·50	***	--	--	***	(2, 6)
	P2: P2 to P3	0·14$^{\mathrm{NS}}$	0·09$^{\mathrm{NS}}$	0·11^{+}	0·00^{--}	0·37$^{\mathrm{NS}}$	0·33$^{\mathrm{NS}}$	0·41$^{\mathrm{NS}}$	*	NS	NS	**	(2)
1987	P1: P1 to P2	0·50	----	----	----	0·49	0·67	0·84	***	--	--	--	(2, 5, 7, 8)
	P1: P2 to P3	0·62	----	----	----	0·41	0·81	0·87	***	--	--	--	(2, 5, 7, 8)
	P1: P1 to P3	0·31	----	----	----	0·20	0·54	0·73	***	--	--	--	(2, 5, 7, 8)
	P2: P2 to P3	0·50$^{\mathrm{NS}}$	----	----	----	0·71***	0·62$^{\mathrm{NS}}$	0·67$^{\mathrm{NS}}$	NS	--	--	--	(2, 5, 8)
Digitaria sanguinalis													
1986	P1 + P2 to P3	0·81	----	0·58	----	0·50	----	----	NS	--	--	--	(2, 5, 9)
1987	P1 + P2 to P3	0·84	----	0·79	----	0·79	----	----	NS	--	--	--	(2, 5, 9)

P1, P2 and P3 refer to the first post-disturbance, second post-disturbance and final censuses, respectively. P1 or P2 before the colon refers to the cohort; the interval after the colon refers to the period over which survival was observed. In addition to the test for overall differences among treatments shown in the column headed Treatment effects, three orthogonal contrasts are shown: T against (vs) NT, till vs. no-till within corn treatments; R vs. NR, rye mulch vs. no rye within corn treatments; Corn vs. Cont., all corn treatments vs. the unmulched controls. A fourth orthogonal contrast of tillage by mulch interaction within corn treatments was significant for the two cases indicated by note (3). Significance of comparisons of survival of the Post 1 and Post 2 cohorts is shown as a superscript to the Post 2 survival data. Statistics: NS not significant; + significant at $P<0{\cdot}10$ level; * significant at $P<0{\cdot}05$ level; ** significant at $P<0{\cdot}01$ level; *** significant at $P<0{\cdot}001$ level.

(1) Due to small expected values, treatments 1 and 2, and treatments 6 and 7 were combined when computing chi-square for the overall treatment effect.

(2) -- indicates that expected values for one or more cells of the contingency table were too low for a valid chi-square test of the contrast.

(3) Interaction of tillage by mulch within corn treatments was significant at $P<0{\cdot}01$.

(4) Insufficient data for statistical comparison of treatments. These data are included solely to show the effect of late season mortality on survival from emergence to seed set.

(5) ---- indicates that the treatment had too few seedlings to provide a basis for computing survival.

(6) Due to small expected values, treatments 8 and 9 were combined when computing chi-square for overall treatment effects.

(7) The predefined contrast between treatments 8 and 9 was significant at the $P<0{\cdot}01$ level.

(8) This ANOVA included a predefined contrast between treatments 1 and 8. The contrast was not significant.

(9) Survival of Post 1 and Post 2 cohorts were not obviously different and were combined to provide sufficient sample size for statistical analysis.

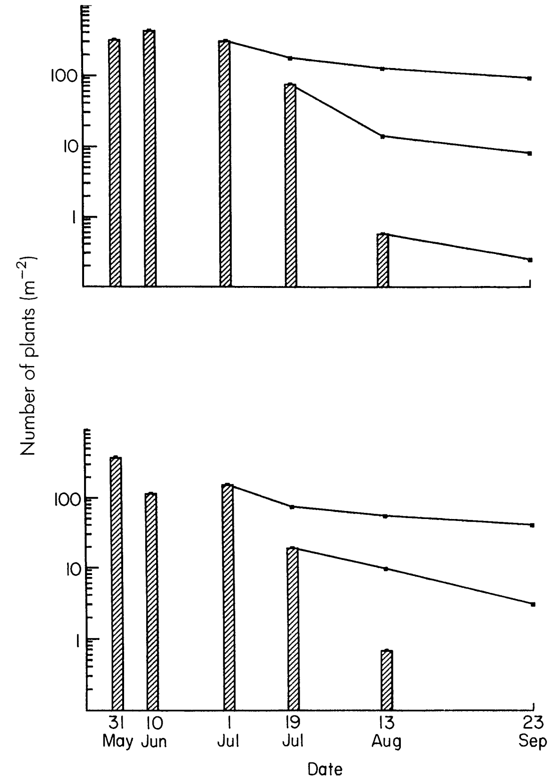

Fig. 2. Emergence and survival of (a) *Amaranthus retroflexus* and (b) *Chenopodium album* in the tilled control without herbicides (treatment 10) in 1987 (number m^{-2}). Bars show emergence of cohorts. Lines show subsequent survival of cohorts. Most censuses took several days; the dates shown were the midpoints of the census intervals.

