

Intraspecific variation in germination response to ammonium nitrate of Powell amaranth (*Amaranthus powellii*) seeds originating from organic vs. conventional vegetable farms

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The primary objectives of this research were (1) to characterize intraspecific variation in Powell amaranth seed germination and emergence response to nitrogen fertilization, and (2) to evaluate whether germination and emergence characteristics varied between seeds from populations originating on organic vs. conventional vegetable farms. We hypothesized that nonherbicide-based weed management and use of slower-releasing forms of N on organic farms may have selected for seeds with lower dormancy and lower germination sensitivity to N fertilization than seeds from conventional farms. Seeds were collected from five conventional and five organic vegetable farms in central New York State. A second generation of seeds, produced under common greenhouse conditions and stored for at least 3 mo at 5 C was tested for both germination in petri dishes and emergence in the field under multiple rates of ammonium nitrate (NH_4NO_3). Both seed germination and emergence were greater for seeds originating from organic compared with conventional vegetable farms. However, seed responsiveness to fertilization did not vary significantly by habitat of origin. Reduced rates or split applications of NH_4NO_3 significantly reduced emergence in the field in 2003 but had no significant effect on emergence in 2004. Large interpopulation variation in germination and emergence patterns suggests that for Powell amaranth and similar weed species, (1) species-level models of emergence may not be very robust across different farms, and (2) the effectiveness of manipulating emergence through soil fertility practices is likely to vary substantially according to farm and year.

Nomenclature: Powell amaranth = green pigweed, *Amaranthus powellii* S. Wats. AMAPO.

Key words: Emergence, dormancy, microevolution, soil fertility.

The ability to predict weed germination and emergence patterns in relation to cropping practices and environmental conditions is useful for successfully managing weeds. Such an understanding can facilitate optimal timing of control practices (Forcella 1998; Grundy 2003), suggest strategies to reduce the synchrony of weed and crop emergence (Dyer 1995), and provide insight into the long-term effects of different management choices on weed population dynamics (Cousens and Mortimer 1995). Assumptions about weed emergence are extremely important in weed-crop competition models because even minor delays in the emergence of weeds relative to crops can significantly shift the competitive balance (e.g., Blackshaw et al. 1981; Brainard and Bellinder 2004; Dieleman et al. 1995). Similarly, weed population dynamic models are often sensitive to assumptions about the proportion of seeds in the seed bank emerging in a given year (Cousens and Mortimer 1995).

Although considerable progress has been made in characterizing the emergence of weed species in response to environmental factors such as temperature and soil moisture (Ghorbani et al. 1999; Myers et al. 2004; Oryokot et al. 1997), intraspecific variation in germination and emergence characteristics of agricultural weeds has received less attention. Evidence from several studies demonstrates large intraspecific variation in germination characteristics of many

weeds (Christal et al. 1998; Naylor and Abdalla 1982) including *Amaranthus* species (Frost and Cavers 1975; McWilliams et al. 1966). Characterization of such variation is critical for (1) interpretation of studies comparing germination characteristics of species or biotypes based on only one or two populations (e.g., Steckel et al. 2004; Weaver and Thomas 1986), (2) assessing the robustness of weed management decision tools across sites (Grundy 2003), and (3) understanding the ability of weed species to evolve rapidly and hence to persist under different management practices (Clements et al. 2004; Mortimer 1997; Rice and Emery 2003).

Mounting evidence from evolutionary biology indicates that selection in natural populations can cause evolutionary shifts in just a few generations, particularly in response to anthropogenic pressures (Clements et al. 2004; Rice and Emery 2003). For weed management, the existence and importance of such microevolution is most apparent in relation to herbicide resistance (Holt and LeBaron 1990). However, the potential for rapid evolution has been demonstrated for other weedy traits that may have important implications for optimizing weed management (Clements et al. 2004; Mohler 2001). For example, Harris et al. (1998) found that seed germination among populations of creeping buttercup (*Ranunculus repens* L.) originating from strawberry (*Fragaria x*

ananassa Duch.) fields was delayed relative to populations originating from pastures and hypothesized that this was because of strong selective pressure from intensive, early weed-control practices in strawberry fields.

