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Corn competition alters the germinability of velvetleaf (*Abutilon theophrasti*) seeds

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Velvetleaf is a troublesome annual weed in many cropping systems of the United States and Canada. Differences in the growing environment of parent plants can influence the number, structure, germinability, and viability of seeds produced. Thus, the effects across a range of competitive environments and corn planting dates on velvetleaf seed production, germination, and seed coat weight were examined under field conditions. Seed production of velvetleaf increased with increasing biomass. Total velvetleaf reproductive output was reduced in competition with corn compared with monoculture stands. Corn planting date had no effect on the dormancy status of seeds, but increased competition from corn resulted in up to a 30% decrease in the proportion of seeds that were dormant. Seed and seed coat weights also decreased for plants of velvetleaf grown in competition with corn compared with those grown in monoculture. These findings suggest that velvetleaf plants growing in relatively noncompetitive environments, such as along field edges or in field areas with poor crop stands, are likely not only to produce a greater number of seeds but also a greater proportion of seeds that are dormant. This alteration in the dormancy status of velvetleaf seeds in the absence or presence of a crop provides unique opportunities for effective long-term management of the soil seedbank in this species, especially for velvetleaf individuals bordering fields or growing in fallow areas that might require more stringent control because of increased seed dormancy.

Nomenclature: Velvetleaf, *Abutilon theophrasti* Medic. ABUTH; corn, *Zea mays* L. 'Dekalb 520RR'.

Key words: Germination, competition, maternal environment, photoperiod, seed coat, dormancy.

Interspecific competition between velvetleaf and corn results in significant economic losses in many North American cropping systems (Spencer 1984). Integrated weed management strategies manipulate interspecific competitive interactions between crops and weeds to suppress weed growth and reproduction (Swanton and Murphy 1996). For example, Teasdale (1998) showed that increasing corn density to at least 90,000 plants ha^{-1} reduced velvetleaf seed production by up to 94% compared with a standard planting density of 64,000 plants ha^{-1}. Moreover, velvetleaf seed production is often eliminated if velvetleaf emergence occurs after the six-leaf stage of corn under this higher corn population density because of lower light availability to the weed. In another study, velvetleaf seed production was reduced from 18,000 to 100 seeds m^{-2} for early- (planted at same time as corn) vs. late-emerging (planted 3 wk after corn) individuals in a corn field in Ohio (Cardina et al. 1995). Similarly, Steinmaus and Norris (2002) reported reductions in velvetleaf seed output from 44,200 seeds $plant^{-1}$ in monoculture stands to 349 seeds $plant^{-1}$ in a corn crop in California. Interspecific competition from soybean [*Glycine max* (L.) Merr.] was also shown to significantly reduce velvetleaf survival and seed production (by up to 82%) relative to velvetleaf plants grown in monoculture (Lindquist et al. 1995). Although numerous studies have demonstrated the deleterious effect of crop competition on velvetleaf seed production, no research to date has examined the effects of competitive interactions on the viability and dormancy status of velvetleaf seeds produced by these plants.

Typically, a high proportion of mature velvetleaf seeds exhibits physical dormancy, a condition in which a hard seed coat prevents imbibition of water necessary for germination (Horowitz and Taylorson 1984, 1985; LaCroix and Staniforth 1964; Warwick and Black 1988). Winter (1960) suggested that the cutinized palisade layer in velvetleaf seeds was largely responsible for their impermeability to water. This layer comprises half the thickness of the velvetleaf seed coat and is discontinuous at the chalazal slit. In members of the Malvaceae such as velvetleaf, water entry is only permitted through the chalazal slit, which in dormant seeds is blocked by the chalazal plug (Baskin and Baskin 1998). The opening and closing of the chalazal plug is affected by seed moisture content (Winter 1960). Horowitz and Taylorson (1984) showed that the permeability of the seed coat to water can be affected by temperature and moisture levels during storage. It is also possible that seed coat impermeability can be influenced by environmental conditions experienced by parent plants during seed development. Velvetleaf plants at a competitive disadvantage relative to corn plants and experiencing reduced light availabilities might divert resources away from reproductive structures such as the seed coat. This could subsequently compromise the integrity of the palisade layer or other components of the seed coat and result in seeds that are permeable to water in regions other than the chalazal slit. Although not possessing physical seed dormancy, buckhorn plantain (*Plantago lanceolata* L. [Plantaginaceae]) seed coat weight increased relative to embryo/endosperm weight when parent plants were grown under increasing temperatures (Lacey et al. 1997). Previous work (Nurse, unpublished data) suggested that environmental stresses such as drought and decreased photoperiod during maturation of velvetleaf seeds might reduce their dormancy, although it was unclear whether this was a result of increased seed coat permeability or some other mechanism.

Late-maturing velvetleaf plants might experience both higher levels of competition from a well-established crop and decreasing photoperiod. Flower initiation in velvetleaf is most rapid under short photoperiods (e.g., 11 h), although this species eventually flowers under longer photoperiods (e.g., 15 h) (Patterson 1995). This shorter interval between maturation, flowering, and seed set suggests that the parent plant will have fewer resources to allocate to reproduction. Species whose seeds possess physical dormancy that germinate early in the season and under longer photoperiods might produce a higher proportion of water-impermeable (dormant) seeds than plants grown under shorter photoperiods. Evenari et al. (1966) found that seeds of *Ononis sicula* Guss. (Fabaceae) had thicker, more impermeable seed coats when grown under a 20-h photoperiod compared with seeds produced by plants grown under an 8-h photoperiod. However, few studies have investigated the effect of photoperiod in species whose seeds exhibit physical dormancy (hardseededness).

No studies have examined the combined effects of corn competition and corn planting date on the viability and dormancy of velvetleaf seeds produced under these conditions. The objectives of this study were to examine the effect of environmental conditions during seed maturation, including competition with corn as well as conditions associated with different corn planting dates (e.g., photoperiod, temperature) on seed production and the proportion of dormant seeds in velvetleaf. We hypothesized that velvetleaf plants grown under stressful conditions (i.e., intense corn competition and short photoperiod) would produce a lower proportion of dormant seeds because of possible reductions in the allocation of available resources to seed coat structures such as the palisade layer.