ENVIRONMENTAL MEASUREMENTS

Three and a half weeks after corn planting in 1986, only treatments 6, 10 and 12 (see Table 1) had light levels less than 100% (Table 6). By July, the light level had increased slightly in treatment 12 due to settling of the dead rye, decreased to 35–40% of ambient in the corn treatments, and declined to 2% of ambient in treatment 10. In 1987 the corn was planted later, and thus light levels in the corn treatments were still 50–70% of ambient in mid-July.

Maximum soil temperatures were much lower in treatment 10 than in other treatments (Table 6). Soil in corn treatments was cooler than soil in unmulched controls.

Discussion

SEEDLING EMERGENCE

Effects of tillage

The difference in emergence of annuals between till and no-till treatments prior to disturbance in 1986 (Table 2) could have resulted from (i) more favourable seedbed conditions in the no-till treatments or (ii) more seeds near the soil surface in the no-till treatments. As weeds were not allowed to set seed in 1985, the second explanation requires that more seeds were killed by the cultivation in till treatments in 1985 than were killed by herbicides in no-till treatments. Weed germination may have been stimulated by cultivation, and the emerging weeds subsequently killed by hoeing. This argument is supported by germination tests run on soil cores collected in autumn 1985 which showed that seeds of most species were more abundant in no-till treatments than in till treatments (C.L. Mohler & M.B. Callaway, unpublished). *Taraxacum* is wind-dispersed and does not persist in the soil seed bank, thus explaining the lack of a difference in emergence between till and no-till for this species (Table 2).

After disturbance, the difference in emergence between till and no-till increased, particularly for *Amaranthus* and *Chenopodium*. Tillage probably stimulated germination, thereby increasing the effectiveness of herbicides in the till treatments.

The contrast between till and no-till in the pre-disturbance censuses in 1987 can be attributed to (i) differences in seed pools created by the seed mortality factors discussed above, and (ii) the larger number of seed-bearing plants in the 1986 no-till treatments (C.L. Mohler & M.B. Callaway, unpublished). After disturbance, these factors continued to operate and, in addition, some seeds in the till plots were probably buried too deeply for successful emergence.

The difference in emergence between till and no-till was less consistent in the control treatments than

Table 5. Proportion of *Amaranthus retroflexus* and *Chenopodium album* seedlings surviving from emergence to seed set in the tilled control without herbicide (treatment 10)

Species	Year	1st Cohort	2nd Cohort	3rd Cohort	Sig.
Amaranthus retroflexus	1986	0·46	0·30	0·19	***
	1987	0·29	0·17		**
Chenopodium album	1986	0·18	0·24	0·05	***
	1987	0·32	0·17		*

Statistical significance is shown for chi-square tests comparing survival of different cohorts in the same year. Tests have 2 degrees of freedom in 1986 and 1 degree of freedom in 1987. * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

in the corn treatments. In 1986 the no-till control (treatment 8) developed a hard crust on the soil surface, which probably contributed to the lower emergence observed for several species (Table 2). This soil crust did not form in the no-till treatments which had corn stalks on the ground from the previous year (treatments 1 & 6). Lower emergence in the no-till control resulted in lower seed production. As a result, the difference in emergence persisted into 1987 when the crust was less pronounced.

Effects of rye mulch

Several studies have shown that rye mulch inhibits emergence and growth of weeds (Barnes & Putnam 1983; Putnam, DeFrank & Barnes 1983; Liebl & Worsham 1983; Bellinder & Warholic 1988).

In this study, rye significantly reduced emergence at one or more censuses for most species (Table 2). Weed emergence was most frequently reduced by rye at pre-disturbance censuses, when the rye was still standing. Before the rye was cut, light levels in the rye plots were somewhat reduced but not sufficiently low to inhibit germination of weed seeds. However, the partial shade cast early in the growing season may have prevented seeds from warming to temperatures suitable for germination. The rye may also have had an allelopathic effect (Barnes & Putnam 1983, 1986; Shilling, Liebl & Worsham 1985).

