

# EXPERIMENTAL ECOLOGICAL GENETICS IN *PLANTAGO*. III. GENETIC VARIATION AND DEMOGRAPHY IN RELATION TO SURVIVAL OF *PLANTAGO CORDATA*, A RARE SPECIES

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## ABSTRACT

*Plantago cordata*, the heart-leaved plantain, is a species of woodland streams that was formerly widespread in the eastern United States, but is now restricted to a few widely scattered localities. Visits to previously sampled sites confirmed that the species is on the decline. Detailed studies were made of populations on one stream system in North Carolina. Demographic studies of an originally vigorous population on a gravel bar showed that the population declined in numbers, average plant size, and reproductive output. The overall population along the whole stream system showed much less change, suggesting frequent localised shifts in population number. Morphological measurements on plants grown from seed under standard conditions showed genetic differentiation between populations within the stream system, as well as extensive genetic variation within populations. Measurements of reproductive effort on field-collected and herbarium specimens showed that *P. cordata* had the fewest seeds per unit leaf area of any *Plantago* species studied. A high rate of habitat destruction, subsequent high adult mortality but low reproductive output, low dormancy and low dispersal capacity between stream systems appeared to be the major reasons for the decline of the species. The requirement of the species for large leaves to intercept light, and extensive roots for anchorage, places limits on evolutionary shifts towards greater reproductive effort. Changes in the dispersal mechanism would entail a major evolutionary reorganisation of the present specialised water dispersal mechanism based on two seeds joined by a spongy placenta. It is emphasised that there is no a priori reason why evolutionary shifts should be more rapid in declining than in stable or increasing populations. Unlike the many weedy species in the genus, *P. cordata* appears to have been adapted to long-standing, stable stream environments of climax hardwood forests, and in spite of considerable physiological flexibility, has a life cycle that is not preadapted to shifting, highly unstable, man-made environments.

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## INTRODUCTION

In spite of the continually growing interest in rare and vanishing plants it is remarkable that almost no studies beyond anecdotal reports exist in the literature of the ecology, population biology, and genetics of rare species. Such information is of considerable interest since it bears on problems of extinction at the population and evolutionary levels. It is pertinent to ask for what reasons a population (or species) loses in the ecological and evolutionary race and how a population 'senses' its own decline and what genetic responses might be expected (cf. Cole, 1954). In addition what impact will persistent rarity have on the evolution of a species, for example with regard to predators and pollinators. As has been pointed out by Antonovics (1976), plants are particularly suited to answering such questions since, as well as being experimentally convenient, they are readily located and can be sampled in various non-destructive ways. From a more practical viewpoint, such studies may be expected to yield information on ecology and life-history that is pertinent to the preservation of the species in question; and such studies may point to general factors, both in the environment and in the biology of a species, that are likely to result in extinction.

The present study examines these questions in relation to *Plantago cordata* Lam., the heart-leaved plantain. This species is characterised by a widespread geographical range, within which it is highly localised. It is found from the Hudson River in New York to the east, south into northern Florida, west as far as central Missouri, and to the north throughout the midwestern states and into Ontario. Despite this wide range, only about three dozen populations of this species have been reported (Svenson, 1935; Clute, 1942; Harper, 1945; Godfrey, 1961; Basset, 1967; Tessene, 1969). It seems to be most common in Missouri where Steyermark (1963) reported it as 'abundant along streambeds.' Tessene (1969) regards *P. cordata* as a victim of civilisation, once common but now becoming extinct. Visiting localities where *P. cordata* had been collected in the past, he found that in many cases the plant was absent and the habitat destroyed by man's activities. The species appears to have become extinct in Michigan (Wagner *et al.*, 1977) and Virginia (Tessene, 1969). The rarity of *P. cordata* is in contrast to other species in the same genus, such as *P. lanceolata*, *P. major*, and *P. rugelii*, which are well known as successful, worldwide weeds.

Typically, *P. cordata* is found growing partially or wholly submerged on gravel bars and along the banks of shallow rock-bottomed streams. The plant may also be found in low-lying woods, usually on the flood plain of a nearby stream. It forms a perennial rosette with a large fleshy upright rhizome and long, thick, cord-like roots which penetrate among, and cling to, rocks on the stream bed. Leaf size and shape vary considerably with season and environmental conditions. The plants range from having large leaves (up to 75 cm in total length), forming 'giant' rosettes in the summer, to bract-like smaller leaves (less than 8 cm in total length) in the winter.

Plants flower in mid to late April and may undergo vegetative reproduction by offshoots from the main stem. Further descriptions of *P. cordata* and its habitat are given by Basset (1967), Basset & Crompton (1968) and Tessene (1969).

This study was undertaken both to investigate possible causes of the rarity of *P. cordata* and to gain insight into population biology and genetic variation of a rare, rather than a common, plantain species. During the course of the study natural populations of *P. cordata* were visited throughout much of its range and detailed studies were made on one population with regard to longevity, reproductive effort, small-scale population differentiation, and genetic variation for quantitative traits.