Materials and Methods

Experimental Design

Field trials were conducted during 2002 and 2003 at the Robert Musgrave Agronomy Research Facility of Cornell University in Aurora, NY. The study site was located on a lima silt loam (fine-loamy, mixed, active, mesic Oxyaquic Hapludalfs) with an organic matter content of 2.6% and pH 7.9. The previous crop grown on the site was glyphosate-resistant soybean.

A split-split-split plot design with four replicates was used. The main plot factor was the competitive environment under which velvetleaf was grown, both in the presence and absence of corn; the subplot factor was corn planting date; and the sub-subplot factor was velvetleaf transplant date. Three corn planting dates were used in both years: May 8, May 30, and June 23. These dates correspond to the range between typical planting (May 8) and late planting (June 23) of corn in central New York state. These planting dates also allowed for comparison of velvetleaf seed development and maturation under photoperiods ranging from about 15 h for the early plantings to about 13 h for the late plantings. No corn was planted for the early (May 8) treatment in 2002 because excessive precipitation prevented the use of planting machinery on the field site. Three velvetleaf seedling transplant dates were established to provide a range of competitive hierarchies between corn and velvetleaf: 14 d before corn emergence (DBE), 0 d after corn emergence (DAE), and 14 DAE. The 14 DBE treatment was established by transplanting velvetleaf seedlings (one- to two-leaf stage) into the field immediately after the seeding of the corn. In early May, corn generally takes between 10 and 14 d to emerge in central New York state; thus, velvetleaf seedlings in this treatment had an approximate 14-d growth advantage over corn.

In early May of each year, the soil was moldboard plowed and disked, and the nonselective herbicide glyphosate[1] was applied at 0.9 kg ai ha^{-1} before corn emergence to control existing vegetation before planting. At corn planting, fertilizer (10-20-20 N-P-K) was added at 224 kg ha^{-1}. Glyphosate-resistant corn cultivar 'Dekalb 520RR' was sown for all corn planting dates at a row spacing of 76 cm and at a density to achieve 70,000 plants ha^{-1}.

Seedling Source

Seeds of velvetleaf used to produce seedlings for this study were randomly collected from a corn field at the Robert Musgrave Agronomy Research facility in September 2001 and were stored dry in the dark at 5 C until required. Only seeds of relatively equal weight (9.0–9.5 mg) were used. In spring 2002 and 2003, seeds were soaked in boiling water in cheesecloth for 10 s then placed on filter paper moistened with distilled water in petri dishes on a lab countertop at room temperature (~ 22 C). Nearly all seeds germinated within 3 d. Individual germinated seeds were placed in peat pots[2] (40 cm^3) containing a 1:1 (v/v) mixture of peat moss and vermiculite. Pots were transferred to a glasshouse under a 14-h photoperiod and 30/15 C (± 3 C) day/night temperatures. On relatively warm (> 15 C) partly cloudy days, pots were moved outdoors to harden seedlings. Seedlings were germinated in separate lots associated with each corn planting date. Seedlings were transplanted into the field at the one- to two-leaf stage for all transplant and corn seeding dates. Velvetleaf seedlings were also planted in plots not seeded to corn for each transplant and corn seeding date (velvetleaf monoculture). Each treatment plot comprised three 9-m rows of velvetleaf seedlings with 25 seedlings planted per row. Seedlings within a row were planted 30 cm apart, resulting in a planting density of 4.2 plants m^{-2}. Plots were weeded regularly both by hand and with a hoe throughout the growing season to remove unwanted weeds. Throughout the growing season, height, number of leaves, and number of capsules for each velvetleaf plant within the middle row of transplants were recorded. At reproductive maturity, aboveground biomass was determined by cutting plants at soil level, drying at a constant 65 C for 48 h, and weighing. Seed and capsule production were also recorded for each plant. At harvest, mature capsules were collected randomly from each of the 25 transplants from the middle row. Seed losses from fruit shattering were minimized by placing the collection bag directly under capsules before removal from plants. Harvested capsules were stored dry at ambient temperature (~ 22–23 C, 50–60% relative humidity) in the laboratory before seed separation.

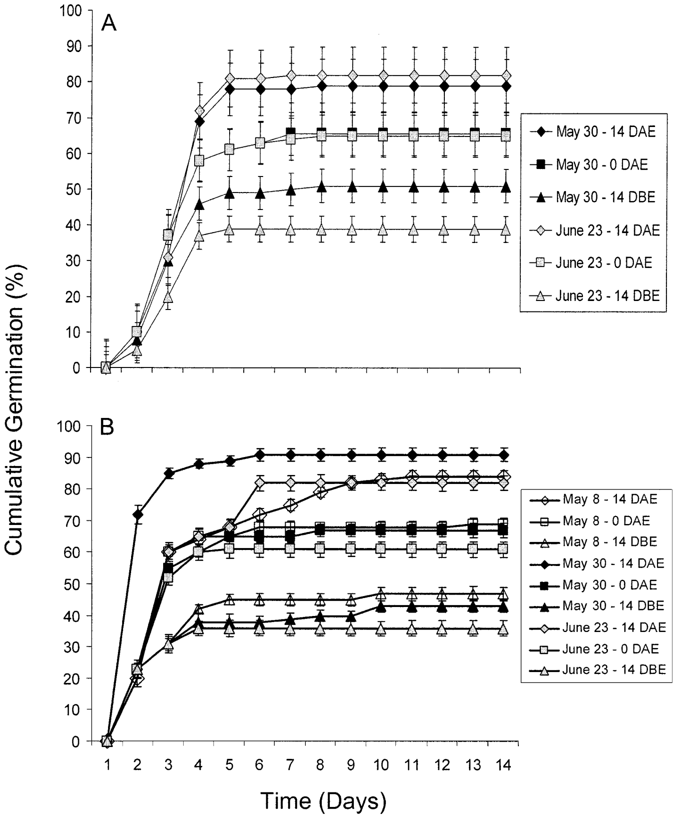

FIGURE 1. Cumulative percent germination of intact velvetleaf seeds produced in competition with corn in (A) 2002 and (B) 2003 for different corn planting dates and competition timings. DAE, days after emergence; DBE, days before emergence. Bars indicate 1 SE above and below the mean.