Two of the four post-disturbance censuses showed significantly less emergence in rye for *Amaranthus*, and similar non-significant trends existed for *Portulaca* and *Chenopodium* (Table 2). Failure of the rye to strongly inhibit emergence later in the growing season may have been due to breakdown of allelopathic compounds, or better soil water retention in rye plots.

The lack of interaction between mulch and tillage was surprising. First, soil temperature would be expected to show less diurnal fluctuation under rye mulch than in unmulched treatments or tilled rye, and temperature fluctuations promote germination of annual weeds (Povilaitis 1956; Thompson, Grime & Mason 1977). Second, less allelopathy could be expected in tilled rye treatments since less rye remained on the soil surface. Third, rye mulch in the untilled treatment might have intercepted some of the herbicides (Banks & Robinson 1982; Ghadiri, Shea & Wicks 1984; Crutchfield, Wicks & Burnside 1985). Any of these factors acting alone would tend to result in an interaction of mulch and tillage. Soil temperature measurements, however, showed no significant differences among the corn treatments (Table 5), and the latter two effects tend to cancel each other. Thus, the lack of significant interaction terms in the ANOVAS may be due to rye replacing the toxic action of herbicides it intercepts.

Effects of the corn crop

In general, emergence was greater in treatments 8 and 9 than in corn treatments (Table 2). The Post 1 census in 1986 was an exception in showing reduced emergence of *Amaranthus* and *Digitaria* in the controls (Table 2). Most of this effect was attributable to the soil crust which formed in the no-till control in 1986. Greater emergence in 1987 control treatments can largely be attributed to greater seed production in 1986 (C.L. Mohler & M.B. Calloway

Table 6. Percentage of ambient light near ground level and peak soil temperatures (°C)

		Corn crop				Controls				Statistics						
Rye tillage treatment		NT 1	T 2	R NT 6	R T 7	NT 8	T 9	R NT 12	T 10	N[¶]	ANOVA	T vs. NT	R vs. NR	Till. × Mulch	Corn vs. Cont.	10 vs. Other
% Light	June 86[*]	100	100	93	100	100	100	81	89	8	***	NS	NS	NS	NS	+
	July 86[†]	36	36	39	36	100	100	89	2	4	***	NS	NS	NS	***	***
	July 87[‡]	59	68	63	54	99	100	92	32	8	***	NS	NS	*	***	***
Soil temperature	July 86[§]	32·6	33·7	33·2	33·9	35·0	34·5	34·2	28·6	7	NS	NS	NS	NS	**	***

[*] Measurements taken from 24 June to 1 July 1986.

[†] Measurements taken from 23 to 24 July 1986.

[‡] Measurements taken from 17 to 27 July 1987.

[§] Measurements taken for block 1 on 7 July 1986, block 3 on 23 July 1986, block 2 on 8 July 1986, blocks 5–8 on 25 July 1986.

[¶] Number of blocks of the experiment which were sampled. July 1986 light measurements were taken in blocks 1–4. Soil temperature measurements were taken in blocks 1–3 and 5–8 (see text).

Significance levels for the ANOVA and for five predefined orthogonal contrasts are shown: T vs. NT, till vs. no-till within corn treatments; R vs. NR, rye mulch vs. no rye within corn treatments; Till × Mulch, till by mulch interaction within corn treatments; Corn vs. Cont., all corn treatments vs. treatments 8 and 9; 10 vs. Other, treatment 10 vs. the other 7 treatments. Significance levels: NS, not significant; + $P < 0·10$; * $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

unpubl.). By July, light levels in the controls were much higher than in corn treatments, contributing to greater differences at the Post 2 census.

Contrary to results for most censuses of the annual weeds, *Taraxacum* emergence was consistently lower in the unmulched controls than in corn treatments (Table 2). Corn debris captured dispersing *Taraxacum* seeds by ensnaring the pappus, and its presence probably also improved moisture conditions at the soil surface. Similar effects were probably also responsible for the high emergence of *Taraxacum* in treatment 12.