Nitrogenous compounds can stimulate germination and emergence of many weed species (Baskin and Baskin 1998; Steinbauer and Grigsby 1957) including redroot pigweed (*Amaranthus retroflexus* L.) (Egley 1989; Gallagher and Cardina 1998; Hurtt and Taylorson 1986) and smooth pigweed (*Amaranthus hybridus* L.) (Teasdale and Pillai 2005). The stimulatory effects of N on seed germination has led to the suggestion that manipulation of the rate and timing of fertilization may facilitate weed management by reducing the number of weeds emerging synchronously with crops (Dyer 1995; Hurtt and Taylorson 1986; Povilaitis 1956). However, attempts to manipulate weed emergence using nitrogenous compounds have met with variable success (Dyer 1995). For redroot pigweed, Hurtt and Taylorson (1986) found emergence increased 71% with application of 34 kg nitrate ha⁻¹, but others found no stimulatory effect of nitrate in the field (Fawcett and Slife 1978; Schimpf and Palmblad 1980). Intraspecific variation in germination response to N fertilizers may account for some of those discrepancies and may limit the success of such strategies. Only a few studies have examined intraspecific variation in sensitivity of seeds to germination stimulants (Agenbag and De Villiers 1989; Cairns and De Villiers 1986) or inhibitors (DiTommaso 2004).

Organic practices may select not only for a different weed flora but also for different traits within resident weed species. Compared with conventional farming practices, organic farming practices often rely on (1) slower releasing forms of N fertilizer (e.g., compost), and (2) nonherbicide-based weed management. Hyvönen et al. (2003) hypothesized that reductions in available N on organic farms would select for less nitrophilic weeds. Similarly, if substantial heritable genetic variation in weed responsiveness to N exists within populations, rapid evolution toward less N-responsive ecotypes may occur on organic farms. Because early emergence of weeds commonly results in higher survival and fecundity (Brainard and Bellinder 2004; Mortimer 1997) and because N is a weaker signal of crop planting on organic farms, germination of seeds evolving on organic farms may be less responsive to N than those evolving on conventional farms receiving readily available inorganic fertilizer.

The fact that organic farms do not use selective herbicides may have important implications for the microevolution of weed seed traits. Weeds like Powell amaranth, which are effectively controlled by herbicides in many crops (e.g., by atrazine in sweet corn [*Zea mays* L.]), are likely to more consistently produce seeds each year on organic farms compared with conventional farms. If so, then production of dormant, persistent Powell amaranth seeds would be less advantageous on organic farms. Assuming that seed dormancy is a heritable trait and that significant trade-offs are associated with production of dormant seeds, microevolution away from seed dormancy would be expected on organic farms. Evidence from other studies suggests that the presence of rotational crops unfavorable to weed growth and reproduction may select for increased seed dormancy and longevity. Naylor and Jana (1976) reported that dormancy was more frequent in seeds of wild oat (*Avena fatua* L.) collected from fields with a history of frequent summer fall-

TABLE 1. Collection site abbreviations and nearby city in Central New York State.

Type and name	Abbreviation	Nearby city
Conventional farms		
Stoughton Farms	SN	Newark Valley
Mandeville Farm	MA	Spencer
Wickham Farms	WI	Burdett
Van Winkel Farm	VW	Nichols
Maple Tree Gardens	MT	Owego
H. C. Thompson Research Farm	FS	Freeville
Organic farms		
Rose Valley Farm	RV	Rose
West Haven Farm	BS	Ithaca
Bloodnick Family Farms	BL	Apalachin
Road's End Farm	RE	Dundee
Starflower Farm	LE	Candor
Blue Heron Farm	BH	Lodi

low than in seeds collected from fields with only occasional summer fallows. Similarly, Powell amaranth seeds collected from fields with a rotation history that included intervals of 3 to 5 yr of perennial alfalfa (*Medicago sativa* L.) were more dormant than seeds collected from habitats with strictly annual cropping systems (Brainard et al. 2005b).

To our knowledge, no previous studies have examined intraspecific variation in weed traits across organic and conventional farms, nor has the extent of intraspecific variation in seed germination responsiveness to N fertilization been examined. Therefore, the primary objectives of our research were (1) to characterize intraspecific variation in Powell amaranth seed dormancy and seed responsiveness to NH₄NO₃ fertilization, and (2) to evaluate whether germination and emergence characteristics varied significantly between seeds originating on organic and conventional vegetable farms. A secondary objective was to assess the effectiveness of reduced rates or split applications of N fertilization in reducing early emergence of Powell amaranth.