#### MATERIALS AND METHODS

The sites visited during this study are listed in Table 1 and include localities within much of the range of *P. cordata*. In North Carolina, this species occurs in scattered

TABLE 1  
SITES FROM WHICH *P. cordata* HAS BEEN RECORDED AND WHICH WERE INVESTIGATED DURING THIS STUDY. IN ALL OF THESE SITES THE PLANTS WERE LOCATED ON A STREAM

<i>Sites visited</i>	<i>Results</i>	<i>Comments</i>
North Carolina Beaverdam Creek, Davidson Co.	Present	Studied in present report.
Ohio 3.2 km E of Peebles, Adams Co.	Present	Plants found in stream at back of quarry, but infrequent. Population did not appear as large as reported by Tessene (1969). Portion of the stream bulldozed, the rest encroached upon by piles of stones from quarry.
Indiana 11.2 km E of Columbia City, Whitley Co.	Absent	Land mostly cultivated with small polluted streams. Generally the area appeared inhospitable for <i>P. cordata</i> .
Illinois Messenger Woods, Willis Co.	Absent	Area is a park. The only stream was explored from one end to the other. Only <i>P. rugelii</i> found.
Mathiessen State Park, La Salle Co.	Absent	Stream located and explored from one end to the other. Extensive populations of <i>P. rugelii</i> but no <i>P. cordata</i> .
Missouri Sugar Creek, 7.6 km SE of Meta, Maries Co.	Present	All Missouri sites in relatively undisturbed areas.
Sugar Creek, 3.2 km SE of Meta, Osage Co.	Absent	
8.8 km E of Anthonies Mill, Washington Co.	Absent	
Lost Creek, 11.2 km SW of Warrenton, Warren Co.	Present	

populations along approximately 3 km of Beaverdam Creek in the southeastern corner of Davidson County (Fig. 1); it has also been reported, but we have not found it, in other parts of the Yadkin River System. The populations on Beaverdam Creek were the source of all material used in this study.

The site of the demographic studies was a gravel bar at the point along the stream indicated in Fig. 1. At this point, the stream is flowing through a bottomland forest. All the plants in a  $3 \times 5 \text{ m}^2$  area were mapped intermittently from April 1974 to April 1977, a period that included four flowering seasons (April readings). On each visit the area was checked for new individuals and plants present were scored for number of leaves, inflorescences, and rosettes. In addition, a more general total population census was made of all plants between the bridge on Slate Mine road and the hog farm, in April 1976, September 1977 and April 1978. The total number of individuals on this stretch of the river was counted, with no attempt made to follow specific plants or their phenology.

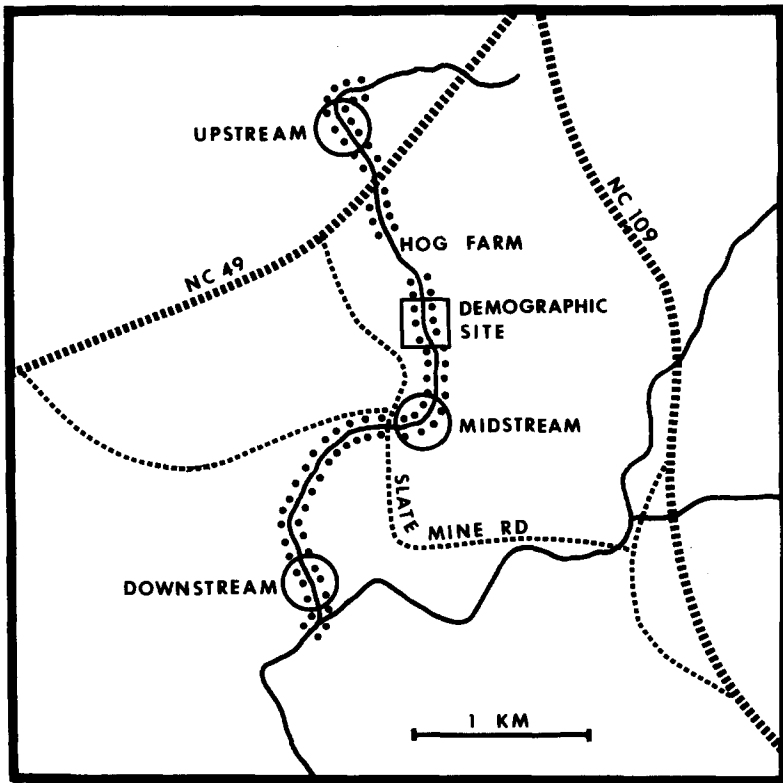


Fig. 1. Map of southwest corner of Davidson County, North Carolina, showing regions (dotted) of Beaverdam Creek where *P. cordata* is found. Positions of the demographic study site, and of the upstream, midstream, and downstream sampling sites are indicated.

