ECOLOGICAL STABILITY: A TEST CASE

Connell and Sousa (1983) questioned whether any ecological community yet studied has conclusively been shown to be stable. The criteria they used in their test for stability were demanding ones: "For a system to be considered stable, there must exist one or more equilibrium points or limit cycles (1) at which the system remains when faced with a disturbing force or (2) to which it returns if perturbed by the force" (p. 790). They further demanded that a disturbed community should resist change for one complete turnover after recovery to satisfy their stability criteria. Not surprisingly given these constraints, Connell and Sousa concluded that "if a balance of nature exists, it has proved exceedingly difficult to demonstrate" (p. 808). Perhaps it would be more accurate to say that stability has proved exceedingly difficult to test. These difficulties were discussed by Williamson (1987).

In this note I wish to draw attention to data from the Park Grass Experiment, perhaps one of the very few studies of terrestrial communities carried out in sufficient detail and for sufficient time to provide a test of stability by Connell and Sousa's rigorous criteria. The Park Grass Experiment (PGE) was begun in 1856 at Rothamsted, Herts, England, as an agricultural experiment to determine the effect of different fertilizers on the hay yield of a species-rich meadow. With some recent modification (Williams 1978), the experiment still continues. A variety of different fertilizer treatments was applied annually to unreplicated plots (of approximately 0.1 ha in area) within the Park Grass Meadow, which was initially of a uniform composition of about 60 species (Lawes et al. 1882). (Details of the experiment are given in Williams 1978.)

Comprehensive botanical analyses of the composition of the plots were made at irregular intervals from 1862, though substantial differences between plots receiving different treatments were observed even before the first systematic survey. Virtually no new species have entered the meadow, and all changes from its original composition have occurred by a process of selective elimination and selective population growth among the original constituent species. Annual determinations of the proportion of grasses, legumes, and other species in the hay were made between 1910 and 1948. Changes in the flora of the PGE can be considered in a hierarchy of three categories: (1) the proportions of grasses, legumes, and other species in the different treatments; (2) the constituent species within the three components; and (3) genetic differentiation within species. The available data in category 1, though only a crude index of community composition, permit us to draw a number of conclusions about the stability properties of the Park Grass plots. The proportion of each of the three floristic components is shown for three representative plots in figure 1.

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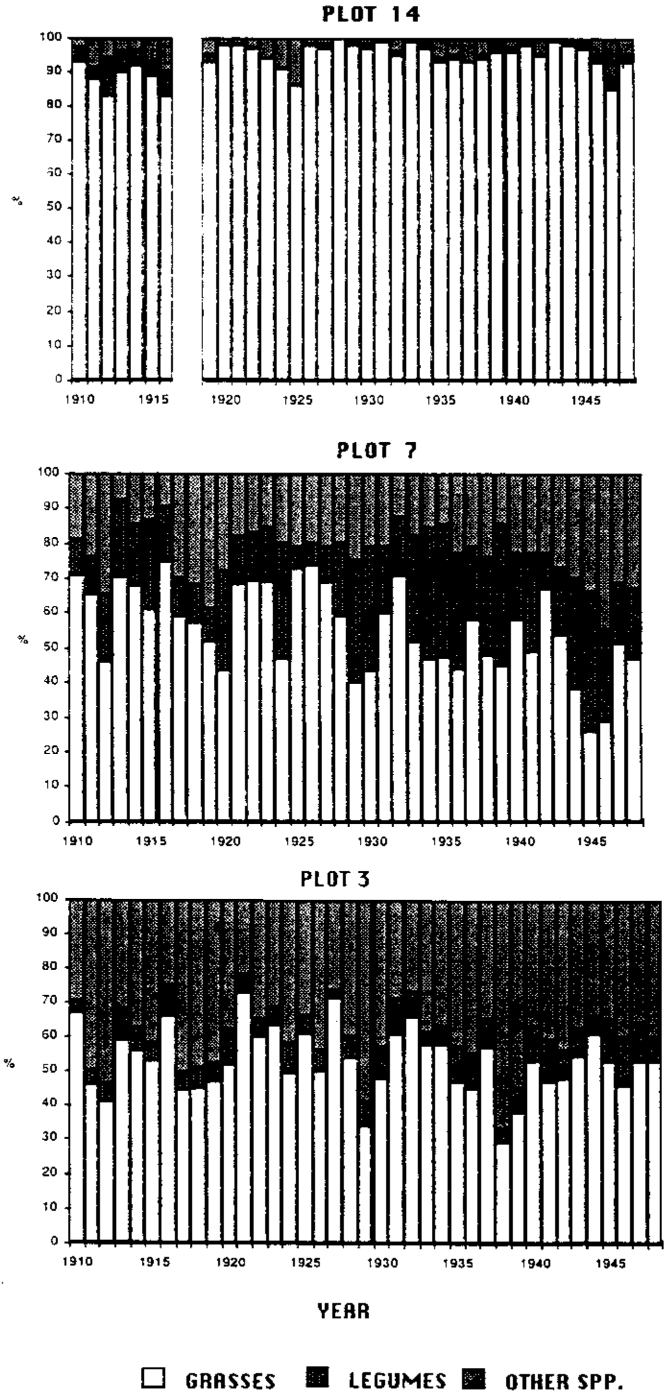

