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THE EFFECT OF COMPETITION AND NUTRIENT AVAILABILITY ON THE GROWTH AND REPRODUCTION OF *IPOMOEA HEDERACEA* IN AN ABANDONED OLD FIELD

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SUMMARY

(1) *Ipomoea hederacea*, a common weed in cultivated fields of eastern North America, disappears quickly following abandonment of farming.

(2) The effects of competition and nitrogen addition on the growth and reproduction of *I. hederacea* were studied during the first year of abandonment.

(3) Competition and fertilization had significant absolute effects on almost all biomass variables measured and few affects on the same variables when they were expressed as percentages of total biomass.

(4) Plants in a fertilized and cleared plot were larger and produced more seed than plants from two other treatment plots and the control plot. Plants in an unfertilized and cleared plot were similar to plants in a fertilized plot which had not been cleared. Plants in a plot which was neither fertilized nor cleared were smaller and produced very few seeds compared with plants in the three treated plots.

(5) The results suggest that *I. hederacea* is eliminated during succession because it is a poor competitor for nitrogen, and that the main result of the competition is a reduction in below-ground biomass.

INTRODUCTION

Ruderal species, most of them annuals, are quickly replaced by other plants during secondary succession on productive sites (Grime 1979) and most are able to persist only in regularly disturbed areas or in locally disturbed sites in areas of continuous vegetation cover (Challenor 1965; Werner 1979). Ruderals may be eliminated for a number of reasons (Angevine & Chabot 1979). Many produce seeds which require light for germination and remain dormant until the soil surface is disturbed (Williams 1973; Baskin & Baskin 1983). Germination may also be inhibited by induced dormancy (Crocker 1916) or chemical inhibition (Wilson & Rice 1968). Other ruderals may become established initially, only to be eliminated because they are unable to compete with more aggressive perennials for space or nutrients or both (Raynal & Bazzaz 1975; Werner 1979; Bookman & Mack 1982; Gross & Werner 1982). This process was referred to as 'scramble competition' (Hils & Vankat 1982). Accumulation of autotoxic substrates may also eliminate some species (Quinn 1974).

Many exotic ruderal species have become established in North America (Muenscher 1955); most are restricted to disturbed sites (Gross 1980; Lee & Bazzaz 1980). *Ipomoea hederacea* (L.) Jacq., a tropical American plant (Crowley 1978), has become an established weed throughout eastern North America (House 1908; Houston 1970; Stroller & Wax 1973). In Maryland, it is the only broad-leaved annual of indeterminate growth

(Harper 1977) that is able to persist in fields treated with pre-emergence herbicides (Upchurch, Selman & Webster 1970).

Following abandonment of farm land, *I. hederacea* is quickly eliminated from the successional community and after the first year is restricted to localized disturbed sites. When fallow fields are returned to cultivation, dormant *I. hederacea* seeds germinate (Crowley 1978), and high population densities are quickly re-established (Upchurch, Selman & Webster 1970; Gomes, Chandler & Vaughan 1978). Why is *I. hederacea* eliminated from the successional community so rapidly?

Ipomoea hederacea is a vine and has a profuse branching habit that should enable it to compete for light adequately (Parrish & Bazzaz 1976). Most seeds are dormant when they are shed, but they germinate readily in both the light and dark following a period of winter stratification (Stroller & Wax 1974). The species is, thus, not eliminated because the seeds on the soil surface remain dormant. *Ipomoea hederacea* is a successful competitor in agricultural fields (Crowley & Buchanan 1978) but little is known about its ability to compete for water and nutrients in abandoned fields. Parrish & Bazzaz (1976) suggested that *I. hederacea* is an ineffective competitor for nutrients and the purpose of this study was to test the hypothesis that the species is eliminated, or becomes a minor species in the vegetation of abandoned fields, because it is a poor competitor for nitrogen.