In May 1974, seeds were collected by family (i.e. common female parent) from three populations (Fig. 1), indicated as upstream (25 families) midstream (21 families) and downstream (5 families). The upstream population (U) is located 180 m upstream from point of intersection of creek with North Carolina state road 49, and the midstream population (M) is about 2.4 km downstream from U just upstream from the intersection of the creek with Slate Mine Road. Both populations are on slate-bottomed streams in fairly undisturbed woods. The downstream population (D), about 1.2 km from M, is composed of widely scattered individuals in an area where the stream has been rerouted due to slate-mining activities. In contrast to U and M, the stream at this point is clay-bottomed and quite exposed. On 25 May 1974, approximately 5 plants from each family were grown from seed in flats in the phytotron, on a long day (16 h) photoperiod. The seedlings were transplanted to individual pots after 21 days. Measurements were made after 36, 81, and 221 days on leaf number, and total length, width, and petiole length of the fourth leaf from the centre of the rosette. At 221 days the plants were measured for inflorescence and shoot number, and a pigmentation index was applied to each plant according to the amount of pigmentation in the petiole (1–5, 5 being heavily pigmented). These data were subjected to the simultaneous test procedure of Gabriel & Vax (1970) for multivariate and univariate comparisons of the three individual populations using analysis of variance.

TABLE 2

TRANSPLANT SITES AND RESULTS. ADULT INDIVIDUALS RAISED FROM SEED IN THE PHYTOTRON WERE TRANSPLANTED DURING SPRING 1975 AND THEN CHECKED DURING SPRING 1977

Site	No. planted	No. surviving
1. Creek in front yard, Parkwood, Durham	9	3 <sup>a</sup>
2. Drainage ditch at roadside, Durham	4	4 <sup>a</sup>
3. Creek off North Flat River, Person Co.	18	8 <sup>a</sup>
4. New Hope Creek, Orange Co.	18	0
5. Silver Hill Mine, in creek, Davidson Co.	9	0
6. Healing Springs, in creek, Davidson Co.	18	3 <sup>a</sup>

<sup>a</sup> Plants flowered.

Following the termination of this study the plants were maintained in the greenhouse until the spring of 1975 when they were transplanted into various stream sites near Durham and in Davidson County (Table 2) to test the ability of adults to survive and grow in environments similar to, but far away from, the Beaverdam Creek area.

Fifteen plants with mature capsules were collected from the M site as part of a comparison of *Plantago* species with regard to reproductive effort (Primack, 1976). Data are presented for five perennial species: two are well-known weeds (*P. rugelii*, *P. major*) and the remaining three (*P. sparsiflora*, *P. tweedyi*, *P. eriopoda*) are in the same section of the genus (*Palaeopsyllium*) as *P. cordata*. The sites of the populations from which plants were obtained for these species are given in Table 3.

The plants collected were all fruiting individuals and were measured for total leaf area, number of inflorescences per individual, number of capsules per inflorescence (based on the number of capsules in the median sized inflorescence), number of seeds per capsule (based on three capsules per plant), and average seed weight (based on 10 seeds). The capsule number, seed number, and seed weight per unit leaf area were then derived from these data for each of the six species. Similar data were obtained for each of these six species from herbarium specimens using the methods of Primack (1976).

TABLE 3

REPRODUCTIVE EFFORT IN NATURAL POPULATIONS AND HERBARIUM SPECIMENS OF SIX *Plantago* SPECIES EXPRESSED IN TERMS OF THE NUMBER OF SEEDS, AND mg OF SEEDS PRODUCED PER 10 cm<sup>2</sup> OF LEAVES. THE MEANS AND STANDARD ERRORS ARE PRESENTED FOR THE LOGARITHMICALLY TRANSFORMED VALUES. SAMPLE SIZES ARE IN PARENTHESES

	<i>No. seeds/10 cm<sup>2</sup></i>	<i>mg seeds/10 cm<sup>2</sup></i>
NATURAL POPULATIONS		
<i>P. cordata</i> (stream edge, Denton, NC)	0.76 ± 0.06 (15)	0.98 ± 0.06 (4)
<i>P. sparsiflora</i> (roadside near pinewoods, Georgetown, SC)	1.02 ± 0.04 (19)	0.96 ± 0.04 (19)
<i>P. tweedyi</i> (mountain meadow, Rabbit Ears Pass, Colo.)	2.15 ± 0.09 (18)	—
<i>P. eriopoda</i> (mountain meadow, Jefferson, Park Co., Colo.)	1.77 ± 0.14 (4)	—
<i>P. rugelii</i> (lawn, Durham, NC)	2.24 ± 0.05 (20)	1.79 ± 0.06 (20)
<i>P. major</i> (field, Newton, Mass.)	2.25 ± 0.08 (20)	1.44 ± 0.08 (20)
HERBARIUM SPECIMENS		
<i>P. cordata</i>	1.15 ± 0.06 (20)	1.29 ± 0.10 (7)
<i>P. sparsiflora</i>	1.42 ± 0.10 (14)	1.33 ± 0.11 (7)
<i>P. tweedyi</i>	2.03 ± 0.07 (20)	1.57 ± 0.17 (4)
<i>P. eriopoda</i>	1.62 ± 0.08 (20)	1.51 ± 0.10 (13)
<i>P. rugelii</i>	2.07 ± 0.09 (18)	1.68 ± 0.10 (16)
<i>P. major</i>	2.50 ± 0.08 (19)	1.67 ± 0.08 (16)