Soil moisture (volumetric water content) was measured by time domain reflectrometry (TDR). Soil moisture probes (30 cm long) were inserted into the soil at a 45 degree angle to measure the soil moisture in the top 20 cm of the soil. One probe was placed within each experimental plot. Measurements by TDR were verified in the lab by drying soil samples of known volume in an oven for 48 h at 105 C and determining volumetric water content.

Germination

In early November of each year, fully ripe capsules were carefully opened by hand, and seed was separated from chaff with sieves. Seeds were then dry-stored at 5 C for 3 mo in paper envelopes until the start of germination experiments in January.

Germination experiments were conducted in a growth chamber at 27/14 C day/night temperatures and a 14-h photoperiod. The photosynthetic photon flux density averaged 150 μmol m^{-2} s^{-1} within the chamber. Thirty seeds from each treatment combination were placed in 9-cm-diam petri dishes on one layer of filter paper moistened with 5 ml of distilled water. Five replications per treatment combination were used, and germination was monitored daily for 14 d. A seed was considered to have germinated when the radicle was at least 1 mm long. Germinated seeds were immediately removed from the dishes. The germination trial was performed twice. Viability of seeds failing to germinate by the end of the 14-d experimental period was assessed by a pressure test in which light pressure was applied to the seeds with forceps. Seeds that collapsed with light pressure or that were heavily colonized by fungi were considered nonviable and excluded from analyses. Viability of the remaining seeds was assessed by the tetrazolium chloride test (Moore 1973). Seeds showing positive tetrazolium staining were considered to be viable but dormant.

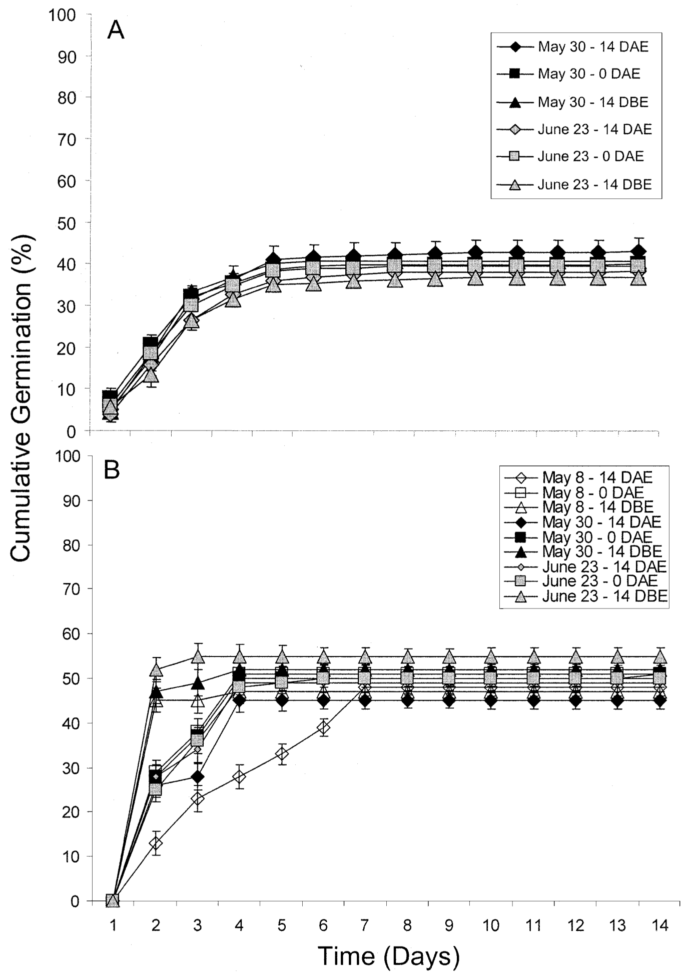

FIGURE 2. Cumulative percent germination of intact velvetleaf seeds produced in monoculture plots in (A) 2002 and (B) 2003 for different corn planting dates and competition timings. DAE, days after emergence; DBE, days before emergence. Bars indicate 1 SE above and below the mean.

Seed Coat Weight

Fifty velvetleaf seeds from each treatment stored at 5 C were randomly selected and placed on filter paper moistened with distilled water in 9-cm-diam plastic petri dishes. Mean dry weight of each set of 50 seeds was obtained before they imbibed water. The seeds were left to germinate on a lab countertop under fluorescent light at ambient room temperature (~ 22 C) for a period of 5 d. At the end of this period, 10 randomly selected germinated seeds from each petri dish were removed and weighed. The seed coat was carefully removed from germinated seeds by applying gentle pressure with metal forceps. In most cases, the seed coat could be separated easily from the embryo. In cases in which the seed coat was not readily removed (~ 2%), the seeds were discarded to ensure that all seed coats in the sample were complete and intact. The wet weight of the 10 seed

TABLE 1. Percent soil moisture in the top 20 cm of the soil profile measured by time domain reflectrometry in 2002 and 2003 over the entire growing season. Plants were grown either alone (monoculture) or with corn at three planting dates (May 8, May 30, and June 23). Data are means, with standard errors shown in parentheses.[a]

	2002		2003	
	Corn	Monoculture	Corn	Monoculture
	%			
May 8				
April	NA	NA	25.64 (1.53)	25.43 (1.34)
May	NA	NA	25.49 (1.53)	23.24 (1.34)
June	NA	NA	23.49 (1.36)	22.59 (1.26)
July	NA	NA	22.58 (1.36)	22.58 (1.26)
August	NA	NA	22.49 (1.36)	21.82 (1.26)
September	NA	NA	23.22 (1.36)	19.58 (1.34)
May 30				
April	24.99 (1.54)	24.92 (1.61)	23.56 (1.46)	21.57 (1.38)
May	23.84 (1.44)	22.63 (1.39)	23.35 (1.35)	21.49 (1.38)
June	21.48 (1.44)	21.48 (1.39)	21.26 (1.35)	20.12 (1.38)
July	21.97 (1.39)	21.52 (1.39)	21.58 (1.35)	19.56 (1.41)
August	23.17 (1.44)	22.71 (1.39)	22.96 (1.46)	19.47 (1.41)
September	23.49 (1.44)	23.78 (1.39)	23.27 (1.46)	19.89 (1.38)
June 23				
April	23.64 (2.11)	19.27 (1.97)	23.54 (1.76)	19.85 (1.89)
May	25.71 (1.97)	19.93 (1.97)	23.79 (1.76)	19.46 (1.89)
June	22.78 (1.97)	18.26 (1.97)	22.57 (1.65)	18.37 (1.96)
July	23.71 (1.97)	19.31 (1.97)	22.98 (1.65)	18.67 (1.96)
August	21.86 (2.11)	19.37 (1.97)	20.59 (1.65)	18.98 (1.89)
September	19.93 (1.61)	17.94 (1.68)	19.43 (1.76)	18.22 (1.89)
ANOVA[b]				
Planting date	*		*	
Crop competition	*		*	
Time	NS		NS	
PD × crop comp	*		*	
PD × crop comp × time	NS		NS	