Materials and Methods

Seed Collection

Seeds from five "conventional" farms (Mandeville Farms [MA], Wickham Farms [WI], Van Winkel Farm [VW], Maple Tree Gardens [MT], and H. C. Thompson Research Farm [FS]) and five organic vegetable farms (West Haven Farm [BS], Bloodnick Family Farms [BL], Road's End Farm [RE], Starflower Farm [LE], and Blue Heron Farm [BH]) in Central New York State were collected from early September to early October in 2002 and 2003 (Table 1). Farms selected had been applying primarily inorganic sources of N (conventional farms) or organic sources of N (organic farms) for at least 10 yr. Within farms, fields were selected that had heavy infestations of Powell amaranth (i.e., mostly fields under pumpkin [*Cucurbita maxima* Duch.] production) and that had been historically under intensive vegetable production with relatively few fallow periods. Fields with a history of fallowing were excluded to control for the potential influence of fallowing on weed seed dormancy (e.g., Naylor and Jana 1976). From each site, seeds from 15 to 20 randomly selected Powell amaranth plants were collected. Because of a lack of Powell amaranth plants in 2003 on two

of the collection sites from 2002 (LE, MT), seeds were collected from two additional farms (Rose Valley Farm [RV] and Stoughton Farms [SN]) in 2003. Powell amaranth was distinguished from close relatives (redroot pigweed and smooth pigweed) by closely examining floral characteristics (Costea et al. 2004). Seeds were separated from reproductive tissue by using a 1.19-mm sieve, followed by air-column separation using a seed blower. Separated seed was stored dry in the dark at approximately 5 °C for 2 mo before germination for production of second generation seeds.

Production of Second Generation Seeds

Maternal environmental conditions can have a significant impact on seed characteristics of redroot pigweed (Chadoeuf-Hannel and Barralis 1982; Gutterman 2000; Kigel et al. 1977) as well as Powell amaranth (Brainard et al. 2005a, 2005c). To control for potential effects of variable maternal environments from which seeds were collected, a second generation of plants was grown under common greenhouse conditions beginning on October 25, 2002, and November 14, 2003. Table 2 summarizes timing and environmental conditions associated with the storage, production, and testing of second-generation seeds. To avoid sampling bias based on dormancy status, 100 randomly selected field-collected seeds from each farm were germinated in 9-cm petri dishes with 5 ml of 0.002 M gibberellic acid (GA₃) in an incubator at 35 °C with a 16 h day length and fluorescent lighting. This treatment resulted in greater than 95% germination of seeds from all populations.

Within 1 d of germination, 10 randomly selected seedlings from each farm were transferred to 10 2-L pots filled with a 1 : 1 peat moss-vermiculite mixture. Pots were placed in a greenhouse set at 26/13 °C day/night temperatures on a 16-h day length, with photosynthetic photon-flux density of approximately 400 μmol m⁻² s⁻¹ from metal halide lamps. Pots were randomly arranged within 10 blocks, each block comprised of one pot from each of the 10 farms. Plants were rerandomized twice weekly, within blocks, during the course of the experiment. Plants were watered as required and fertilized weekly with 15-5-15 (N-P-K) soluble fertilizer beginning 2 wk after seeding. Seeds from each plant were harvested 4 to 5 wk following anthesis. Because individual plants reached anthesis and produced mature seeds at different times, seeds from all plants were stored in paper bags in this same greenhouse until final plant harvest. Seeds were then separated from reproductive tissue as described previously and transferred to a refrigerator set at 5 °C until needed for assessing emergence under field conditions (Table 2).

Emergence Testing in the Field

Four days before sowing seeds, Williamson silt loam soil (Coarse-silty, mixed, active, mesic Typic Fragiudept) was collected from an agricultural field (known through preliminary greenhouse germination testing to have very low density of *Amaranthus* seeds) and mixed with a nutrient-free potting soil to create a 4 : 1 : 1 mixture of soil : peat : vermiculite. On June 15, 2003, and June 16, 2004, 100 randomly selected second-generation seeds from a single farm were sown at a depth of approximately 1 cm in two rows in 1-L pots. In both years, seeds originating from all 10

TABLE 2. Summary of timing and environmental conditions associated with seed harvest, storage, production, and testing for 2002 to 2003 and 2003 to 2004 trials.

	Dates	
	2002 to 2003 Trial	2003 to 2004 Trial
Collection of seeds from farms	Sept.–Oct. 2002	Sept.–Oct. 2003
Storage of field collected seed	Sept.–Nov. 2002	Sept.–Nov. 2003
Dormancy breaking in growth chamber	Oct. 22, 2002	Nov. 11, 2003
Production of second-generation seed	Oct. 25, 2002	Nov. 14, 2003
Seeding date	Nov. 30, 2002–Dec. 15, 2003	Dec. 17, 2003–Jan. 12, 2004
Dates of anthesis	Dec. 31, 2002–Jan. 17, 2003	Jan. 21, 2004–Feb. 19, 2004
Harvest dates ^b	Dec. 31, 2002–Jan. 31, 2003	Jan. 21, 2004–Feb. 26, 2004
Storage of second-generation seed	Jan. 31, 2003–	Feb. 26, 2004–
In glasshouse ^c	30/25 °C day/night; paper bags	June 22, 2004–July 1, 2004
In cooler ^d	5 °C; dark	June 16, 2004–Sept. 1, 2004
Growth-chamber testing of germination	30/25 °C day/night; light; NH ₄ NO ₃	
Field testing of emergence	See Table 4	

^a See Materials and Methods section for details.