## RESULTS

Nine sites where *P. cordata* had been found by previous workers were visited but this species was found at only four (Table 1). In addition, many streams that appeared suitable were explored in all of the states listed in Table 1, but no additional populations of *P. cordata* were located. The sites in Ohio and Indiana had been highly disturbed by a nearby quarry and farms, respectively. The Illinois and Missouri sites, however, appeared to have undergone no conspicuous habitat destruction since the last collection. These results support the contention (Tessene, 1969) that *P. cordata* is on the decline throughout most of its range except in central Missouri where several flourishing populations were found.

The population size within the demographic study plot declined over four years (Table 4). Only two new plants were seen during this period; one arose from seed and the other sprouted from a root. The major period of mortality was between April

TABLE 4

NUMBER OF PLANTS, PERCENT INDIVIDUALS IN FLOWER, MEAN NUMBER OF INFLORESCENCES PER FLOWERING INDIVIDUAL, AND MEAN NUMBER OF LEAVES PRESENT ON FLOWERING AND NON-FLOWERING PLANTS IN *Plantago cordata* AT THE DEMOGRAPHIC STUDY PLOT ON BEAVER DAM CREEK

Year	No. of plants	% Flowering	Mean number of inflorescences per flowering individual	Mean number of leaves Flowering	Mean number of leaves Non-flowering
1974	54	74	5.08	11.0	6.2
1975	49	65	3.27	9.0	5.7
1976	23	9	1.00	6.5	5.4
1977	19	21	1.50	7.0	4.9

1975 and April 1976. The difference in size between surviving (8.38 leaves) and non-surviving (7.25 leaves) between these periods was not significant ( $t_{47} = 1.323$ ;  $p < 0.2$ ): mortality was essentially random with respect to size. During the study period there was a general reduction in plant size in terms of leaf number (Table 4 and Fig. 2), inflorescence number (Table 4 and Fig. 3) and percentage of

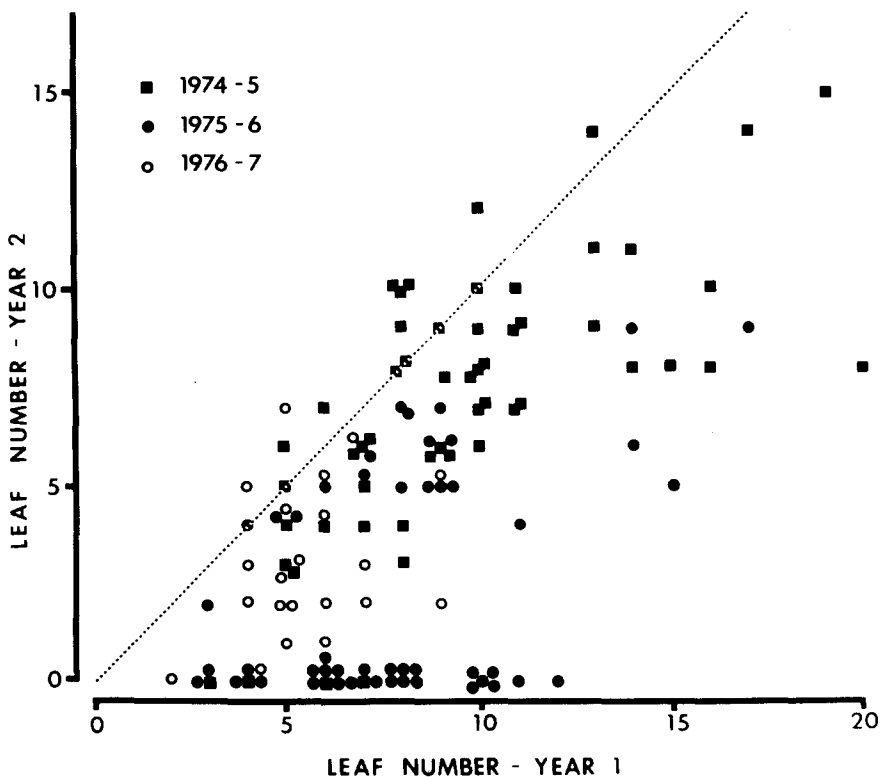


Fig. 2. Leaf number per plant in successive seasons at the demographic study site.