Treatment 10

Because treatment 10 received no weed control, even in 1985, many weeds grew to large size and produced huge numbers of seeds. The substantially greater emergence of all species at the pre-disturbance censuses in this treatment relative to the tilled control receiving herbicide (treatment 9) (Table 3) can therefore be attributed to a much larger seed pool (C.L. Mohler & M.B. Callaway, unpubl.). Seedlings began to emerge just a few days after tillage in treatment 10, unlike other treatments, where seedling emergence was delayed for 5–6 weeks. *Amaranthus* and *Chenopodium* quickly established a closed canopy, substantially reducing light levels relative to other treatments (Table 6). Declining light levels under the weed canopy probably caused the substantial decline in seedling emergence at succeeding censuses (Figs 1 & 2).

Emergence after tillage was much lower in treatment 10 than before tillage (Table 3). This was probably due to burial of the previous year's seed crop, as well as the destruction during tillage of some seeds which were in the process of germination.

At the pre-disturbance censuses, only *Portulaca* had lower emergence in treatment 10 than in 9 (Table 3). Several authors have reported that *Portulaca* germinates best at relatively high temperatures (Povilaitis 1956; Hopen 1972; Vengris, Dunn & Stacewicz-Sapuncakis 1972). The low pre-disturbance emergence for this species may have been due to lower early season soil temperatures caused by a greater residue of dead weeds. In addition, the *Portulaca* seed pool in 1987 was lower in treatment 10 due to greater competition from other weed species the previous year (C.L. Mohler & M.B. Callaway, unpubl.).

SEEDLING SURVIVAL

Effects of tillage

At the outset of the experiment, weed seedlings were expected to survive better in the more friable seedbed of the tilled treatments. However, *Amaranthus* and the Post 2 *Chenopodium* cohort in 1986 had lower survival with tillage. The explanation is obscure. One hypothesis is that the looser soil in the tilled treatments may have dried more rapidly, causing the seedlings to desiccate. Probably corn stalks and other organic matter on the soil surface of no-till treatments maintained a more favourable soil moisture environment. The problem with differences in drought stress as an explanation for the lower survival in tilled treatments is that tiny, newly emerged seedlings should be most sensitive, yet significant differences in survival of the Post 1 cohort did not develop until the second sampling interval, when plants were larger and air temperatures lower.

Effects of the corn crop

It was not surprising that the presence of corn reduced survival in a few cases (Table 4). More remarkable was the finding that survival of *Amaranthus*, *Chenopodium* and *Digitaria* in the cropped treatments was frequently similar to that in the controls (Table 4). Apparently, these annual weeds are adapted to persist for long periods in the shade of the crop, even if growth is virtually halted by the low light levels. Any growth that the weed makes, even if it is barely more than conversion of seed reserves to roots and shoot, is conserved and converted back to seeds at the end of the season.

Selection obviously favours those individuals which reproduce prior to death, so one might expect weeds to flower in response to deepening shade. However, the photoperiod sensitivity of these weeds (Peters & Dunn 1971; Vengris, Dunn & Stacewicz-Sapuncakis 1972; Weaver & McWilliams 1980) seems to override any flowering response to shade. In most cropping systems the crop will die or be harvested before weeds are killed by frost. As crop harvest provides a second opportunity for growth, flowering in response to shade would often prove maladaptive.

In general, *Portulaca* showed lower survival in corn treatments than the other species (Table 4). This result superficially contradicts Vengris, Dunn & Stacewicz-Sapuncakis (1972) who found that *Portulaca* grew well in controlled conditions resembling the understorey of a corn crop in late summer. In their growth chamber study, seedlings were well established before being subjected to low levels of green light, whereas in this study, most of the mortality occurred when the seedlings were still in the cotyledon stage. In a field experiment by Vengris, Dunn & Stacewicz-Sapuncakis (1972), *Portulaca* plants emerging later than mid-July showed negligible growth when subjected to 76% shade. Conceivably, still deeper shade or similar shade in a less favourable growing season could lead to substantial mortality.

The better survival in the corn treatments of the Post 2 cohorts of several species (Table 4) was interesting given that these plants established in an environment with substantially higher interspecific competition. Possibly, some plants of the Post 1 cohort failed to adjust to changing conditions as the corn canopy developed above them. However, a simpler explanation is that because the Post 2 cohort flowered very early in life it was not exposed to mortality factors as long as the earlier emerging cohort.