FIG. 1.—The proportion of dry matter (first hay harvest) composed of grasses, legumes, and other species in three unlimed plots of the Park Grass Experiment between 1910 and 1948. No data are available for plot 14 in 1917 and 1918. The annually applied fertilizer treatments were as follows: plot 3, no fertilizer; plot 7, P K Na Mg; plot 14, N P K Na Mg. (Data from Williams 1978.)

TABLE 1

LINEAR-REGRESSION COEFFICIENTS FOR TRENDS IN THE BIOMASS OF THE VEGETATION COMPONENTS IN UNLIMED SECTIONS OF THE PARK GRASS EXPERIMENT, 1906–1938

Plot No.	Sample Size	Grasses (b)	Legumes (b)	Miscellaneous Species (b)
3	33	−0.27	−0.007	−0.31
7	33	−3.10	−0.09	−0.90
14	18	−6.60**	−2.90	−0.65

NOTE.—Changes in biomass (b) are measured in g m^{-2} yr^{-1}. Data are from Silvertown 1979.
** $P < 0.01$. Other values of coefficient b shown here are not significant.

Evidence from data in categories 2 and 3 is also relevant. Ramet populations of grassland plants have relatively rapid population turnover times, on the order of years rather than decades (Harper 1977; Silvertown 1987). No demographic data exist for plants in the PGE, though significant genetic differentiation has occurred between populations of the grass *Anthoxanthum odoratum* in different plots in less than 40 yr (Snaydon and Davies 1972, 1982), indicating a rapid turnover of genets in this species. The rapidity with which changes in botanical composition occurred after the initiation of the experiment in 1856, and after changes in liming treatments in 1965 (Williams 1978), also indicates the potential for fast directional change in this community. The result of these initial changes and the divergent communities that were produced in plots 3, 7, and 14 (fig. 1) should be compared with the relative stability in the composition of these plots between 1910 and 1948. The permanent changes in soil conditions introduced by the fertilizer treatments had lasting effects on community composition. By contrast, short-term perturbations appear not to have produced lasting changes. Figure 1 shows obvious changes from year to year in the relative proportions of the three components in the plots, presumably caused by climatic variation from year to year (Cashen 1947; Silvertown 1980). However, there were no systematic trends of increase or decrease in the biomass of any of the three components in plots 3 or 7 during the period shown and only a minor, though significant, decrease in the biomass of grasses in plot 14 (table 1). The crude level of this analysis, which divides the plant community into only three components, obscures trends in the abundance of some individual species (Bergh 1979). The relatively stable ratios of the grasses, legumes, and miscellaneous species are all the more remarkable in view of these changes in their constituent species and suggest that the abundance of components and of species may be independently regulated (Silvertown 1980).

Connell and Sousa (1983) recognized that disturbance is such a frequent phenomenon in many communities that the effects of a new disturbance can obscure the signs of recovery from a previous one. This is true of the PGE plots, and for this reason it is not easy to pick out a particular disturbance event and its consequences. Extensive statistical analysis of the annually collected PGE data has not revealed the regulatory processes that maintain the stable composition of the plots, but this seems to be because these processes operate rapidly, within a growing season (Silvertown 1980; Thórhallsdóttir 1984). Nevertheless, it seems clear that the PGE passes Connell and Sousa's strict test of stability: the community is frequently perturbed, the composition of the plots does remain within recognizable bounds, and this stability has been observed over a long period, given the demonstrated capacity of the system for rapid and dramatic change. The PGE provides us with a unique data set, but is its stability unique too?

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