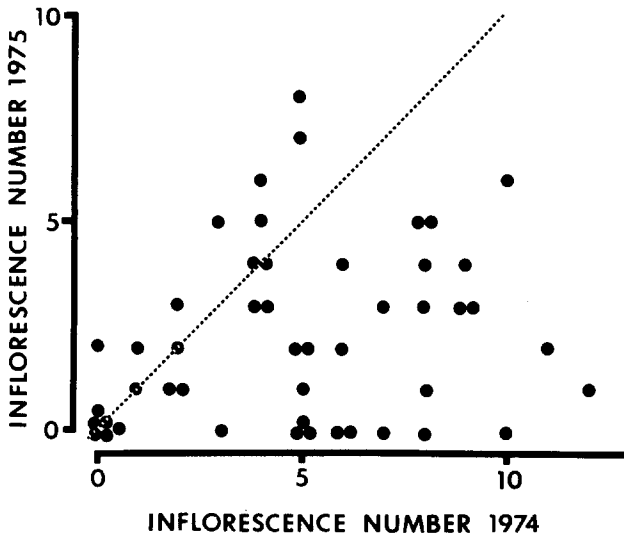


Fig. 3. Inflorescence number per plant in 1974 and 1975 at the demographic study site.

plants in flower (Table 4). This drop in flowering occurred in spite of the fact that the plants were older and at a lower density each year.

The overall population census gave the following results: 1976, 808 individuals; 1977, 597 individuals; 1978, 556 individuals. The population had declined much less than in the demographic study plot.

In the phytotron study, there were significant differences between the upstream (U), midstream (M) and downstream (D) populations (Table 5). Much of the difference between the three populations is to be found in the seedling characters: D in particular appears to differ greatly from U and M in that D seedlings had fewer and smaller leaves. The overall size of the D leaf blades remained significantly smaller than those of U and M through the second set of measurements. The D leaves were significantly narrower than leaves from U and M throughout the experiment. The number of inflorescences per plant increased towards the downstream population, whereas number of leaves decreased, suggesting a cline of increased reproductive effort in populations from further downstream.

There was significant variation between families within populations for 14 of the 15 characters (Table 5). This indicates that there exists a detectable level of genetic variation for these characters within *P. cordata*.

The reproductive effort studies on field-collected and herbarium material showed that *P. cordata* and *P. sparsiflora*, two species which are regarded as rare, had the lowest reproductive effort in both the field and herbarium data (Table 3). The weedy species *P. rugelii* and *P. major* had the highest reproductive efforts.



TABLE 5

MEANS AND STANDARD DEVIATIONS FOR THE FIFTEEN CHARACTERS IN U, M, AND D. GROUPS OF MEANS UNDERLINED ARE NOT SIGNIFICANTLY DIFFERENT ACCORDING TO GABRIELS STP AT THE 0.05 SIGNIFICANCE LEVEL. SAMPLE SIZES ARE INDICATED IN PARENTHESES AT THE HEAD OF THE FIRST THREE COLUMNS. SIGNIFICANCE OF DIFFERENCES BETWEEN FAMILIES WITHIN POPULATIONS BASED ON F RATIO (55 AND 177 DEGREES OF FREEDOM) FOR BETWEEN AND WITHIN FAMILIES

	U (117)		M (97)		D (15)		Significance of differences between families within populations
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	
Leaf number 1	<u>4.9</u>	<u>0.42</u>	<u>4.7</u>	<u>0.58</u>	<u>4.4</u>	<u>0.51</u>	1.55*
Leaf length 1	<u>5.7</u>	<u>1.44</u>	<u>5.5</u>	<u>1.55</u>	<u>4.3</u>	<u>1.35</u>	2.43***
Leaf width 1	<u>2.5</u>	<u>0.66</u>	<u>2.6</u>	<u>0.76</u>	<u>1.8</u>	<u>0.51</u>	2.06***
Petiole length 1	<u>1.2</u>	<u>0.46</u>	<u>1.2</u>	<u>0.48</u>	<u>0.9</u>	<u>0.41</u>	2.77***
Leaf number 2	<u>6.5</u>	<u>1.41</u>	<u>6.6</u>	<u>1.38</u>	<u>6.9</u>	<u>1.30</u>	1.70**
Leaf length 2	<u>19.9</u>	<u>3.84</u>	<u>20.5</u>	<u>4.40</u>	<u>17.8</u>	<u>3.91</u>	2.20***
Leaf width 2	<u>7.7</u>	<u>1.62</u>	<u>7.9</u>	<u>1.81</u>	<u>6.7</u>	<u>0.47</u>	1.22
Petiole length 2	<u>8.8</u>	<u>2.56</u>	<u>9.1</u>	<u>2.67</u>	<u>7.5</u>	<u>2.34</u>	3.10***
Leaf number 3	<u>21.6</u>	<u>10.6</u>	<u>21.2</u>	<u>9.76</u>	<u>19.8</u>	<u>12.8</u>	1.68**
Leaf length 3	<u>19.4</u>	<u>4.33</u>	<u>19.8</u>	<u>4.72</u>	<u>20.2</u>	<u>3.95</u>	1.53*
Leaf width 3	<u>5.5</u>	<u>1.28</u>	<u>5.8</u>	<u>1.50</u>	<u>4.9</u>	<u>0.81</u>	2.17***
Petiole length 3	<u>9.3</u>	<u>3.03</u>	<u>9.4</u>	<u>3.41</u>	<u>10.1</u>	<u>2.48</u>	1.34*
Inflorescence number	<u>2.1</u>	<u>2.82</u>	<u>2.9</u>	<u>2.98</u>	<u>4.1</u>	<u>3.01</u>	2.11***
Rosette number	<u>2.8</u>	<u>1.89</u>	<u>2.9</u>	<u>1.82</u>	<u>2.4</u>	<u>2.41</u>	1.80***
Petiole pigmentation	<u>2.2</u>	<u>0.71</u>	<u>2.2</u>	<u>0.68</u>	<u>2.1</u>	<u>0.52</u>	2.23***

