DEVELOPMENT OF SPECIES DIVERSITY IN SOME MEDITERRANEAN PLANT COMMUNITIES*

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Introduction

Changes in plant species composition during succession are interpreted as the result of a dynamic equilibrium between colonization, persistence and extinction of species.

Early successional communities are composed of species with a short life span (Odum 1969, Salisbury 1942). In more mature communities, most of the species are chamaephytes and phanerophytes which tend to persist together for a long time. Earlier dynamic models of ecosystems as suggested by Margalef (1957, 1968) and Odum (1969) mainly postulate that, during succession, the biomass increases, as primary production does, while diversity originally increases and decreases toward the final stage of succession afterwards; fluctuations are damped and stability increases. These earlier hypotheses have been criticized by Drury & Nisbet (1973), May (1973), Colinvaux (1973) and Horn (1974). In recent studies (Connell & Slatyer 1977, Grime 1977, Grubb 1977, Whittaker 1977, Whittaker & Levin 1977, Huston 1979) one has tried to synthesize empirical results and proposed more elaborate models to explain successional patterns and community diversity, stability and organization.

Two ecological problems were especially emphasized:
1. The substitution of species during the succession.
2. The cohabitation of species in mature communities.

Most studies on plant succession have been carried out in non-mediterranean countries. In this paper our main purpose is to compare the results achieved in the field of vegetation dynamics with those in the French Mediterranean region and to treat in particular:

1. The evolution of species richness in the course of an old field succession, ending in an oak forest (Quercus pubescens) and the mechanisms causing a substitution of species. Here our investigations concentrate on a. lifeforms as an expression of stature and species life span, and b. dispersal means as an expression of the capability of species to colonize a new habitat.
2. The tendency of species to evolve towards coexistence in more mature communities such as a Quercus pubescens forest. This has been investigated by means of three variables: a. the stratification of species and foliage, b. the relation of species to a resource gradient such as light, c. the phenology of species. These variables may be considered as indicators of community organization and resource allocation.

Our contribution consists of two parts, dealing with 1. changes during succession towards a Quercus pubescens forest, 2. community structure in relation to the organization of two Quercus pubescens forests representing the final stage of succession.

Study area

The investigation sites are located in the region of the
Hautes Garrigues du Montpellierais, North of Montpellier, at an elevation of 230 m. The average annual precipitation amounts to 120 cm with maxima in spring and autumn. Evergreen forests dominated by Quercus ilex, deciduous forests dominated by Quercus pubescens, and mixed formations including both species are considered as the mature formations of the region. This mature vegetation was phytosociologically described as a transition between the Quercetum ilicis galloprovineiatis and the Querceto - Buxetum (Braun-Blanquet 1936, Braun-Blanquet et al. 1952). In coppices of Quercus pubescens we find some septentrional species which extend southward of their usual habitat because of the special ecological conditions of the deciduous coppice (Blondel 1941).

The succession study was carried out in adjacent abandoned vineyards and olive groves on marly soil, in two localities at 30 km distance in Le Causse de la Selle and in La Boissière, with a Quercus pubescens forest as the potential vegetation. Data were collected during 1977 and 1978 from sites on 19 old fields which were abandoned for 4, 8, 9, 10, 12, 14, 15, 16, 17, 20, 21, 25, 30, 50, 54, 58, 62, 72, resp. 125 years. Some fields were reinvestigated in the second year. At La Boissière only the earlier stages from 1 to 25 years were analysed.

The two old field series are very similar in major successional trends and constitute parallel series according to factorial analysis of correspondances (Benzecri et al. 1973) based on the floristic composition of the sites (see appendix).

Horizontal, vertical and temporal patterns of plant species in the final stage, i.e. the forest, were studied in two Quercus pubescens stands, sampled in the La Rouvière forest at 50 m distance from the La Boissière old fields. The two stands had no human influence after cutting in 1945. The forest was earlier destroyed by fire in 1918 and 1923; while grazing occurred in the area during the 17th century and between 1840 and 1930 (Vidal 1979).

Table 1. Classification of dispersal types according to Molinier & Müller (1938) and van der Pijl (1972) slightly simplified.

| BAROCHORES | Diaspores fall by their own weight |
| ANEMOCHORES | Diaspores moved by wind |
| ZOOCHORES | Diaspores normally dispersed by animals |
| AUTOCHORES | Diaspores moved by their own weight |
| HYDROCHORES | Diaspores moved by water |

Methods

Two different sampling schemes were used for the old field sere and the forest. In the old field sere, species richness of all sites was analyzed in areas of (20 m x 1 m) for herbaceous species and (20 m x 10 m) for woody species. Cover of species was taken as importance value and determined by the line interception method (Canfield 1941, Buell & Cantlon 1950) along a 20 m transect. The age of the fields (number of years after abandonment) was determined according to information from the landowners and by means of woody species if present on the site.

To identify species dispersal means we used the classification of diaspores (Table 1) proposed by Molinier & Müller (1938) and van der Pijl (1972). Only three dispersal types were analyzed: barochory, anemochory and zoochory.

Life forms types sensu Raunkiaer were determined through own observations and further based on reviews of species life forms in the mediterranean region by Blondel (1941) and Braun-Blanquet et al. (1952). The frequency of dispersal and life form types are expressed as the number of species belonging to a type relative to the total number of species in the sample.

In the forest communities vertical and horizontal structure was studied along a 32 m transect. The presence of each species was registered in units of 10 cm height and 10 cm length from the zero to the 2 m level, along the transect.

The vertical vegetation profile above 2 m was determined with the optical point-quadrat method developed by McArthur & Horn (1969), using a 50 mm camera.