[a] Abbreviations: Comp, competition; PD, planting date; NA, not available; ANOVA, analysis of variance; NS, not significant.
[b] An asterisk indicates $P < 0.05$.

coats was measured before placement into paper envelopes. The seed coats were then dried at a constant temperature of 65 C for 48 h and weighed.

Seeds not germinating in this experiment were considered dormant. Dormant seeds in each treatment were subsequently placed in boiling water for 10 s to break dormancy. Germination and seed coat measurements of these seeds were then determined as previously described for nondormant seeds.

Statistical Analysis

Data for the germination, seed weight, and seed coat experiments were analyzed separately by analysis of variance with PROC GLM (SAS 1999). All percentage data from the germination experiment were arcsine square root transformed to homogenize variances. Data from the seed weight and seed coat experiment did not require transformation. Differences between treatments were established at the 5% level of significance with the LSMEANS function of SAS. Regression analysis for reproductive output vs. biomass was generated with PROC REG (SAS 1999).

Results and Discussion

Influence of Corn Planting Date and Competition Timing on Germination

The germinability of mature seeds did not differ with corn planting date for velvetleaf individuals grown in the presence of corn in either 2002 or 2003 (Figure 1). This result was surprising given the strong influence decreasing photoperiod has been shown to have on the growth and reproductive output of velvetleaf (Oliver 1979; Patterson 1995). Similarly, velvetleaf plants grown in monoculture also produced seeds that did not differ in germinability between corn planting dates in both 2002 and 2003 (Figure 2). Early-season precipitation (i.e., May) was above average in both 2002 (126 mm; 80 mm long-term average) and 2003 (114 mm). McDonald and Riha (1999) suggested that factors such as early season drought might influence the growth of velvetleaf and increase its competitiveness with corn. Thus, it seems that ample moisture available in the spring of 2002 and 2003 might have masked potential differences in germinability among treatments.

Velvetleaf transplanted in corn plots 14 DAE produced 15 and 32% more nondormant seeds than were produced by velvetleaf plants transplanted either at corn emergence (0

DAE) or 14 DBE, respectively, in 2002 (Figure 1A), and 11 and 42% in 2003 (Figure 1B). These findings support our original hypothesis that velvetleaf individuals experiencing high stress during maturation (i.e., that are at a competitive disadvantage relative to corn, 14 DAE) produce higher proportions of nondormant seeds. Timing of competition did not influence velvetleaf seed dormancy in monoculture stands (Figure 2).

Maximum cumulative germination differed between velvetleaf seeds grown in competition with corn and those grown in monoculture stands (Figures 1 and 2). Seeds produced in monoculture stands had a maximum germination of approximately 45% (Figure 2), whereas seeds grown in competition with corn had maximum germination of up to 90% (Figure 1). This is a clear indication of the influence of competition. If only the 14 DBE competitive timing is considered (Figure 1), the average cumulative germination (40%) does not differ from the average cumulative germination for seed grown in monoculture stands (45%) (Figure 2). Thus, velvetleaf individuals growing along field margins (monoculture) or that germinate early and are able to overtop a corn canopy (14 DBE) could produce seed that is highly dormant.

In both 2002 and 2003, percent soil moisture was significantly different between planting dates of corn (Table 1). However, soil moisture did not differ over the growing season (April–September) within each planting date. Interestingly, soil moisture was significantly higher in plots containing both corn and velvetleaf than in monoculture plots of velvetleaf. It was expected that the added competition from corn would have reduced water content available to the velvetleaf plants; however, this appears not to be the case. Evaporation of water from bare soil in monoculture plots is not believed to be the major factor explaining the observed differences because water loss from evaporation at the soil surface is relatively small. Soil moisture values (monthly averages) obtained in this study were below field capacity (39% volumetric water content at − 30 kPa), but they were above the permanent wilting point (18% volumetric water content at − 1,500 kPa) for the soil.

In 2002, the weight of velvetleaf seeds did not differ across corn planting dates, although a decreasing trend was observed. There was, however, a significant decrease in seed weight for velvetleaf plants grown with corn compared with plants grown in monoculture (Figure 3A). In 2003, the weight of velvetleaf seeds decreased at later planting dates and for plants grown with corn (Figure 3B). It was expected that seed weight would decrease in seeds produced by parent plants grown under the shorter photoperiods experienced at later plantings. Surprisingly, in both years, velvetleaf seed weight was not influenced by transplant date relative to the corn planting. However, overall reproductive output by velvetleaf plants was reduced by later corn planting dates. As photoperiod decreased with later plantings, reproductive output in velvetleaf also decreased relative to plant biomass, as shown by the lower regression slope values in both the corn and monoculture environments in 2002 (Figure 4). This was not always the case in 2003 because the regression slope increased in monoculture stands as photoperiod increased (Figures 5A and 5C) and in competition with corn as photoperiod decreased (Figures 5D and 5F). In 2002, competition with corn reduced seed production in velvetleaf