The results of the transplant experiments (Table 2) confirmed that *P. cordata*, if transplanted as an adult, could persist, flower and set fruit in several areas beyond the specific locality where it was found. However, seedling establishment was not observed in any of these transplant sites. More general observations indicated that *P. cordata* is easy to grow both as a greenhouse and garden plant without the requirement for submergence or a specialised watering regime. The species could also grow in standing water. It could be regenerated from root cuttings and from petiole stalks pretreated with IAA (indole 3 acetic acid) (cf. Wu & Antonovics, 1975).

## DISCUSSION

*P. cordata* is listed as an endangered species by the US Department of the Interior (1976) and there is no question that the species is on the decline and becoming restricted to a few widely scattered localities from what was formerly a very widespread distribution. It has become extinct in several states and in others is represented by only one or two localities. Tessene (1969), in an extensive review of the species, records 76 collection localities for the 60-year period from 1840–1900, and only 39 from 1900–1960 in spite of the greatly increased collection rate this century. Tessene (1969) failed to find it in 15 out of 22 sites where it had been collected before, and in our study we failed to find it in five out of nine sites.

At our study site in North Carolina, a general population census was only carried out over two years, in which the population declined by 31 %: however, little can be concluded from this since the study was short-term and no life-history data were obtained with which a population projection might be made. On the particular gravel bar on which detailed demographic studies were carried out, the local subpopulation showed a marked decline. The gravel bar remained superficially unchanged, but there were presumably local changes in substrate composition, water level, or canopy, which were responsible for the decline. Given also the general physical instability of gravel bars, we are left with the view of *P. cordata* as a plant living in a locally unstable habitat. At the local level, subpopulations are probably subjected to frequent extinctions.

The reasons for the decline of any species can be viewed at two levels, namely ecological and evolutionary, i.e. we can ask what factors are responsible for the decline in the population and what are the nature of the evolutionary changes that the species might undergo in response to such a decline. From an ecological viewpoint it is clear that destruction of the habitat is responsible for many of the population extinctions: Tessene (1969) makes an impressive list of such changes. They fall into two categories, namely destruction of stream systems (drainage, ditching, damming and rerouting), and clearing of surrounding woodlands (to make pastures, fields, university campuses, and housing developments). The detrimental effect of such clearance is not exposure to full sun since *P. cordata* is found at times growing in open areas. For example, localised clearing of trees around the Bridge on Beaver Dam Creek has resulted in large, vigorous plants in that area. Instead the effects are probably the result of a changed hydrology. There is an increased frequency and intensity of severe flooding and scouring, and more generally an increase in erosion followed by silting up of formerly rock-bottomed streams. The effects of these on *P. cordata* are probably serious, since it is a broadleaved plant that offers much resistance to flowing water: on Beaver Dam Creek after storms we have seen the leaves become very shredded. It also relies on fibrous roots which clasp rocks for maintaining a foothold when streams flood. Clearly changes in the substrate, an increase in flow rate, or physical destruction of the rocky areas in which it grows will result in plants being destroyed.

Of particular interest is the fact that in some areas where *P. cordata* has disappeared (e.g. Port Huron, Michigan: Tessene, 1969; Missouri sites: present study) the habitat appears superficially still suitable for the species. Here its disappearance may be related either to clearance of woods within the same watershed or other direct pollution effects. That such indirect habitat destruction may be important is very pertinent to establishing sufficiently large areas within which the species could be conserved. In general such 'cryptic' habitat destruction may be far more common than we realise.