^b Seeds of each plant were harvested 4 to 5 wk after anthesis.

^c Seeds from all plants were stored in the glasshouse until harvest of the last plant.

^d Seeds were stored in a cooler until use in either the growth chamber or the field experiments.

collection sites of the previous fall were included. In 2004, two additional populations (MT and LE), originating from the fall of 2002, were included as controls to help distinguish effects due to year from effects due to population. Main plots measuring 2 by 2 m were arranged in a randomized, complete-block design with six replicates. One pot from each farm was randomly placed in 1 of 10 (2003) or of 12 (2004) locations (subplots) within each main plot. Pots were buried so that the soil level in the pot corresponded to the level of adjacent field soil, with approximately 1 cm of the pot rim exposed. Pots were surrounded by landscaping cloth and covered with aluminum screening to prevent seed losses or gains during soil splashing from heavy rainfall events. Ammonium nitrate fertilizer (34-0-0, N-P-K) was applied at either 45 or 180 kg N ha⁻¹ either all at once or in two equal, split applications. Fertilizer was dissolved in water and sprayed on main plots using a CO₂ backpack sprayer equipped with tee-jet 8002 vs nozzle at 207 KPa. Initial applications (at 22.5, 45, 90, or 180 kg ha⁻¹) were made on June 16, 2003, and June 18, 2004 (1 or 2 d after seeding, respectively). The second application (at either 22.5 or 90 kg ha⁻¹) for split-application treatments was made on August 7, 2003, and August 10, 2004, respectively. Emergence was monitored twice weekly for the first 3 wk and then 1- to 2-wk intervals, thereafter. Emerged seedlings were counted and then removed by clipping them at the soil surface. Other nontarget weed seedlings were also clipped at the soil surface and removed.

Germination Testing

The effect of ammonium nitrate concentration and light treatment on germination of second generation seeds from each farm of origin was tested in petri dishes in a growth chamber. Fifty randomly selected seeds from each farm of origin were placed in 9-cm petri dishes with two sheets of filter paper saturated with 5-ml solutions of 0, 0.002, or 0.02 M NH₄NO₃. Dark germination was tested by wrapping petri dishes in two layers of aluminum foil. Three replicates of each light, by fertilizer, by farm combination were placed randomly in a single-growth chamber set at 30/25 C day/night temperatures with a photoperiod of 16/8 light/dark and photosynthetic photon-flux density of approximately 150 μmol m⁻² s⁻¹. Germinated seeds (radicle > 2 mm) in light treatments were counted daily and removed for 10 d. Germinated seeds in the dark treatments were counted following removal of aluminum foil on day 10. Viability of second-generation seeds from each farm was tested separately by germinating seeds in petri dishes with 5 ml of 0.002 M GA₃ and incubating at 35/30 C day/night temperatures on a 16-h day length with fluorescent lighting. As with field-collected seed, this treatment resulted in very high germination percentages (> 97% for all populations). The viability of seeds that did not germinate following GA₃ treatment was tested by assessing the pressure required to crush dried seeds (Sawma and Mohler 2002). Germination and emergence data are presented as percentage of viable seeds.

Statistical Analysis

Germination and emergence data were analyzed using the general linear model procedures of the Statistical Analysis