MATERIALS AND METHODS

The research was conducted at the Smithsonian Environmental Research Center on the inner coastal plain of Chesapeake Bay approximately 14·5 km south of Annapolis, Anne Arundel County, Maryland (38°53′20″N, 76°33′20″W). The study area was a portion of a maize (*Zea mays*) field that was in the first year of abandonment following more than 15 years of continuous maize cultivation. Maize was harvested in autumn of 1980 and no cultivation followed until this study began. *Ipomoea hederacea* was well established in the field and occurred in 69 of 100 plots (each of 1 m^2) that were sampled prior to abandonment. Four areas were chosen and each was divided into 400 plots each 1 × 1 m. In each area, all the 400 plots received one of the following treatments: (i) F-W, fertilizer added and all plants removed; (ii) NF-W, no fertilizer added and all plants removed; (iii) F-NW, fertilizer added and no plants removed; and (iv) (control) NF-NW, no fertilizer added and no plants removed. Commercial-nitrogen fertilizer (Sudbury Laboratory, Sudbury, Massachusetts) was applied to each plot in June, July, and August at a rate of 11 g N m^{-2}. In the middle of each plot (1600 total) was placed a bamboo stake by which were sown *I. hederacea* seeds. After the seeds had germinated, all but one plant was removed from each plot. On three sampling dates, ten plots were selected randomly from each treatment and the plants were harvested. The F-W and NF-W plots were maintained free of competitors throughout the growing season.

Harvested plants were divided into the following components: leaves; stems; flower buds; flowers; fruits; seeds; and roots, and dried at 80 °C to constant weight. In addition, stem lengths were measured and the numbers of leaves, stems, flower buds, flowers, fruits, and seeds were counted. Analyses of variance were performed on each variable to determine if there were effects due to the presence of other vegetation, and referred to as competition (C), fertilization (F), and time (T), with interaction effects between F and T and between C and T. Analyses were performed on arc sin transformed and untransformed data but, because there were no differences in the results, untransformed data only are presented. Analysis of variance tests were also performed on: total weight (the sum of stem, leaf, flower buds, flowers, fruits, and root weights); vegetative growth (the sum of stem, leaf and root weights); sexual reproductive effort (the sum of flower bud, flower, fruit, and seed weights); and root to shoot quotient (the sum of weights of stem, leaf and reproductive parts divided into the root weight). To determine if there were shifts in the amount of weight allocated to each plant component, analyses of variance were also performed on stem, fruit, bud, flower, seed, vegetative growth and reproductive effort weights, all as percentages of total weight.

On sample day 95, all vegetation was removed from ten (50 × 50 cm) quadrats given each of F-NW and NF-NW treatments. Each quadrat was positioned so that a planted *I. hederacea* was at the centre. The vegetation was clipped at the ground surface, separated by species in the laboratory, and dried at 80 °C to constant weight. Composite samples of the vegetation were prepared for nitrogen analyses by grinding in a Wiley Mill. The *I. hederacea* plants from each area were prepared separately for nitrogen analysis, as were *I. hereracea* plants collected in the nearby field. All nitrogen analyses were performed in triplicate by the National Marine Fisheries Laboratory at Beaufort, North Carolina using spark emission spectroscopy. Limits of detection for the spectroscope are 0–400 μg N. The coefficient of variation for replicate samples is 10%, which includes errors associated with sample preparation as well as analytical error.

RESULTS

Fertilization significantly affected all biomass variables except number and weight of flower buds and weight of flowers (Table 1). When biomass variables were converted to percentages of the total biomass, only the percentage root weight was significantly affected by fertilization (Table 1). The presence of other vegetation significantly affected all biomass and number variables except the weight of fruits, while among the percentage variables only the percentage weight of leaves and roots were significantly affected (Table 1). All biomass and percentage variables except the weight of fruits and sexual reproductive effort changed significantly with time (Table 1). In general, the interaction effects were fewer than the main effects. There were eleven significant interactions between fertilization and time and nineteen significant interactions between competition and time (Table 1). The biomass, number, and percentage values for almost all variables were in the order F-W > NF-W > F-NW > NF-NW, and the values almost always increased from sample day 34 to sample day 95 (Figs 1 & 2).