Given that populations may be frequently destroyed it is still pertinent to enquire why the species does not re-establish in new areas. Although Tessene (1969) states

the species has an 'apparent lack of ecological plasticity', our transplant experiments suggest that the species could survive in a fairly wide range of habitats. This is supported by the ease with which the plant can be grown under a wide range of conditions. However, in nature, the survival of the species over long periods of time will depend on the formation of new populations in different streams. Yet the establishment of a population on a stream is probably a relatively uncommon event, being dependent upon seed transport from other streams. There are several difficulties inherent in this. First, seeds of *P. cordata* have a limited dormancy period (Tessene, 1969); only three out of thirty seeds germinated after having been dried and stored for three months, in contrast to seeds of other *Plantago* species which showed about 90% germination following the same treatment (Primack, 1976). Tessene (1969) states that the seeds live 'only about a month in storage at 40°F' (4.5°C). This implies that seeds of *P. cordata* must become established as seedlings within a few weeks of being shed. Secondly, the seeds are adapted to water dispersal, in that the two seeds from one capsule remain attached to a spongy placenta. They are therefore well suited to re-establishment within the same river-system, but otherwise have no special mechanism for dispersal across land between streams. Thirdly, such transport between streams would probably have been carried out by large animals and the habitat destruction mentioned earlier would have the synergistic effect of increasing distances between suitable habitats and inhibiting the movement of seed-transporting mammals. And finally, *P. cordata* produces relatively few seeds. In fact it has the fewest seeds per plant and lowest reproductive effort of any *Plantago* species studied (see also, Primack, 1976).

The low reproductive effort of *P. cordata* as well as of *P. sparsiflora*, another rare species from the coastal plain of the Carolinas, raises the question of whether the process of extinction, in that it produces a protracted period of decline in population numbers, has led to the evolution of delayed reproduction and low reproductive effort, as would be predicted from basic theory of life history evolution (Cole, 1954). While this possibility cannot be readily dismissed, at least in the case of *P. cordata*, there are good reasons for predicting a low reproductive effort on purely ecological grounds. There are demands on the species to produce extensive roots for anchorage, to produce large, broad leaves for light interception since it often grows in shade of woodlands, yet its probability of establishment by seed seems highly risky: under these conditions a low investment in reproduction in any one year would be favoured. If the low reproductive effort is in any sense the result of population decline, it is probably at the level of the local subpopulation: at this level there would be selection for persistence and a protracted reproductive output. With regard to *P. sparsiflora*, we know little of its biology: it too is a wetland species, occurring on the coastal plain wet savannahs. The populations we have found have been from roadside drainage ditches. Otherwise the ecology of this species is likely to be very different from that of *P. cordata* and it would repay further study.

Where species have long life-spans and low reproductive rates, an increase in adult

mortality can be disastrous for population numbers. In this regard there are remarkable, almost uncanny, parallels between the population biology of *P. cordata* and the Californian condor, *Gymnogyps californianus* (Mertz, 1971). Both species were widespread and common in the early 1800s but are now highly localised and endangered; both species are large (*P. cordata* may have leaves reportedly as long as 1 m, the largest of any plantain species); both species have low reproductive rates and produce few large seeds/eggs; both species are potentially long-lived (although definitive data on *P. cordata* are scant in this regard). It is therefore likely that species with long life-spans and low reproductive rates are in greater danger of extinction in both plants as well as animals.

It has been frequently postulated that rare species are in some sense genetically depauperate, so that although there may be no particular pressures on them to evolve, they are nonetheless 'losers' in the evolutionary race. The few studies on this subject have provided no convincing evidence for this. For example, Babbel & Selander (1974) found that several edaphically restricted species in Texas had not much lower levels of genetic variation than did closely related species occupying a wider range of habitats. The present study has also revealed both population differences and family differences in a number of morphological traits that are in all likelihood genetically based. Although the possibility of maternal effects cannot be excluded in analyses based on seed collected in the field by female parent, it seems unlikely that such effects by themselves would produce population and family differences of the magnitude observed. Moreover, *P. cordata*, although capable of self-fertilisation (Tessene, 1969; and we have seen isolated individuals set seed in the greenhouse), is highly protogynous; outcrossing certainly occurs frequently in nature. The results therefore suggest that in spite of its rarity, *P. cordata* is not devoid of genetic variability: indeed within populations it is variable for almost every character studied and the differences between populations indicate a degree of localised adaptation that would have been surprising twenty years ago (see Antonovics, 1971). Tessene (1969) concludes on the basis of general observations that there is a 'lack of morphological variability in *P. cordata* throughout its range.' However, the genetic studies reported here show that there is considerable genetic variability for morphological traits.

The evidence of genetic variation begs the question of whether this variation is likely to be useful in the evolutionary survival of the species in response to its changed habitat. The localised differentiation that has occurred is probably important. The downstream population was found in the most extreme disturbed habitat, and it was most different from the midstream and upstream populations which were growing in habitats more 'typical' for *P. cordata*. Its smaller leaves and greater reproductive effort are adaptive for a habitat with greater light intensity, possibly greater flooding, and perhaps greater population turnover.