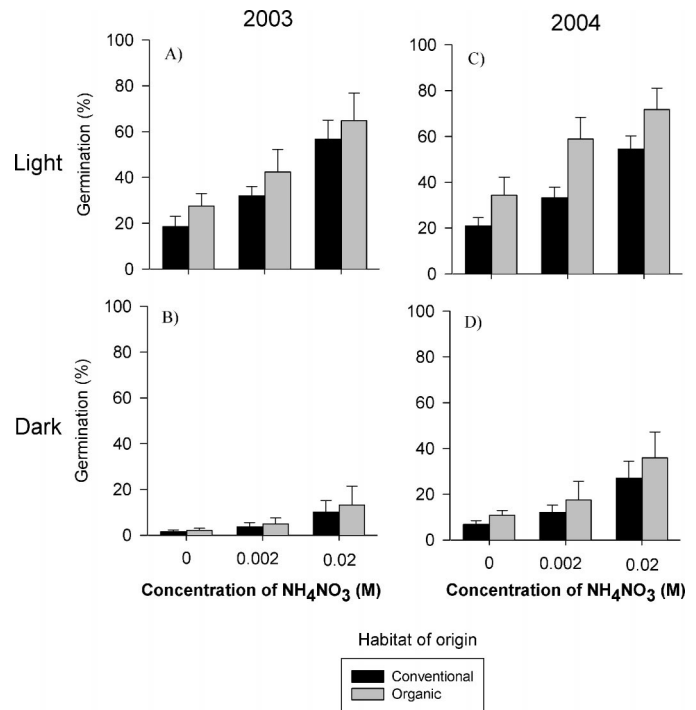


FIGURE 1. Mean germination percentages of seeds of Powell amaranth based on habitat of origin and ammonium nitrate (NH₄NO₃) concentration (A and B) in 2003 and (C and D) 2004 in (A and C) light or (B and D) darkness. All seeds were tested at 30/25 C day/night temperatures in petri dishes in a growth chamber. Bars indicate 1 SE above the mean.

System (SAS 2001). Germination data were square root transformed, and emergence data were either not transformed or log transformed as needed to improve assumptions of normality and equal variance of population distributions. The relationship between early fertilization rate (22.5, 45, 90, or 180 kg ha⁻¹) and early emergence (evaluated at 18 or 20 d after seeding in 2003 and 2004, respectively) was estimated using linear regression. The effects of total fertilization rate, fertilization timing, and habitat of origin on final emergence (cumulative emergence at 93 and 92 d after seeding in 2003 and 2004, respectively) were assessed using three-way ANOVA. These relationships were also tested for seeds from individual farms to characterize emergence patterns for different individual populations.

Results and Discussion

Habitat Effects on Germination and Emergence

Germination in petri dishes was significantly influenced by habitat of origin (Figure 1). Seeds collected from organic farms had significantly higher germination in light than those from conventional farms ($P = 0.031$). For example, 55% of seeds from organic farms germinated in 2004 compared with 36% for seeds from conventional farms.

As with germination in petri dishes, cumulative emergence in the field was higher for seeds originating from organic farms than for those originating on conventional farms, although this difference was only marginally significant in 2003 (Table 3). In 2004, final cumulative emergence (averaged across fertilization levels) for seeds originating from organic farms was 48%, compared with 37% for seeds originating from conventional farms.

TABLE 3. Cumulative emergence of Powell amaranth seedlings as a percentage of seeds sown, by habitat and fertilization treatment, in 2003 and in 2004. Data are means with standard errors in parentheses. Summary of ANOVA also shown.

Treatment	Early emergence ^a		Final emergence ^b	
	2003	2004	2003	2004
Conventional				
45 kg ha ⁻¹ split	5 (1)	12 (3)	25 (8)	33 (5)
45 kg ha ⁻¹ early	6 (1)	16 (5)	24 (6)	37 (5)
180 kg ha ⁻¹ split	7 (2)	16 (5)	40 (8)	38 (6)
180 kg ha ⁻¹ early	10 (3)	13 (4)	31 (6)	39 (5)
Organic				
45 kg ha ⁻¹ split	5 (2)	17 (5)	36 (8)	44 (6)
45 kg ha ⁻¹ early	7 (2)	16 (4)	31 (5)	46 (5)
180 kg ha ⁻¹ split	8 (3)	20 (6)	44 (7)	52 (5)
180 kg ha ⁻¹ early	10 (4)	14 (4)	39 (6)	48 (4)
ANOVA ^c				
Habitat	NS	NS	+	**
Rate ^d	*	NS	*	NS
Timing ^e	NA	NA	NS	NS
Habitat by rate	NS	NS	NS	NS
Habitat by timing	NA	NA	NS	NS
Rate by timing	NA	NA	NS	NS

^a Emergence 18 or 20 d after seeding in 2003 and 2004, respectively.

^b Emergence 93 or 92 d after seeding in 2003 and 2004 respectively.

^c + P < 0.10; * P < 0.05; ** P < 0.01; NS, P > 0.10; NA, not applicable.

^d For early emergence, rate corresponds to early rate (22.5, 45, 90, or 180 kg ha⁻¹), whereas for late emergence, rate corresponds to total rate (45 or 180 kg ha⁻¹).

^e For early emergence, timing and its interactions were not included because the second application occurred after early emergence counts.

Higher germination and emergence of Powell amaranth originating from organic farms compared with conventional farms is consistent with the hypothesis that historic control of Powell amaranth on organic farms was less variable than control on conventional farms, resulting in reduced selection pressure for seed dormancy. Our field observations suggest that the conventional vegetable farms in this study had greater crop-to-crop variability in control of weeds because of the use of highly effective herbicides in some crops (e.g., atrazine in sweet corn) and lack of effective control in other crops (e.g., pumpkin). Organic farms, in contrast, tended to have a moderate density of Powell amaranth in a larger proportion of crops.

