update

Plant demography: what do we know?

by Miguel Franco* and Jonathan Silvertown**

It is a curious fact about the history of population biology that botanists were slow to apply demographic analysis to plant populations. This is true, even though the modern founders of this now well-established subject have uncovered antecedents among rangeland scientists, foresters, agronomists, and even the odd ecologist who censused plants (Harper, 1977; White, 1985). A crude indication of the time lag between the development of animal and plant demography is provided by the dates of publication of two review papers that can be considered milestones in their respective subjects. Deevy's *Life Tables for Natural Populations of Animals* was published in 1947 and Harper and White's *The Demography of Plants* was published in 1974. Harper's *Population Biology of Plants* came out in 1977.

What is now known? How far have plant demographers caught up? In the course of a comparative survey of plant demography using published sources we have identified 529 papers covering 585 species. This sample of the literature is not definitive, but it is large enough to allow us to make some judgements about the subject's development. Figure 1 shows the trend in the number of demographic studies published per year over the last fifty years. It omits most of the Soviet literature, which has been catalogued by T.A.Rabotnov (1980–81).

A survey of the literature

This information comes from a bibliographic database we have compiled to help us in a comparative study of plant life history evolution and demography. The database does not contain the demographic data themsevles, and we are still analysing these. Papers vary a great deal in the amount of information they contain and more than a handful of articles with the terms population dynamics or demography in the title contain no such information at all. All papers included in the database contain, as a minimum, information on survivorship of ramets or genets either determined directly or from the age structure of the population. Such information is often found in papers without any keywords in the title or abstract that would allow them to be identified by a computer search without generating many redundant references. We therefore began by manually searching every issue of 20 key botanical and ecological journals published between 1970 and 1985. The papers identified in this way were used to find further papers by scanning the literature cited in them. Since 1985 we have kept the database up-to-date by the use of *Current Contents* and *Current Advances in Ecological and Environmental Sciences*. Each paper identified in our search has been scanned by at least two members of our project team.

Table 1 summarizes the characteristics of over 550 species. Breaking the sample down by biogeographic regions, species in the Nearctic (45%) and Palaearctic (33%) are best represented. Very similar numbers of herbs have been studied in these two regions, but there are many more demographic studies of trees and shrubs in the Nearctic than in the Palaearctic region. Since we have excluded studies of intensively managed populations such as plantation forests, the greater number of Nearctic studies of trees probably reflects the much greater extent of primary forest that survives in North America than in Europe, outside the species-poor boreal forest. Shrubs are demographically better studied in the Nearctic than the Palaearctic because of the long-term studies done in the deserts of the American southwest (Goldberg and Turner, 1986). Why have there not been any demographic studies in the shrub communities of Southern Europe?

Trees are much better studied than other growth forms in the neotropics, which is to be expected, but the almost complete absence of studies of vines is remarkable given their abundance, though perhaps it is not so surprising given the difficulties they present the investigator. The low figure for tree studies in the Ethiopian region is an underestimate because we have omitted some African studies where turnover and mortality rates have been given for whole stands rather than for individual species. Results from long-term permanent-plot studies at Barro Colorado Island, Panama, Pasoh in Malaysia, at Los Tuxtlas, Mexico and elsewhere will soon increase the number of demographic studies of tropical trees by an order of magnitude. At the moment, in the sample as a whole, studies of herbs greatly outnumber studies of trees (379 spp. *vs.* 106 spp.) but this can be expected to change.

Looking next at the habitat distribution of the species studied, nearly a quarter occur in grassland, with species of deciduous and evergreen forest sharing second place. The number of arable (weed) species studied underestimates the total volume of work in this habitat because so much of it has been concentrated on just a few

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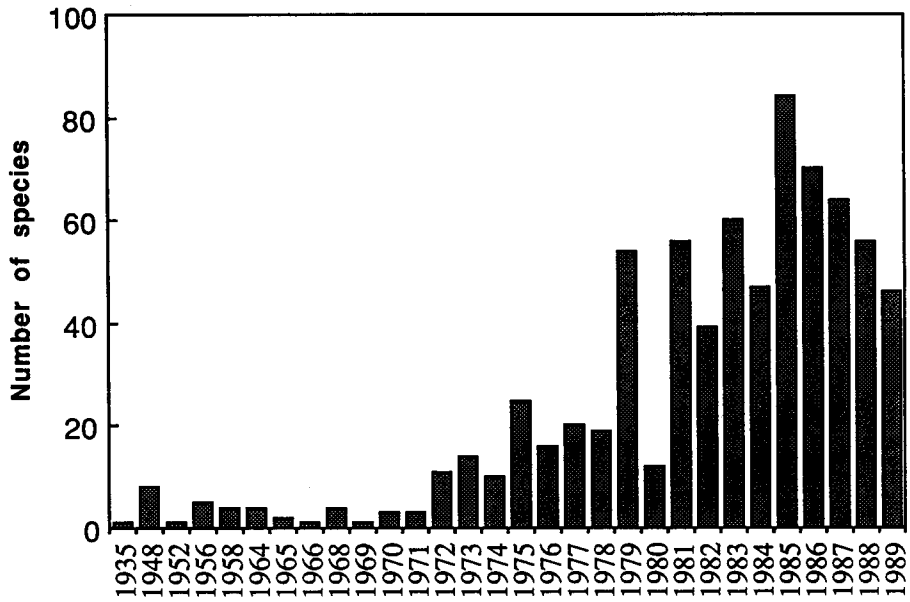

Fig. 1. The number of demographic studies of plant species published per year between 1935–89. We found no studies published in the years omitted from the early part of this period.