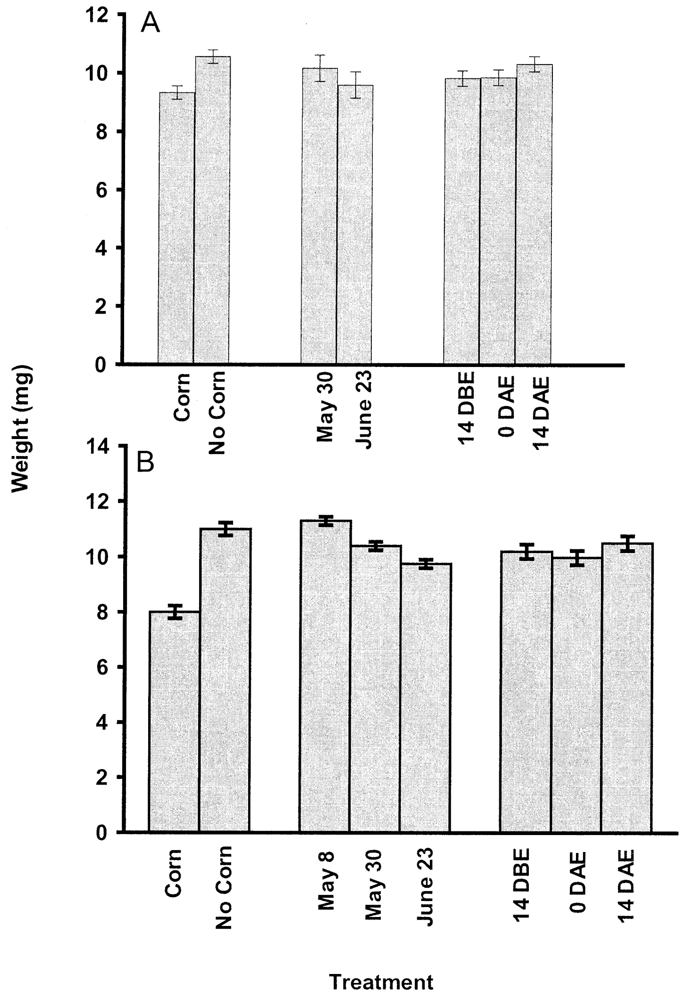

Figure 3. Mean weight of intact velvetleaf seeds produced in monoculture and mixture (with corn) plots planted at different corn planting dates and competitive intensities in (A) 2002 and (B) 2003. DAE, days after emergence; DBE, days before emergence. Bars indicate 1 SE above and below the mean.

to < 2,000 seeds for the May 30 planting (Figure 4B) and to only 200 seeds for the June 23 planting (Figure 4D). In contrast, 14,000 and 10,000 seeds were produced in monoculture plots for the May 30 and June 23 plantings, respectively (Figures 4A and 4C). Corn competition resulted in similar reductions in seed number and biomass in 2003, in which seed production was reduced in some cases by up to 5,000 seeds in plants of similar size (Figure 5). Patterson (1995) reported significant reductions in velvetleaf height, total biomass, and seed production for plants subjected to short photoperiods (e.g., < 13 h) during vegetative growth. Clearly competition with corn combined with decreasing photoperiod substantially reduced the size and reproductive output of velvetleaf relative to plants grown in a pure stand.

Corn planting date did have a significant effect on leaf and capsule number, but not on plant height in either 2002 or 2003 (Table 2). Under the longer photoperiod experienced during the early plantings, velvetleaf leaf number and capsule production increased. As expected, velvetleaf individuals growing in monoculture and not competing with corn produced a significantly higher number of leaves and more capsules. Additionally, plants with greater biomass had higher reproductive output (Figures 4 and 5). These differ-

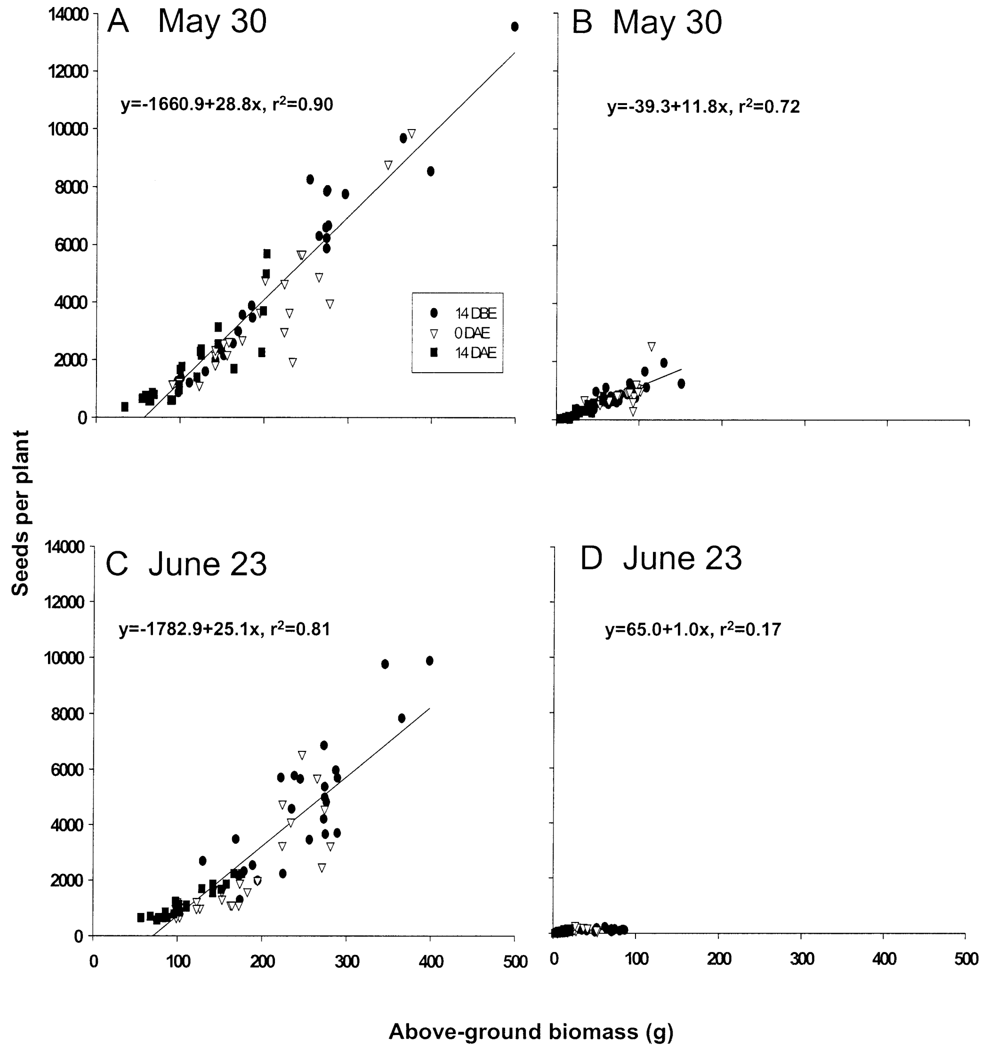

FIGURE 4. Regression of velvetleaf aboveground biomass vs. total seed production in monoculture (A, C) and in competition with corn (B, D) at two corn planting dates in 2002. Photoperiod decreased (A > C and B > D) within each environment. DAE, days after emergence; DBE, days before emergence.