Response to N Fertilization

Seeds from organic and conventional farms did not differ in their germination response to N in either year (the interaction between N fertilization and habitat of origin was not significant) (Figure 1). Seeds from both habitats had increased germination at higher rates of N fertilization in both light and darkness (P < 0.0001). For example, in 2004, germination in light of seeds collected from conventional farms increased from 21 to 55% with the addition of 0.02 M NH₄NO₃. Similarly, germination of seeds collected from organic farms in the same year increased from 35 to 72% with the addition of 0.02 M NH₄NO₃. Germination in darkness also increased significantly with addition of NH₄NO₃ in both years and for both habitats of origin.

In 2003, both early and final emergence was significantly greater at higher rates of fertilization (Table 3). For example, emergence at 18 d after seeding was twice as high in treatments receiving 180 kg ha⁻¹ NH₄NO₃ than in treatments receiving 22.5 kg ha⁻¹. Final emergence was roughly 33% higher at 180 kg ha⁻¹ compared with the 45 kg ha⁻¹ rate. In contrast, in 2004, emergence was not significantly influenced by fertilization rate.

Contrary to our hypothesis, the responsiveness of emergence to N did not vary significantly by habitat of origin as shown by the nonsignificant interactions between habitat and fertilization rate and between habitat and timing (Table 3). In 2003, seeds from both organic and conventional vegetable farms had greater emergence at higher N rates, whereas in 2004, seeds from both habitats were unresponsive to N. Differences in responsiveness to N between years were probably because of field environmental conditions, rather than intrinsic differences in seeds because (1) seeds from 2004 that did not respond to fertilization in the field were highly responsive to N rate in controlled petri dish conditions (Figure 1), and (2) emergence of control seeds collected in fall 2002 and tested both in 2003 and 2004 (MT population) responded to fertilization in 2003 (Figure 2) but not in 2004 (data not shown). Differences in response to N cannot be easily explained by temperature or rainfall because temperature and rainfall during June and July (the period of greatest N response in 2003) were very similar in both years (Table 4). A more likely explanation is that, in 2004, background levels of N or other chemical stimulants to germination (e.g., ethylene) were greater than in 2003 and sufficiently high to result in high levels of germination even at low N-application rates.

Lack of differentiation across habitats in responsiveness to N fertilization may have been due to several factors. First, the historic availability of N in the soil following field preparation may not have been sufficiently different on the organic and conventional farms to select for different response types. Although available N is higher for many synthetic fertilizers, N levels from organic sources of fertilizer, such as decomposing leguminous cover crops or chicken manure can also be very high (Cooperband et al. 2002; Teasdale and Pillai 2005), and soil disturbance itself may result in levels of available N that stimulate maximum germination. Second, the assumption that early emergence is advantageous may not hold for many crops. Although early emerging weeds generally have greater fecundity, they may also suffer higher mortality where effective early weed management tools are used (Mortimer 1997). Such trade-offs between fecundity and survival suggest that the optimal time of emergence is likely to vary by crop and management practice, resulting in contradictory selective pressures. Third, responsiveness to fertilization may not be a heritable trait or may be correlated with other heritable traits (e.g., seed dormancy or seed size) that respond to different selective pressures. Fourth, given that persistent seed banks tend to slow the rate of evolution, microevolutionary changes in N responsiveness may not have accumulated yet. Several farms in this study were less than 15 yr old. Finally, founder effects may have been more important in explaining differences between populations than evolution. Without knowing the initial distribution of traits within each population, assessing