Because patterns were constant for almost all variables, total weight will be used to demonstrate the effects of fertilization, competition and time. Fertilization effects can be demonstrated by comparing plants in the F-W and NF-W plots and plants in the F-NW and NF-NW plots. *Ipomoea hederacea* plants in the F-W plot were 4·5, 2·3 and 8·7 times larger than plants in the NF-W plot on sample days 34, 63 and 95, respectively (Fig. 3). Fertilization effects were even more pronounced in the uncleared plots, where plants in the F-NW plot weighed 57·3 and 62·9 times more than plants in the NF-NW plot on sample days 63 and 95, respectively. Plant weights in the same two plots were not different on sample day 34 (Fig. 3), indicating that the fertilization effect occurred later in uncleared plots.

Competition effects can be shown by comparing plants in the F-W and F-NW plots and plants in the NF-W and NF-NW plots. The mean plant weight was reduced by 48·5, 4·7 and 9·5 times on the three sample dates in the F-NW plot compared with plants in the F-W

TABLE 1. Results of analysis of variance tests in an experiment comparing the effects of fertilization and competition on biomass variables, per plant of *Ipomoea hederacea* in Maryland, U.S.A.

	Main effects			Interactions	
	Fertilization (F)	Competition (C)	Time (T)	F × T	C × T
Stem length	**	***	***	*	***
Stem weight	***	***	***	***	***
Leaf number	***	***	***	N.S.	**
Leaf weight	***	***	**	*	**
Number of flower buds	N.S.	***	***	N.S.	***
Flower bud weight	N.S.	***	***	N.S.	***
Number of flowers	*	***	***	N.S.	***
Weight of flowers	N.S.	***	***	N.S.	***
Number of fruits	**	**	**	*	*
Weight of fruits	*	N.S.	N.S.	N.S.	N.S.
Number of seeds	***	***	***	***	***
Weight of seeds	***	***	***	***	***
Number of branches	***	***	***	**	***
Root weight	**	***	***	N.S.	***
Total vegetative weight	***	***	***	***	***
Sexual reproductive effort	*	*	N.S.	N.S.	N.S.
Root-Shoot quotient	**	***	***	N.S.	**
Weight of stems (% of total)	N.S.	N.S.	***	N.S.	***
Weight of leaves (% of total)	N.S.	***	***	*	***
Weight of roots (% of total)	***	***	***	*	*
Weight of buds (% of total)	N.S.	N.S.	***	*	N.S.
Weight of flowers (% of total)	N.S.	N.S.	***	N.S.	*
Weight of fruits (% of total)	N.S.	N.S.	***	N.S.	N.S.
Weight of seeds (% of total)	N.S.	N.S.	***	N.S.	N.S.
Vegetative growth (% of total)	N.S.	N.S.	***	N.S.	N.S.
Sexual reproduction effort (% of total)	N.S.	N.S.	***	N.S.	N.S.

Significance symbols: *, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$; ***, $P < 0{\cdot}001$; N.S., not significant ($P \geqslant 0{\cdot}05$).

plot. Competition effects were even more severe in the unfertilized plots as plants in the NF-NW plot were 10·7, 120 and 68·2 times smaller than plants in the NF-W plot.