In the absence of corn competition, survival from emergence to seed set was high for all four species. Only the Post 1 cohort of *Chenopodium* in 1986 suffered extreme mortality in the open treatments. This census was followed by a hot, dry period which probably accounted for the severe mortality. Since *Amaranthus*, *Portulaca* and *Digitaria* are C_4 plants (Pearcy, Tumosa & Williams 1981; Miyanishi & Cavers 1980; Hallberg & Larsson 1981) and *Portulaca* is succulent, it is not surprising that these species survived the drought period better than *Chenopodium*, a C_3 species (Chu *et al.* 1978).

The three broadleaved species are native to North America (Gleason 1952; Miyanishi & Cavers 1980; Weaver & McWilliams 1980) and are attacked by a variety of insects and diseases (Vengris, Dunn & Stacewicz-Sapuncakis 1972; Bassett & Crompton 1978; Miyanishi & Cavers 1980; Weaver & McWilliams 1980). However, the high survival in open conditions implies that natural enemies were ineffective once the plants had emerged from the soil. Other investigators have also observed high rates of survival for some annual weeds in agricultural systems (Sagar & Mortimer 1976; Mortimer 1983; Fernandez-Quintanilla *et al.* 1986), except where post-emergence control measures have been applied (e.g. Ballaré *et al.* 1987). Given the very high fecundity of these species (Peters & Dunn 1971; Vengris, Dunn & Stacewicz-Sapuncakis 1972; Bassett & Crompton 1978; Weaver & McWilliams 1980; C.L. Mohler, unpubl.), the relatively high survivorship implies that most mortality occurs in the soil prior to emergence. This hypothesis will be discussed further elsewhere.

Treatment 10

The declining mortality rates for *Amaranthus* and *Chenopodium* in treatment 10 (Figs 1 & 2) further supports the idea that once these species have established, resources are largely conserved until seed set. The first post-disturbance cohorts of both species experienced moderate mortality during the first census interval as tiny seedlings died of desiccation and other causes. Thereafter, these individuals grew very tall (1·5 m) and wand-like but suffered relatively lower mortality (Figs 1 & 2). Later cohorts emerged in the shade of earlier cohorts (Table 6) and may have suffered from below-ground competition as well. As a result, relatively high mortality rates were prolonged (Figs 1 & 2). Consequently, the survival of later cohorts from emergence to seed set was poorer (Table 5). Unlike the Post 2 cohort in other treatments, the second and third post-disturbance cohorts in treatment 10 emerged mid-season, thus having a substantial period of exposure to mortality factors.

Overall, this study demonstrated that tillage and the presence of a crop substantially affect the emergence and survival of weeds. The effects of tillage on emergence were remarkably consistent across weed species which maintain a soil seed bank. The absence of tillage frequently improved both emergence and survival. Under the conditions of this experiment, the existence of a mulch of dead rye had only a weak effect on emergence and no effect on survival.

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References

Ballaré, C.L., Scopel, A.L., Ghersa, C.M. & Sánchez, R.A. (1987) The demography of *Datura ferox* (L.) in soybean crops. *Weed Research*, **27**, 91–102.

Banks, P.A. & Robinson, E.L. (1982) The influence of straw mulch on the soil reception and persistence of metribuzin. *Weed Science*, **30**, 164–168.

Barnes, J.P. & Putnam, A.R. (1983) Rye residues contribute weed suppression in no-tillage cropping systems. *Journal of Chemical Ecology*, **9**, 1045–1057.

Barnes, J.P. & Putnam, A.R. (1986) Evidence for allelopathy by residues and aqueous extracts of rye (*Secale cereale*). *Weed Science*, **34**, 384–390.

Bassett, I.J. & Crompton, C.W. (1978) The biology of Canadian weeds. 32. *Chenopodium album* L. *Canadian Journal of Plant Science*, **58**, 1061–1072.

Bazzaz, F.A. (1983) Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. *Disturbance and Ecosystems* (eds H.A. Mooney & M. Godron), pp. 259–275. Springer-Verlag, New York.

Bellinder, R.R. & Warholic, D.T. (1988) Comparison of five herbicide programs for no-tillage sweet corn. *Proceedings of the Northeastern Weed Science Society*, **42**, 216–220.

Brenchley, W.E. & Warrington, K. (1933) The weed seed population of arable soil. II. Influence of crop, soil and methods of cultivation upon the relative abundance of viable seeds. *Journal of Ecology*, **21**, 103–127.

Chancellor, R.J. (1964) The depth of weed seed germination in the field. *Proceedings of the 7th British Weed Control Conference*, pp. 607–613.