However, it seems unlikely that *P. cordata* can adapt to the large-scale habitat

destruction that has taken place. Indeed its disappearance is evidence that it has not done so. Such habitat destruction seems to have been more drastic and to have occurred at too great a rate for evolutionary change to keep pace. This is particularly true since the evolutionary changes would have to be complex and would entail important conflicts. For example, increasing its probability of dispersal to new habitats would require a greater seed output. If this were achieved by an increase in resources devoted to reproduction, then presumably there would be a corresponding decrease in leaf area (and hence reduced photosynthesis in what often is already a very shaded habitat) or decrease in root production (and hence reduced anchoring to the substrate). The relative importance of these various pay-offs remains to be quantified, but they would undoubtedly be severe: even within Beaverdam Creek conflicts are seen at the population level between inflorescence and leaf number. If the greater seed output were achieved by partitioning differently resources currently available for reproduction, this would require reorganisation of the placental attachment point that serves as a float and a decrease in seed size. This in turn would have serious consequences. The large seeds are clearly an adaptation to rapid establishment under low light intensity in a shifting river system. Their lack of dormancy is also a clear adaptation to rapid establishment in early spring when water levels and temperatures are moderate and the canopy is not completely closed: partial dormancy with precise control of germination is therefore also unlikely to be adaptive. In the stable stream environments of mature forests, these conflicts are not serious, but when mortality is increased and dispersal becomes more difficult, they become almost insurmountable.

In addition to these difficulties, the species would have to undergo concomitant physiological adjustments and changes in relation to new competitive stresses it may meet. For example, *Plantago rugelii* is frequently a coloniser of semi-open, flood plain areas near creeks. It would presumably serve as a powerful competitor, reducing the probability of *P. cordata* occupying this particular niche. The only evolutionary escape we can visualise is in the direction of plants similar to those in the downstream population at Beaver Dam Creek, i.e. plants in more open habitats, with less premium on leaf area, greater photosynthetic rates and therefore an ability to maintain anchorage, reduced resistance to water flow, and increased seed production. However, it must be emphasised that the species as a whole, or indeed a population, cannot sense its own extinction in any mechanistic sense. There is no particular reason why a population that is declining should undergo any more rapid evolutionary change than one which is constant or even increasing in size: the processes of reproduction and mortality are universally present in all populations. Therefore those individuals which maximise their genetic contribution to future generations relative to that of others (by increasing reproductive output and/or decreasing mortality) will be favoured. There is no *a priori* reason to believe that such differential contribution will be greater in a declining or an increasing

population. Looked at from a broad evolutionary context, extinction is an integral part of the normal evolutionary process, and is not necessarily dependent on drastic environmental change (Van Valen, 1973). One would therefore not anticipate accelerated evolutionary rates in response to declining population size. These arguments also apply in general terms in situations where the population decline is associated with a change in the environment. An altered environment would stimulate evolutionary change regardless of whether the population expands or declines, since now in both circumstances new and different gene combinations would be favoured.

The conservation of *P. cordata* in a greenhouse or botanical garden context should generate no real difficulties. Nor would it seem particularly difficult to re-establish the species in particular streams in view of the relative success of our transplants. Clearly one would like more information about the substrate requirements and hydrological characteristics of appropriate streams, and more information on precisely how specialised the conditions have to be for germination and establishment. But in spite of its rarity it is a flexible and durable species.

We have largely been concerned here with the causes of rarity and extinction, rather than with justifying why a particular species should be conserved. Nevertheless it is appropriate to mention that *P. cordata* is a unique native North American species of *Plantago*. It is the only true semi-aquatic member of the genus in North America, it has many unique morphological features, it is an impressive plant with giant leaves that has considerable horticultural interest, it belongs to a group with herbal and medicinal properties, and it is in a highly diversified genus that is in itself interesting from an evolutionary standpoint (Stebbins & Day, 1967). It is also the one rare plant species that has been the object of considerable scientific study both here and by Tessene (1969). It would therefore be very regrettable if this 'great species of *Plantago* . . . of an incredible magnitude,' as it was described in 1773 by William Bartram (Harper, 1945), one of the early plant explorers, should remain only as an ignoble herbarium specimen.

#### ACKNOWLEDGEMENTS

The authors would like to thank L. Wu for his assistance in the field work, and L. Reinertsen Meagher for her helpful comments on an earlier draft of the manuscript. T. Meagher and R. Primack were supported during this research by National Institute of Health Graduate Traineeships through NIH grant No. GM02007-08 administered by the University Program in Genetics of Duke University. The phytotron studies were supported by National Science Foundation Grants No. GB-28950-1A and No. BMS71-00947-A02. The field work was supported by National Science Foundation grant No. GB35470 to J. Antonovics.

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