Fertilization-time and competition-time interactions were obvious for all treatments except NF-NW (Fig. 3). Evidence for fertilization-competition interactions, which could not be tested significantly, was seen for plants in the NF-W and F-NW plots compared with plants in the F-W and NF-NW plots. Plants in the NF-W plot were larger than plants in the F-NW plot by sample day 63 (Fig. 3), suggesting that competition had a greater effect in reducing growth than fertilization did in increasing growth, but there were no differences between plants in the same plots on sample day 95 (Fig. 3), suggesting that the two test variables had equal and opposite effects. The same time and treatment relationships were found for almost all weight and number variables (Fig. 1) except root-shoot quotients. The root-shoot quotients were larger for plants in uncleared plots

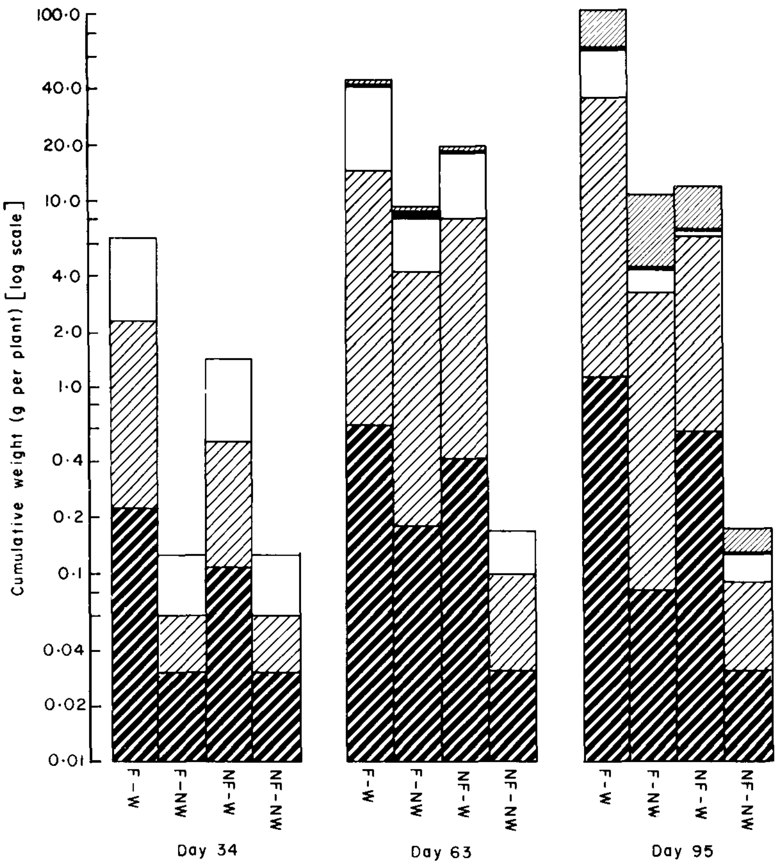

FIG 1. Cumulative mean weight of roots, stems, leaves, buds and flowers, and fruits and seeds for *Ipomoea hederacea* on sample days 34, 63, and 95 in plots on an old field in Maryland, U.S.A. Sample sites are: F-W, fertilized and cleared; F-NW, fertilized and uncleared, NF-W, unfertilized and cleared; NF-NW, unfertilized and uncleared; (▩), fruits and seeds; (■), buds and flowers; (□), leaves; (▨), stems, (▨), roots.

than in the cleared plots (means 0·38 and 0·15 respectively) on the first sampling date (Fig. 4), but there were no differences between plants in NF-W and F-NW plots. The root-shoot quotients of plants in the NF-NW plot continued to be higher on the second and third sample dates while those of plants in the F-NW plot declined by sample day 63 and were similar to those of plants in the F-W plots on sample day 95.

Plants had produced mature seeds at all sites by sample day 95, but there were large between-plot differences in seed production. A mean of only 2·0 $\pm$ 6 (1 S.E., $n = 10$) seeds per plant were produced in the NF-NW plot, compared with 677 $\pm$ 148 in the F-W plot. There were no differences between the mean number of seeds in the NF-W plots (138 $\pm$ 47) compared with the F-NW plots (147 $\pm$ 38), although both values were smaller than the number of seeds (315 $\pm$ 86) on plants in the nearby maize field which, however, still had only half the number of seeds found on plants in the F-W plot.