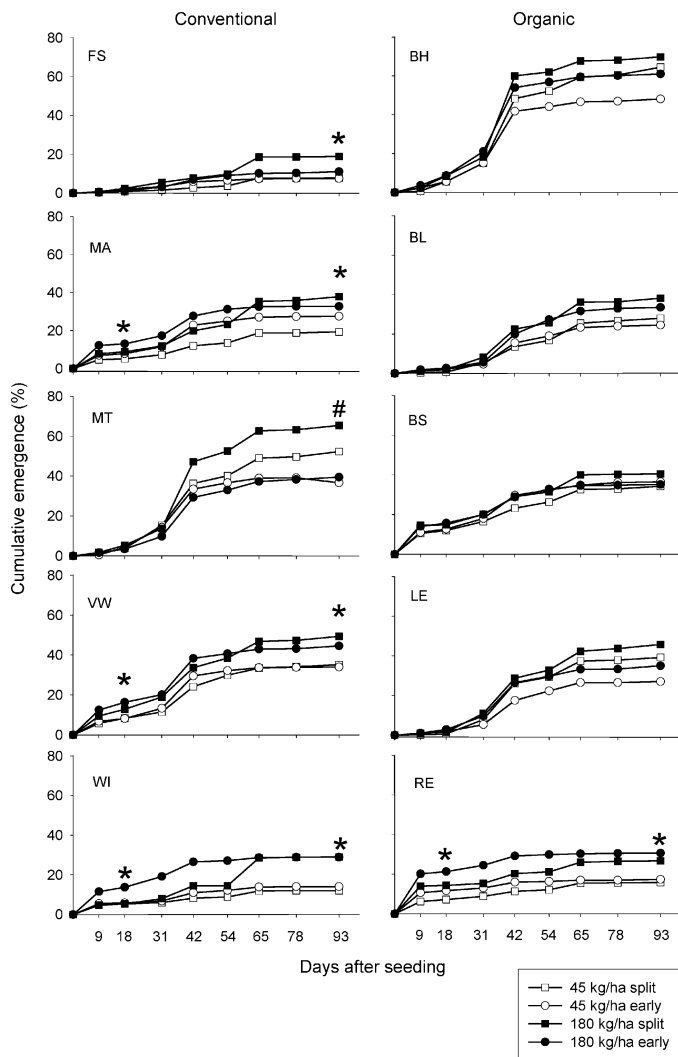


FIGURE 2. Mean cumulative emergence of seedlings as a percentage of seeds sown, by farm of origin and by fertilization treatment, 2003. An * at 18 d indicates that early emergence was significantly greater at higher fertilization rates (the slope of linear regression of emergence as function of four initial fertilizer rates was significantly greater than zero at $P < 0.05$ level). An * at 93 d indicates that emergence was significantly greater at the high total fertilization rate (ANOVA $P < 0.05$), whereas a # indicates that split application significantly reduced total emergence (ANOVA $P < 0.05$). Abbreviations: FS, H. C. Thompson Research Farm; MA, Mandeville Farms; MT, Maple Tree Gardens; VW, Van Winkel Farm; WI, Wickham Farms; BH, Blue Heron Farm; BL, Bloodnick Family Farms; BS, West Haven Farm; LE, Starflower Farm; BH, Blue Heron Farm. All sites located in Central New York State.

the evolutionary trajectory resulting from different management practices is difficult.

Whether results of this study can be generalized to other weed species and beyond the farms sampled in this study is debatable. For species with different sensitivity to management practices (e.g., herbicides), organic weed management practices may produce more variation in density than conventional practices, resulting in completely different selective pressures than those experienced by Powell amaranth in our study. With respect to historic management effects, it is important to note that our study sampled exclusively from fields with a history of intensive vegetable production and minimal historic following. Particularly on organic farms, following is often a critical component of soil and pest management (Grubinger 1999) and may select for greater weed seed dormancy (Naylor and Jana 1976; Brainard et al. 2005b). Therefore, caution should be exercised in generalizing our results to other species and farms.

It is also important to consider that results from this study reflect a specific and narrow set of maternal, storage, and seed-testing conditions. The seeds tested were grown under minimal stress under long days in pots in a greenhouse. Because maternal environmental conditions, including day length (Kigel et al. 1977), nutrient stress (Brainard et al. 2005c) and shade (Brainard et al. 2005a; Kigel et al. 1977), influence seed dormancy, a different choice of maternal environments would undoubtedly have resulted in different levels of seed germination. Similarly, seeds were stored dry at 5 C for at least 3 mo before testing. Seeds stored under these artificial conditions may behave differently from those subjected to overwintering in the soil, where fluctuating temperatures and moisture and exposure to germination stimulants like nitrogen and ethylene can influence seed dormancy (Baskin and Baskin 1998; Egley 1989) and, possibly, responsiveness to N.

Farm-to-Farm Variation in Emergence Patterns

Habitat-level analysis obscures considerable variation in emergence patterns based on farm origin (Figures 2 and 3). In 2003, emergence within 18 d of seeding was significantly stimulated by fertilization for seeds from four farms (MA, VW, WI, RE). For these farms, early emergence was between 49 and 66% lower at the lowest fertilization rate compared with the highest rate. Total emergence by 93 d was significantly stimulated by N fertilization for the same four populations and population FS. In general, splitting applications at either rate had no significant effect on total emergence but reduced early emergence of N responsive seeds.

TABLE 4. Average monthly temperature and precipitation, and 30-yr average for June to September 2003 and 2004 in Ithaca, NY.