Table 1. The number and percentage of plant demographic studies, classified by biogeographic region, habit, habitat and life history of the species. The column totals for habit and habitat are not identical because the two samples were drawn separately from a larger total that includes some species that were incompletely described

	Nearctic 45%	Neotropical 6%	Palaearctic 33%	Ethiopian 2%	Oriental 6%	Australian 8%	Total	%
Habit								
Herb	163	9	161	6	16	24	379	68
Shrub	40	3	10	1	2	11	67	12
Tree	46	21	12	2	13	12	106	19
Vine	1	1	0	0	0	0	2	0
Σ	250	34	183	9	31	47	554	
Habitat								
Alpine	11	6	7	2	0	0	26	5
Arable	5	2	20	1	5	3	36	6
Grassland	63	3	44	1	3	21	135	24
Shrubland	10	0	4	1	0	8	23	4
Desert	42	1	12	0	1	3	59	11
Dune	11	0	28	0	0	1	40	7
Marsh	8	0	16	0	0	4	28	5
Deciduous forest	51	1	33	0	2	1	88	16
Evergreen forest	22	21	13	4	10	7	77	14
Other	27	1	6	1	9	0	44	8
Σ	250	35	183	10	30	48	556	
Life history								
Semelparous	11%	6%	17%	10%	3%	4%	12%	
Annual	24%	3%	28%	0%	17%	17%	23%	
Clonal	19%	20%	29%	50%	23%	10%	22%	

economically important species such as *Avena fatua* and *Cyperus esculentus*.

The quantity and quality of studies

The simple life history classification shown in Table 1 indicates that a surprisingly large proportion (12%) of species studied are semelparous perennials and that annuals are also well represented. In both cases this probably reflects the fact that species with short lifespans are easy to study. This does not apply to clonal species, which are nevertheless well represented, especially in the Palaearctic. In the plant kingdom as a whole the range of life histories and plant habits is unequally represented among plant families (e.g. Silvertown, 1983). How biased is plant demography with respect to the taxonomic diversity of the plant kingdom? The 580 species in our sample represent 99 families, 28 of which have five or more species in the sample. In the world flora the most speciose families are the *Compositae* (*c.* 25,000 spp.), the *Orchidaceae* (*c.* 18,000 spp.), the *Leguminosae* (*c.* 17,000 spp.) and the *Gramineae* (*c.* 9000 spp.) (Heywood, 1978). With the exception of the orchids (only nine demographic studies) these are also the best studied families with 72 species for the *Compositae*, 42 for the *Leguminosae* and 75 for the *Gramineae*. Among less speciose families there are bigger discrepancies between family size and the number of species studied. For example nearly 10% of the 250 species in the *Pinaceae* have been studied demographically, but only nine of *c.* 1000 species of *Fagaceae*, six of *c.* 2000 species of *Cactaceae* and six of 2780 species of *Palmae*.

In simple numerical terms plant demography has barely begun to sample the diversity of the plant kingdom. It is worrying therefore that the number of species studied appears to have peaked in 1985 and that there has been a decline since then (Fig. 1). Nearly 600 species studied is a superficially impressive quantity of knowledge, but the quality of most of the studies is low. Most have used low sample sizes, very few have attempted to estimate the variance in any vital rates, let alone partition this variance between spatial and temporal components or to estimate their heritability. Most studies are also incomplete in one way or another, often omitting the fate of seeds in the soil. The good news is that although plant demography may have passed its peak quantitatively, we have the impression that the quality of recent studies is showing a definite improvement.

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13th Annual Spring Systematics Symposium Evolutionary Ethics

by Olivier Rieppel*

On May 12, 1990, about 400 scholars and students gathered at the Field Museum of Natural History, Chicago, to attend the 13th Annual Spring Systematics Symposium on Evolutionary Ethics organized by Matthew H. Nitecki. In his introduction to the symposium programme, Nitecki traced evolutionary ethics from Herbert Spencer's Social Darwinism through Darwin, Haeckel, T.H. Huxley and G.E. Moore up to the modern sociobiology debate and to the dispute over 'right' moral grounds and their justification in the antagonism of opposite political powers. After enthusiastic words of welcome from the Vice President of Research and Collections, Jonathan Haas, who emphasized the Field Museum's interest and honour to serve as a hosting institution for this well-established and popular symposium series, the audience were taken on a *tour de force* by 11 speakers, covering the topic of evolutionary ethics from a truly interdisciplinary point of view, rating the power of human thought and free will against the power of natural selection.

The first three speakers on the symposium were Robert R. Richards, Chicago, Michael Ruse, Guelph, and Elliott Sober, Wisconsin–Madison. The dispute springing up between Richards' 'revised version' of evolutionary ethics and Ruse's approval of sociobiology, almost legendary

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