Cumulative percentage allocations for weight components are shown in Fig. 2. The only

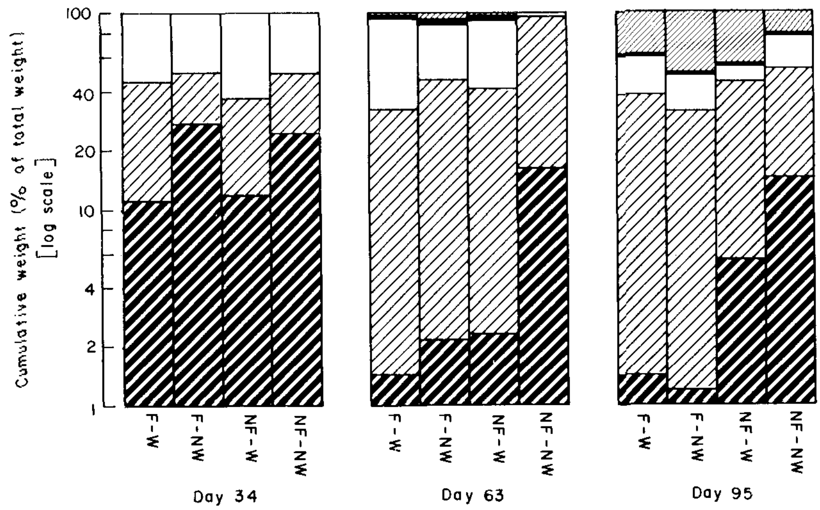

FIG. 2. Cumulative weights as percentages of total weight per plant of roots, stems, buds and flowers, and fruits and seeds of *Ipomoea hederacea* in plots on an old field in Maryland, U.S.A. on sample days 34, 63, and 95. Symbols as in Fig. 1.

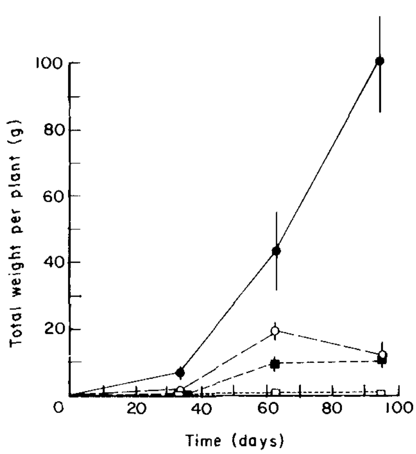

FIG. 3. Mean (±1 S.E., $n = 10$) total weight of *Ipomoea hederacea* plants in treatment plots on an old field in Maryland, U.S.A., on sample days 34, 63, and 95. Symbols: (●), F-W; (■), NF-W (○), F-NW; (□), NF-NW; (F), fertilized; (W), weeded; (N), not.

significant fertilization effect was for percentage root weight (Table 1). Plants in the unfertilized plots allocated more biomass to roots (12·3 ± 1·5%) (±1 S.E., $n = 10$) than plants in the fertilized plots (7·7 ± 2·1%). Competition effects were significant for percentage leaf biomass and percentage root biomass. Plants in the two cleared plots (F-W and NF-W) had significantly more biomass in leaves (44·3 ± 4·1%) than did plants in the uncleared (F-NW, NF-NW) plots (36·7 ± 3·0%). Plants in the uncleared plots allocated more biomass to roots (14·5 ± 2·1%) than plants in the cleared plots (5·9 ± 1·5%).