Chu, C., Ludford, P.M., Ozbun, J.L. & Sweet, R.D. (1978) Effects of temperature and competition on the establishment and growth of redroot pigweed and common lamb's-quarters. *Crop Science*, **18**, 308–310.

Cousens, R., Moss, S.R., Cussans, G.W. & Wilson, B.J. (1987) Modeling weed populations in cereals. *Reviews in Weed Science*, **3**, 93–112.

Cousens, R. & Moss, S.R. (1990) A model of the effects of cultivation on the vertical distribution of weed seeds within the soil. *Weed Research*, **30**, 61–70.

Crutchfield, D.A., Wicks, G.A. & Burnside, O.C. (1985) Effect of winter wheat (*Triticum aestivum*) straw mulch level on weed control. *Weed Science*, **34**, 110–114.

Cussans, G.W. (1976) The influence of changing husbandry on weeds and weed control in arable crops. *Proceedings of the 1976 British Crop Protection Conference: Weeds*, pp. 1001–1008. British Crop Protection Council, Croydon.

Deevey, E.S. (1947) Life tables for natural populations of animals. *Quarterly Review of Biology*, **22**, 283–314.

Fernandez-Quintanilla, C. (1988) Studying the population dynamics of weeds. *Weed Research*, **28**, 443–447.

Fernandez-Quintanilla, C., Navarrete, L., Andujar, J.L.G., Fernandez, A. & Sanchez, M.J. (1986) Seedling recruitment and age-specific survivorship and reproduction in populations of *Avena sterilis* L. ssp. *ludoviciana* (Durieu) Nyman. *Journal of Applied Ecology*, **23**, 945–955.

Froud-Williams, R.J., Chancellor, R.J. & Drennan, D.S.H. (1981) Potential changes in weed floras associated with reduced cultivation systems for cereal production in temperate regions. *Weed Research*, **21**, 99–109.

Froud-Williams, R.J., Chancellor, R.J. & Drennan, D.S.H. (1984) The effects of seed burial and soil disturbance on emergence and survival of arable weeds in relation to minimal cultivation. *Journal of Applied Ecology*, **21**, 629–641.

Gallaher, R.N. (1978) Benefits of killed rye for a mulch in no-tillage cropping systems. *Proceedings, Southern Weed Science Society*, **31**, 127–133.

Ghadiri, H., Shea, P.J. & Wicks, G.A. (1984) Interception and retention of atrazine by wheat (*Triticum aestivum* L.) stubble. *Weed Science*, **32**, 24–27.

Gleason, H.A. (1952) *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*. Hafner, New York.

Hallberg, M. & Larsson, C. (1981) Compartmentation and export of $^{14}\mathrm{CO}_2$ fixation products in mesophyll chloroplasts from the C_4 plant *Digitaria sanguinalis*. *Archives of Biochemistry and Biophysics*, **208**, 121–130.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, New York.

Hopen, H.J. (1972) Growth of common purslane as influencing control and importance as a weed. *Weed Science*, **20**, 20–23.

Jones, R. (1966) Effect of seed bed preparation on the weed flora of spring barley. *Proceedings of the 8th British Weed Control Conference*, pp. 227–228.

Koskinen, W.C. & McWhorter, C.G. (1986) Weed control in conservation tillage. *Journal of Soil and Water Conservation*, **41**, 365–370.

Liebl, R.A. & Worsham, A.D. (1983) Tillage and mulch effects on morningglory (*Ipomoea* spp.) and certain other weed species. *Proceedings of the Southern Weed Science Society*, **36**, 405–414.

Miyanishi, K. & Cavers, P.B. (1980) The biology of Canadian Weeds. 40. *Portulaca oleracea* L. *Canadian Journal of Plant Science*, **60**, 953–963.

Mohler, C.L. (1991) Effects of tillage and mulch on weed biomass and sweet corn yield. *Weed Technology*, **5**, 545–552.

Mortimer, A.M. (1983) On weed demography. *Recent Advances in Weed Research* (ed. W.W. Fletcher), pp. 3–40. Commonwealth Agricultural Bureau, Oxford.

Mortimer, A.M. & Firbank, L.G. (1983) Towards a rationale for the prediction of weed infestations and the assessment of control strategies. *10th International Congress on Plant Protection*, Vol. 3, pp. 146–153. British Crop Protection Council, Croydon.