	Temperature			Precipitation		
	2003	2004	30 yr	2003	2004	30 yr
	C			cm		
June ^a	17.3	16.9	18.0	3.5	3.1	4.9
July	20.4	19.9	20.4	17.3	17.9	9.0
August	20.7	19.4	19.6	9.8	19.4	8.6
September	15.8	17.0	15.2	14.2	13.1	9.8
Average/total	18.5	18.3	18.3	44.8	53.5	32.3

^a Includes period after seeding only.

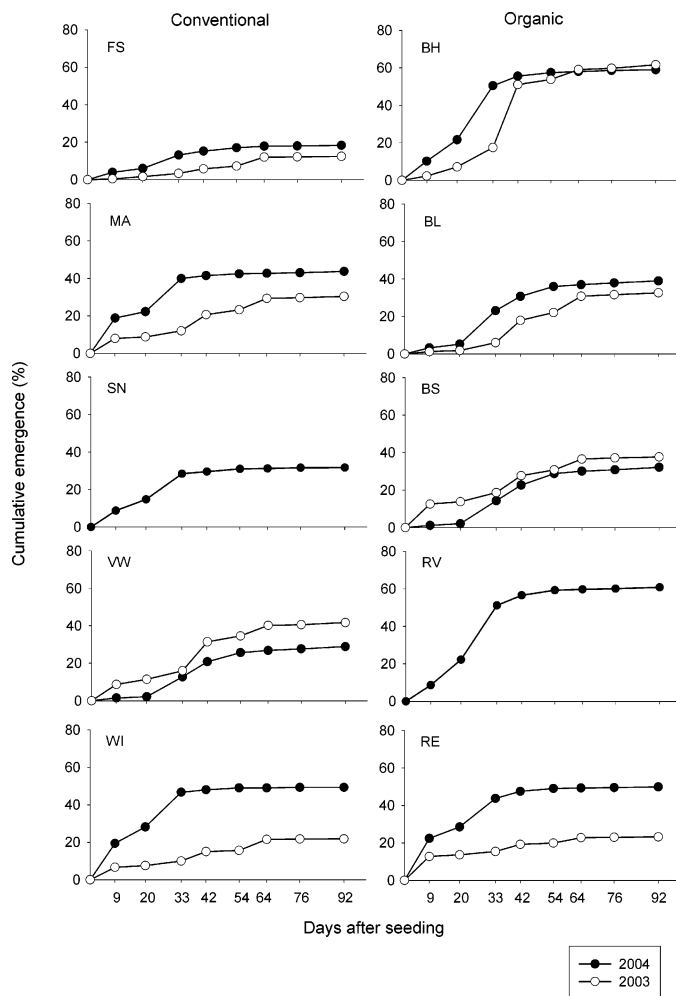


FIGURE 3. Mean cumulative emergence of seedlings as a percentage of seeds sown, by farm of origin, in 2003 and 2004. Because fertilizer treatment had no effect on emergence in 2004, data for each farm is averaged over all fertilization treatments. Average emergence for 2003 is included for comparison. Note that seeds from SN and RV farms were not included in the 2003 experiment. Abbreviations: FS, H. C. Thompson Research Farm; MA, Mandeville Farms; SN, Stoughton Farms; VW, Van Winkel Farm; WI, Wickham Farms; BH, Blue Heron Farm; BL, Bloodnick Family Farms; BS, West Haven Farm; RE, Road's End Farm. All sites located in Central New York State.

However, for the MT population, split applications increased total emergence.

The timing of emergence also varied significantly by farm origin in both years (Figures 2 and 3). For example, in 2003, the greatest emergence occurred between 31 and 42 d for seeds from BH, LE, MT and VW populations but within 9 d of seeding for MA, RE and BS populations.

Such intraspecific variation in the rate of emergence has important implications for the optimal timing of weed management practices. For example, cultivation within the first 2 wk would dramatically reduce density of the RE population but have very little effect on the BL and LE populations. Such results suggest that species-level models of emergence patterns (e.g., Forcella 1998) may not be very robust across different farms. Observed intraspecific variation in N response across populations (Figure 2) also suggests that the effectiveness of manipulating emergence through soil fertility practices is likely to vary substantially according to farm and year.

Acknowledgments

This research was funded through a CSREES/NRI Competitive Grants Program award (2002-35320-12681). We thank the Bloodnick, Bokaer-Smith, Davis, Johns, Kuhlman, Leed, Mandeville, Ostfield, Stern, Stoulke, Stoughton, White, Wickham, and Van Winkle families for their hospitality, for access to their Powell amaranth seeds, and for information on their cropping practices. Valuable field assistance from Nathan Hubert and Scott Morris was also much appreciated. We also thank Françoise Vermeulen for help with statistical analysis.

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Received November 1, 2005, and approved January 13, 2006.