Table 2 shows the density and biomass of plants in the F-NW and NF-NW plots on sample day 95. Approximately twenty-five species occured in the plots sampled in the

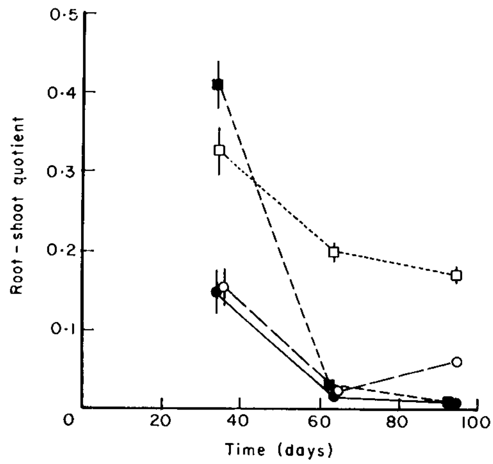

FIG. 4. Mean root-shoot quotients (± S.E., $n = 10$) for *Ipomoea hederacea* in plots on an old field in Maryland, U.S.A., on sample days 34, 63, and 95. Symbols as in Fig. 3.

TABLE 2. The mean above-ground dry weight biomass (g m^{-2}) of plants in two unweeded areas (NW) in an experiment in Maryland, U.S.A., in which plots were either fertilized (F) or unfertilized (NF). Values for mean total density (plants $m^{-2} \pm$ 1 S.E., $n = 10$) and biomass (g $m^{-2} \pm$ 1 S.E., $n = 10$) are also given. A dash (—) indicates that the species was absent. Nomenclature follows Radford *et al.* (1968).

Species	Plot F-NW	Plot NF-NW
Acer rubrum	0·02	—
Ambrosia artemisiifolia	0·34	5·81
Aster sp.	0·03	—
Bidens bipinnata	1·85	—
Campsis radicans	4·00	11·11
Cyperaceae	0·04	0·05
Erigeron canadensis	85·27	38·05
Ipomoea sp.	0·03	0·37
Juncus tenuis	0·29	0·37
Liquidambar styraciflua	0·07	0·11
Oenothera sp.	0·40	6·11
Panicum sp.	0·05	—
Perilla frutescens	—	0·24
Phytolacca americana	0·02	—
Polygonum pennsylvanicum	2·27	—
Prunus serotina	0·04	—
Rumex acetosella	0·02	—
Rumex sp.	—	0·90
Setaria sp.	0·41	—
Solanum caroliniense	9·67	18·69
Trifolium sp.	2·53	0·75
Trifolium repens	—	0·01
Poaceae	0·29	3·00
Unidentified seedlings	0·01	0·06
Mean total density (plants m^{-2})	87 ± 13	60 ± 11
Mean total biomass (g m^{-2})	441 ± 144	342 ± 66

F-NW area compared with approximately fifteen species in the NF-NW area. *Erigeron canadensis L.* and *Solanum caroliniense* L. dominated both areas. Although the differences were not significant, both mean density and mean biomass were higher in the F-NW area.

TABLE 3. Nitrogen concentrations of *Ipomoea hederacea* subjected to combinations of fertilization (F) and removal of competition (W), or lack of both (NF, NW) and in the adjacent maize field in Maryland, U.S.A. Nitrogen concentrations are also given (as percentages of dry weight) for vegetation in the two uncleared areas. All values are mean (± 1 S.E., $n = 6$).

	F-W	NF-W	F-NW	NF-NW	Maize field
I. hederacea	3·23 ± 0·19	2·34 ± 0·04	3·28 ± 0·28	1·86 ± 0·23	2·64 ± 0·01
Other plants	—	—	2·64 ± 0·02	1·73 ± 0·01	—

Ipomoea hederacea and other plants in the F-NW area had higher tissue-nitrogen concentrations than plants in the NF-NW area (Table 3). There were no differences in nitrogen concentrations of *I. hederacea* in the F-NW and F-W areas. *Ipomoea hederacea* in the NF-W area had lower nitrogen concentrations (as percentage of dry weight) (2·34 ± 0·04%) (±1 S.E., $n = 6$) than plants in the fertilized plots, similar to *I. hederacea* in the maize field, and higher than *I. hederacea* in the NF-NW area.