Moss, S.R. (1979) The influence of tillage and method of straw disposal on the survival and growth of blackgrass, *Alopecurus myosuroides*, and its control by chlortoluron and isoproturon. *Annals of Applied Biology*, **91**, 91–100.

Pareja, M.R., Staniforth, D.W. & Pareja, G.P. (1985) Distribution of weed seed among soil structural units. *Weed Science*, **33**, 182–189.

Pearcy, R.W., Tumosa, N. & Williams, K. (1981) Relationship between growth, photosynthesis and competitive interactions for a C_3 and a C_4 plant. *Oecologia*, **48**, 371–376.

Peters, R.A. & Dunn, S. (1971) Life history studies as related to weed control in the Northeast. 6. Large and small crabgrass. *Bulletin of the Storrs Agricultural Experiment Station*, **415**, University of Connecticut.

Pollard, F. & Cussans, G.W. (1976) The influence of tillage on the weed flora of four sites sown to successive crops of spring barley. *Proceedings of the 1976 British Crop Protection Conference: Weeds*, pp. 1019–1028. British Crop Protection Council, Croydon.

Povilaitis, B. (1956) Dormancy studies with seeds of various weed species. *Proceedings of the International Seed Testing Association*, **21**, 88–111.

Putnam, A.R. & DeFrank, J. (1983) Use of phytotoxic plant residues for selective weed control. *Crop Protection*, **2**, 173–181.

Putnam, A.R., DeFrank, J. & Barnes, J.P. (1983) Exploitation of allelopathy for weed control in annual and perennial cropping systems. *Journal of Chemical Ecology*, **9**, 1001–1010.

Roberts, H.A. (1981) Seed banks in soils. *Advances in Applied Biology*, **6**, 1–55.

Robinson, E.L., Langdale, G.W. & Stuedmann, J.A. (1984) Effect of three weed control regimes on no-till and tilled soybeans (*Glycine max*). *Weed Science*, **32**, 17–19.

Sagar, G.R. & Mortimer, A.M. (1976) An approach to the study of the population dynamics of plants with special reference to weeds. *Applied Biology*, **1**, 1–47.

Shilling, D.G., Liebl, R.A. & Worsham, A.D. (1985) Rye (*Secale cereale* L.) and wheat (*Triticum aestivum* L.) mulch: the suppression of certain broadleaved weeds and the isolation and identification of phytotoxins. *The Chemistry of Allelopathy* (ed. A.C. Thompson), pp. 243–271. A.C.S. Symposium Series 268.

Snedecor, G.W. & Cochran, W.G. (1967) *Statistical Methods*, 6th edn. Iowa State University Press, Ames, Iowa.

Thompson, K., Grime, J.P. & Mason, G. (1977) Seed germination in response to diurnal fluctuations of temperature. *Nature*, **267**, 147–149.

Triplett, G.B. Jr & Little, G.D. (1972) Control and ecology of weeds in continuous corn grown without tillage. *Weed Science*, **20**, 453–457.

Van Esso, M.L., Ghersa, C.M. & Soriano, A. (1986) Cultivation effects on the dynamics of a Johnson grass seed population in the soil profile. *Soil & Tillage Research*, **6**, 325–335.

Vengris, J., Dunn, S. & Stacewicz-Sapuncakis, M. (1972) Life history studies as related to weed control in the northeast. 7. Common purslane. *University of Massachusetts Agricultural Experiment Station Research Bulletin* 598.

Weed Science Society of America. (1989) *Herbicide Handbook of the Weed Science Society of America*, 6th edn. Weed Science Society of America, Champaign, Illinois.

Weaver, S.E. & McWilliams, E.L. (1980) The biology of Canadian weeds. 44. *Amaranthus retroflexus* L., *A.powellii* S. Wats. and *A.hybridus* L. *Canadian Journal of Plant Science*, **60**, 1215–1234.

Wesson, G. & Wareing, P.F. (1969) The role of light in the germination of naturally occurring populations of buried weed seeds. *Journal of Experimental Botany*, **20**, 402–413.

Wilson, H.P., Mascianica, M.P., Hines, T.E. & Walden, R.F. (1986) Influence of tillage and herbicides on weed control in a wheat (*Triticum aestivum*)-soybean (*Glycine max*) rotation. *Weed Science*, **34**, 590–594.

Wilson, R.G., Kerr, E.D. & Nelson, L.A. (1985) Potential for using weed seed content in the soil to predict future weed problems. *Weed Science*, **33**, 171–175.

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