ences in growth and reproduction could be a result of decreased competition in velvetleaf monoculture plots compared with mixture plots with corn. Shading by the corn canopy caused a significant increase in velvetleaf height relative to plants grown in monoculture. Bello et al. (1995) reported similar findings for velvetleaf grown under artificial shading.

Timing of Competition Influences Seed Production

It is well documented that velvetleaf seed production is significantly reduced when competing with corn relative to plants grown in monoculture (Cardina et al. 1995; Steinmaus and Norris 2002; Teasdale 1998). This reduction in velvetleaf seed production in the presence of corn could be a result of a decrease in resources allocated to reproduction. Our study further expands on the effect of corn on velvetleaf by examining the dormancy status of those seeds that are produced in this interspecific competitive environment. In both 2002 and 2003, the competitive status of velvetleaf relative to that of corn had a significant effect on seed production (Figures 4 and 5) and on the ability of seeds produced to germinate (Figure 1). Bello et al. (1995) showed that velvetleaf plants grown in monoculture at densities ranging from 6,500 to 15,100 plants ha^{-1} and under artificial shade had growth and seed production decreases of up to 94% relative to nonshaded plants. Moreover, the proportion of dormant seeds produced by shaded plants was reduced by 20% relative to seeds produced by nonshaded plants. Clearly, a reduction in available resources, especially light, could not only reduce the number and weight of seeds produced but also the proportion of dormant seeds. Our findings are consistent with the conclusions of Baloch et al. (2001) that as velvetleaf seed weight increased so did dormancy. Rees (1996) also suggested that heavier seeds should be more dormant than lighter seeds because larger seeds have more resources for establishment after dispersal than smaller seeds. However, the prediction by Rees (1996) that interspecific competition under a closed canopy should result in an increase in seed weight is not consistent with the results of our study. That seed weight did not vary between the different velvetleaf transplant treatment dates in corn might reflect a minimum threshold seed weight resulting from corn competition that is independent of the competition timing established by the different transplant dates.

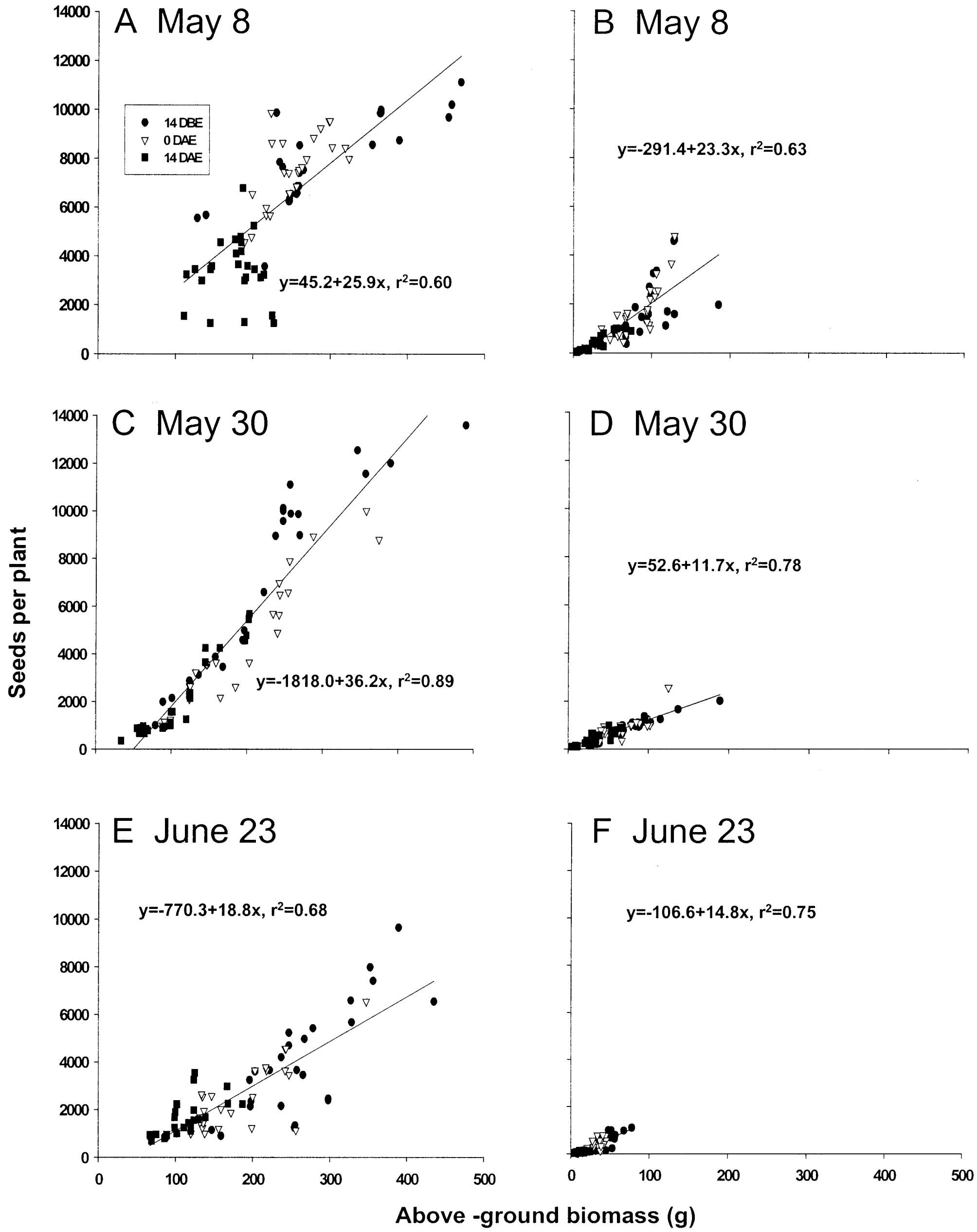

FIGURE 5. Regression of velvetleaf aboveground biomass vs. total seed production in monoculture (A, C, E) and in competition with corn (B, D, F) at three corn planting dates in 2003. Photoperiod decreased (A > C > E and B > D > F) within each environment. DAE, days after emergence; DBE, days before emergence.