DISCUSSION

Like other ruderal species found in arable fields or disturbed sites (Parrish & Buzzaz 1976; Gross 1980), *Ipomoea hederacea* showed a significant reduction in growth and reproduction due to interspecific competition. Negative effects due to competition were, however, somewhat ameliorated by the addition of nitrogen fertilizer. These results extend the suggestion of Parrish & Bazzaz (1976) that *I. hederacea* is a poor competitor for nutrients even though, as a vine, it should be able to compete successfully for light. Parrish & Bazzaz (1976) also reported that *I. hederacea* contains proportionally higher tissue nutrient concentrations than do other old field species, a result which suggests that *I. hederacea* has a high N requirement. In this study, *I. hederacea* also had slightly higher tissue-N concentrations than competing plants in its immediate environment (Table 3). With the addition of fertilizer, *I. hederacea* was apparently able to compete successfully for nitrogen, and plants in the F-NW plots were almost identical in size and reproductive output to plants in the NF-W plots (Figs 1 & 2). These results agree with the finding of Raynal & Bazzaz (1975) that competition for nutrients is one of the most important processes in early stages of old field succession. Why can *I. hederacea* not successfully compete with other species?

Since *Ipomoea hederacea* is a vine, it should not be eliminated through competition for light (Quinn 1974; Parrish & Bazzaz 1976) but, like many old-field species, it has a very small root-shoot quotient compared with perennial species (Abrahamson 1979). The mean (for the three sample dates) root-shoot quotient ranged from 0·18 to 0·35 for plants in the NF-NW area, which is near the mean of 0·17 given by Abrahamson (1979) for old-field annuals. Plants in the NF-NW area had higher quotients throughout the study (Fig. 4). Plants in the F-NW plots also had higher quotients on sample day 34, but by sample day 63 the quotients had declined to values similar to plants in the F-W and NF-NW plots (Fig. 4). This suggests that the plants in the NF-NW plots produced more root biomass in response to nitrogen limitation. Moisture could also have been limiting, but Parrish & Bazzaz (1976), James, Oliver & Chandler (1977), and Whigham & Orbach (1981) found that water did not limit the growth of *I. hederacea* or any old-field species when they were grown in competition. Nutrients other than nitrogen could limit *I. hederacea* growth, but this seems unlikely as Parrish & Bazzaz (1976) found that *I. hederacea* had proportionally lower tissue-nutrient concentrations for other macro-nutrients.

Ipomoea hederacea is eliminated from early successional communities because it cannot compete for nutrients. Plants in 1-year old abandoned fields are stunted and produce very few seeds. For *I. hederacea* to persist in the successional community, large numbers of seeds would have to be produced annually since buried seeds do not germinate (Gomes, Chandler & Vaughan 1978). Because few, if any, seeds are produced by plants in abandoned fields, the species would be eliminated until the next disturbance. It is not known how long a field would have to remain undisturbed before the buried seed pool would be depleted (Stroller & Wax 1974; Harper 1977). Viable *I. hederacea* seeds may be found in the top 20 cm of soil that has been undisturbed for at least 10 years.

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REFERENCES

Abrahamson, W. G. (1979). Patterns of resource allocation in wildflower populations of fields and woods. *American Journal of Botany*, **66,** 71–79.

Angevine, M. W. & Chabot, B. F. (1979). Seed germination syndrome in higher plants. *Topics in Plant Population Biology* (Ed. By O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven), pp. 188–207. Columbia University Press, New York.

Baskin, J. M. & Baskin, C. C. (1983). Germination ecology of *Veronica arvensis*. *Journal of Ecology*, **71,** 57–68.

Bookman, P. A. & Mack, R. N. (1982). Root interaction between *Bromus tectorum* and *Poa pratensis*: a three dimensional analysis. *Ecology*, **63,** 640–646.

Challenor, R. J. (1965). Emergence of weed seedlings in the field and the effects of different frequencies of cultivation. *Report of the Seventh British Weed Control Conference*, pp. 599–606. British Crop Protection Council, Brighton.

Crocker, W. (1916). Mechanisms of dormancy in seeds. *American Journal of Botany*, **3,** 99–120.

Crowley, R. H. (1978). *Ecological factors contributing to the prevalence of morning glories* (Ipomoea *spp.) as weeds*. Ph.D. thesis, Auburn University.

Crowley, R. H. & Buchanan, G. B. (1978). Competition of four morning glory (*Ipomoea* spp.) with cotton (*Gossypium hirsutum*). *Weed Science*, **26,** 484–488.

Gomes, L. F., Chandler, J. M. & Vaughan, C. E. (1978). Aspects of germination, emergence, and seed production of three *Ipomoea* taxa. *Weed Science*, **26,** 245–248.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, New York.

Gross, K. L. (1980). Colonization of *Verbascum thapsus* (mullein) of an oilfield in Michigan: experiments on the effects of vegetation. *Journal of Ecology*, **68,** 919–927.

Gross, K. L. & Werner, P. A. (1982). Colonizing abilities of 'biennial' plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology*, **63,** 921–931.

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

Hils, M. H. & Vankat, J. L. (1982). Species removals from a first-year old-field plant community. *Ecology*, **63,** 705–711.

House, H. O. (1908). The North American species of the genus *Ipomoea*. *Annals of the New York Academy of Science*, **18,** 181–263.

Houston, W. (1970). The ten worst weeds of field crops: morning glories. *Crop Soils*, **23,** 9–10.

James, T. A., Oliver, L. R. & Chandler, J. M. (1977). Soil moisture competition between four morning glory species and cotton. *Proceedings of the Southern Weed Science Society*, **30,** 363.

Lee, T. D. & Bazzaz, F. A. (1980). Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *Journal of Ecology*, **68,** 813–821.

Muenscher, W. C. (1955). *Weeds*. Macmillan, New York.

Parrish, J. A. D. & Bazzaz, F. A. (1976). Underground niche separation in successional plants. *Ecology*, **57**, 1281–88.

Quinn, J. A. (1974). *Convolvulus sepium* in old field succession on the New Jersey Piedmont. *Bulletin Torrey Botanical Club*, **101**, 89–95.

Radford, A. E., Ahles, H. E. & Bell, C. R. (1968). *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapel Hill.

Raynal, D. J. & Bazzaz F. A. (1975). Interference of winter annuals with *Ambrosia artemisiifolia* in early successional fields. *Ecology*, **56**, 35–49.

Stroller, E. W. & Wax, L. M. (1973). Periodicity of germination and emergence of some annual weeds. *Weed Science*, **21**, 574–580.

Stroller, E. W. & Wax, L. M. (1974). Dormancy changes and the fate of some annual weed infestations under field conditions. *Weed Science*, **18**, 206–214.

Upchurch, R. P., Selman, F. L. & Webster, H. L. (1970). Utility of maintained weed infestations under field conditions. *Weed Science*, **18**, 206–214.

Werner, P. A. (1979). Competition and coexistence of similar species. *Topics in Plant Population Biology* (Ed. by O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven), pp. 287–310. Columbia University Press, New York.

Whigham, D. F. & Orbach, D. (1981). Ecological studies of an old-field weed: *Ipomoea hederacea*. *The Association of Southeastern Biologists Bulletin*, **28**, 73.

Williams, E. D. (1973). Seed germination of *Agrostis gigantea* Roth. *Weed Research*, **13**, 310–324.

Wilson, R. E. & Rice, E. L. (1968). Allelopathy as expressed by *Helianthus annus* and its role in old-field succession. *Bulletin of the Torrey Botanical Club*, **95**, 432–48.

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