Competition timing also significantly influenced the number of velvetleaf leaves and capsules produced in both 2002 and 2003 (Table 2). In general, as competition increased (i.e., with later velvetleaf transplant dates, 0 DAE and 14 DAE), the number of leaves and capsules decreased. Velvetleaf plant height was not influenced by velvetleaf transplant date relative to corn.

Seed Coat Weight

Corn Planting Date and Environment

Seed coat weights were determined for a subset of dormant and nondormant velvetleaf seeds in an attempt to determine the possible mechanism for changes in the proportion of dormant seeds between the various corn planting dates and competitive environment treatments. In 2002, seed coat weight in nondormant seeds decreased significantly at later planting dates for velvetleaf plants grown with corn (Table 3). There was no difference between seed coat weights for the May 30 planting, but a significant planting date effect was found for the June 23 corn planting. Corn planting date did not affect seed coat weight in monoculture. In 2003, differences in seed coat weight between nondormant and dormant seeds increased as planting date was delayed. Seeds from velvetleaf plants grown in competition with corn showed a significant decrease in seed coat weight at later planting dates. In general, the weight of seed coats from dormant seeds was greater than for nondormant seeds in the same treatments.

In both 2002 and 2003, the proportion of the seed coat

TABLE 2. Capsule number, height, and leaf number of velvetleaf plants in 2002 and 2003. Plants were grown either alone or with corn at three planting dates and under three competitive environments. Data are means, with standard errors shown in parentheses.[a]

	Capsule number		Plant height		Leaf number	
Treatment	2002	2003	2002	2003	2002	2003
	No.		m		No.	
Corn planting date						
Monoculture						
May 8	NA	200 (24)	NA	1.95 (0.2)	NA	102 (28)
May 30	176 (13)	194 (18)	1.85 (0.2)	1.97 (0.1)	75 (13)	86 (4)
June 23	125 (15)	136 (19)	1.73 (0.1)	1.83 (0.1)	47 (5)	53 (3)
Corn						
May 8	NA	7 (2)	NA	2.56 (0.2)	NA	10 (2)
May 30	16 (3)	5 (3)	2.13 (0.3)	2.23 (0.2)	11 (2)	14 (2)
June 23	2 (1)	4 (1)	2.10 (0.1)	1.76 (0.1)	7 (2)	3 (1)
ANOVA[b]						
Corn planting date	*	*	NS	NS	*	*
Crop competition	*	*	*	*	*	*
PD × crop comp	*	*	NS	NS	*	*
Competition						
Monoculture						
14 DBE	NA	196 (15)	NA	1.75 (0.1)	NA	106 (15)
0 DAE	176 (13)	183 (12)	2.23 (0.2)	2.12 (0.2)	102 (6)	100 (8)
14 DAE	181 (12)	189 (12)	1.96 (0.2)	2.02 (0.2)	56 (3)	45 (3)
Corn						
14 DBE	NA	15 (3)	NA	1.95 (0.2)	NA	15 (1)
0 DAE	12 (2)	13 (3)	2.13 (0.1)	2.06 (0.2)	8 (2)	10 (1)
14 DAE	5 (2)	7 (2)	2.02 (0.2)	2.04 (0.1)	2 (1)	5 (1)
ANOVA[b]						
Timing	*	*	NS	NS	*	*
Crop competition	*	*	NS	NS	*	*
Timing × crop comp	*	*	NS	NS	*	*

[a] Abbreviations: DBE, days before corn emergence; DAE, days after emergence; comp, competition; PD, planting date; NA, not available; ANOVA, analysis of variance; NS, not significant.
[b] An asterisk indicates $P < 0.05$.

weight relative to the total seed weight was greater in dormant compared with nondormant seeds within the same treatment. Barnett (1976) reported that as much as 69% of the variation in the dormancy of pine (*Pinus* spp.) seeds was due to the proportion of the seed coat weight relative to the total seed weight. The increased restriction to water uptake, and thus embryo expansion, by the heavier seed coats were thought to be responsible for the increased proportion of dormant seeds. In a similar study with loblolly pine (*Pinus taeda* L.), Barnett (1997) also demonstrated the profound effect that maternal environment and, more specifically, the seed coat proportion of total seed weight have on the dormancy status of seeds. Consistent with their previous work, the greater the proportion of the seed coat mass relative to the total seed mass, the larger the proportion of dormant seeds.

Competition Timing and Growing Environment

Transplant timing had no effect on seed coat weight in either velvetleaf monoculture or mixture plots with corn. However, seeds produced in plots with corn had lower mean seed coat weights than seeds produced in monoculture plots (Table 3). In monoculture plots, seed coat weight did not differ between nondormant and dormant seeds in 2002, but did differ in 2003. Dormant velvetleaf seeds produced in corn mixture plots and at a competitive disadvantage (14 DAE) produced seed coats significantly heavier than nondormant seeds within the same treatment in both years. One plausible explanation for these findings is that, under intense competition, plants alter the type of storage compounds in their seeds (Rees 1996). The proportion of seed coat weight to total seed weight was higher in dormant than in nondormant seeds in both 2002 and 2003. This proportion did not differ in nondormant seeds for the different transplant dates in both years. For dormant seeds however, the proportion of the total weight allocated to the seed coat decreased when velvetleaf transplant date was delayed in monoculture plots, and it increased in mixture plots with corn as velvetleaf transplant date was delayed in 2003. It remains unclear what specific role seed coat weight might play in the regulation of velvetleaf seed dormancy because it is not the only factor controlling dormancy.

Management Implications

Consistent with our initial hypothesis, we found a higher proportion of dormancy in heavier than in lighter seeds. Velvetleaf individuals germinating early in the growing season (i.e., 14 DBE) and under the longest photoperiod

TABLE 3. Seed coat weight and proportion of seed coat weight relative to total seed weight for dormant compared with nondormant velvetleaf seeds in 2002 and 2003. Plants were grown either alone or with corn at three planting dates and under three competitive environments. Data are means, with standard errors shown in parentheses.[a]

Treatment	Seed coat weight				Proportion of total seed weight			
	Nondormant		Dormant		Nondormant		Dormant	
	2002	2003	2002	2003	2002	2003	2002	2003
	mg				%			
Corn planting date								
Monoculture								
May 8	NA	4.51 (0.08)	NA	4.50 (0.10)	NA	42.1 (1.0)	NA	42.0 (1.0)
May 30	4.54 (0.08)	4.49 (0.10)	4.53 (0.07)	4.71 (0.09)	42.8 (1.1)	42.0 (0.9)	42.7 (1.1)	44.0 (0.8)
June 23	4.47 (0.11)	4.31 (0.06)	4.73 (0.07)	4.69 (0.07)	42.6 (1.2)	42.0 (1.0)	45.1 (1.3)	45.5 (1.5)
Corn								
May 8	NA	4.21 (0.04)	NA	4.28 (0.06)	NA	42.3 (1.3)	NA	42.8 (1.1)
May 30	4.22 (0.05)	3.98 (0.03)	4.41 (0.09)	4.08 (0.04)	43.4 (1.1)	42.3 (1.3)	45.3 (1.2)	43.4 (1.1)
June 23	3.79 (0.06)	3.91 (0.03)	4.23 (0.14)	4.01 (0.04)	43.6 (1.2)	42.2 (1.1)	48.6 (1.5)	43.1 (1.5)
ANOVA[b]								
Corn planting date	*	NS	NS	*	NS	NS	*	NS
Crop competition	*	*	*	*	NS	NS	*	NS
PD × crop comp	NS	NS	NS	NS	NS	NS	NS	NS
Dormant × nondormant	*	*	—	—	*	*	—	—
Dormancy × crop comp	*	*	*	*	NS	NS	*	NS
Dormancy × corn planting	NS	*	NS	*	NS	NS	*	NS
Dormancy × corn planting × crop comp	*	*	*	*	NS	NS	NS	NS
Competition								
Monoculture								
14 DBE	4.52 (0.11)	4.25 (0.11)	4.72 (0.08)	4.78 (0.07)	43.2 (1.1)	41.5 (1.5)	45.2 (0.9)	46.9 (1.2)
0 DAE	4.64 (0.07)	4.53 (0.12)	4.67 (0.06)	4.76 (0.07)	42.8 (1.2)	41.6 (0.9)	43.1 (0.9)	43.7 (0.6)
14 DAE	4.23 (0.12)	4.23 (0.08)	4.28 (0.05)	4.25 (0.08)	41.2 (1.3)	41.1 (1.2)	41.7 (0.6)	41.3 (1.1)
Corn								
14 DBE	4.03 (0.11)	3.98 (0.06)	4.06 (0.08)	4.12 (0.09)	43.6 (1.1)	41.4 (1.1)	44.1 (1.2)	43.0 (0.7)
0 DAE	3.96 (0.07)	3.99 (0.07)	4.42 (0.12)	4.36 (0.09)	44.5 (1.3)	41.4 (0.9)	49.7 (1.4)	45.4 (0.9)
14 DAE	4.27 (0.02)	4.12 (0.10)	4.73 (0.18)	4.98 (0.11)	41.0 (1.1)	40.1 (0.8)	45.5 (0.9)	48.3 (1.3)
ANOVA[b]								
Timing	NS	NS	NS	NS	*	NS	*	*
Crop competition	*	*	*	*	NS	NS	*	NS
Timing × crop comp	*	*	*	NS	NS	NS	NS	NS
Dormant × nondormant	NS	*	—	—	*	*	—	—
Dormancy × crop comp	*	*	NS	*	NS	NS	NS	NS
Dormancy × timing	*	NS	*	*	NS	NS	NS	NS
Dormancy × timing × crop comp	*	*	*	NS	NS	NS	NS	NS

[a] Abbreviations: DBE, days before corn emergence; DAE, days after emergence; comp, competition; PD, planting date; NA, not available; ANOVA, analysis of variance; NS, not significant.
[b] An asterisk indicates $P < 0.05$.

(> 14 h) produced heavier seeds. Velvetleaf grown in competition with corn had lower seed and seed coat weights and proportion of dormant seeds. Thus, velvetleaf plants growing late in the season within a closed corn canopy might not only produce fewer seeds but also a greater proportion of seeds that are not dormant. These differences in the dormancy of velvetleaf seeds produced under these unfavorable growing conditions could be from a reallocation of resources away from seed coat structures. However, on the basis of our results within monoculture plots, velvetleaf plants growing along field edges or in field areas having poor crop stands, in which interspecific competition might be minimized, will likely produce heavier and more dormant seeds. Seeds produced from these velvetleaf plants will be most problematic for future crop management in these fields because of increased dormancy and longevity in the soil seed bank. Our findings provide additional support for the need to establish a crop canopy as early as possible before weed germination and emergence because this will not only minimize yield losses, but also the dormancy of weed seeds. Furthermore, special attention and effort should be directed toward not allowing velvetleaf plants growing along field edges or in crop fields with poor stands to produce seed. Conversely, velvetleaf plants escaping control or germinating late in the season but growing under a corn canopy might not require as intense late-season control as is often thought for species having a high proportion of dormant seeds. These plants are not only less capable of reducing crop yields, but many of the seeds they produce will have decreased dormancy, thereby increasing the likelihood of successfully controlling emerging seedlings the following spring. Future work should include more detailed investigations of the structural components of the seed coat and possible genetic controls of seed dormancy in this species. Additional research is also required to determine whether our findings with corn could be extended to other crops with different growth patterns and canopy architectures and to weed species with similar or different seed dormancy mechanisms.

Sources of Materials

[1] Glyphosate, Monsanto Co., 800 North Lindbergh Boulevard, St. Louis, MO 63167.

[2] Peat pots, Griffin Greenhouse and Nursery Supplies, P.O. Box 1588, Auburn, NY 13021.

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