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Secondary succession following cultivation in an arid ecosystem: The Owens Valley, California

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Few old-field succession studies have been conducted in arid ecosystems and there is some question if classical secondary succession occurs in arid environments. In order to determine if old-field succession does occur under arid conditions, we sampled 40 previously-cultivated sites abandoned over a period of 29–80 years in the Owens Valley, California. We compared vegetation development at these 40 old fields to vegetation composition on 17 adjacent uncultivated reference sites. We were interested in determining if 1) seral communities could be identified, 2) these communities expressed predictable and progressive patterns, and 3) if so, whether the seral patterns indicated divergent or convergent successional pathways.

The 57 sites separated into 6 separate seral communities. Two seres were identified, one progressing toward a big sagebrush late-seral community and the other with fourwing saltbush as the characteristic species. Based on multivariate statistical analysis, the two seres were likely to continue on divergent pathways for 100–140 years, after which the saltbush sere may converge toward the late-seral sagebrush community. Both localized and broad-scale factors were important in defining successional patterns in this arid environment. Our results support the concept that classical old-field succession does occur in arid regions.

1. Introduction

Old-field succession has been widely studied. However, few of these studies have been in arid regions. Secondary succession in general has been much less studied in arid regions than in more mesic regions. It has been hypothesized that successional processes that occur in other regions may not function similarly in arid regions, and that the concept of succession itself may not be valid in arid ecosystems (see discussions in Carpenter et al., 1986; Toft and Elliott-Fisk, 2002; Webb et al., 1987).

The Owens Valley of eastern California is located between the Sierra Nevada Mountains to the west and the White and Inyo Mountains to the east in the transition area between the Mojave and Great Basin Deserts. Death Valley occurs immediately east of Inyo Mountains. The region is in the rain shadow of the Sierras, with the Owens Valley receiving an average annual precipitation of 10–15 cm. Although located in an arid region, agriculture was widely practiced a century ago. The Owens River flows through the Valley and along the river floodplain groundwater is often found within 1–5 m of the surface. Around 1920, almost 10,000 hectares were under cultivation in the Owens Valley (Sauter, 1994). During the 1920s, the City of Los Angeles began large-scale purchase of farms, causing an 80% reduction in cultivated land by 1935, and additional abandonment of fields has occurred since then. Secondary succession has occurred on most of the land permanently abandoned to cultivation. However, several areas abandoned around 1970 remain largely devoid of perennial vegetation, raising questions regarding the rate of natural recovery on these sites.

This abandonment of a large number of fields over a relatively long period of time (50 years) provided an opportunity to identify a series of chronosequences from which patterns of old-field succession in an arid region could be quantified. Our purpose in this study was three-fold. First, we wanted to determine if patterns of old-field succession could be recognized and, if so, to identify seral stages and quantify rates of change. In essence, we were interested in determining if old-field succession even occurred in this arid system. If it did, it should be identifiable by several basic characteristics of succession. At a minimum, it would be a process

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that could be identified to be orderly and directional, there should be an increase in structure and diversity of the plant community, and there should be clear shifts in seral species composition during the chronosequences (Odum, 1971:251). Second, we wanted to determine if secondary succession on these sites resulted in a single sere, or if multiple pathways were evident. Lastly, we wanted to determine that if multiple pathways were evident, was there any indications that the different seres would eventually converge, or did it appear that succession on these sites was divergent.

2. Methods

2.1. Field methods

Our study sites were selected so as to form a set of chronosequences. The use of chronosequences is a standard method of determining rates and patterns of secondary succession (Carpenter et al., 1986; Coffin et al., 1996; Costello, 1944; Knops and Tilman, 2000; Paschke et al., 2000; Romme and Knight, 1981; Thorne and Hamburg, 1985; Webb et al., 1987). The primary limitation of the use of chronosquences is the assumption that the included sites supported similar vegetation prior to disturbance and that the environmental history since disturbance has been similar among the sites. However, for long-term studies where initial data are not available, there are no alternatives to the use of chronosequences and the technique can provide useful information.

We included three criteria for the selection of study sites. (1) To form a chronosequence, there had to be several sites within a general area, each with similar soils and topographic position, but with a different and identifiable end of cultivation date. (2) Each site had to have information relative to types of crops grown and post-cultivation land use. (3) There had to be a nearby reference site. A reference site was defined as an uncultivated area with similar soils and depth to water as the old-field site, and which supported native perennial vegetation similar to what could be assumed to have been on the old-field site had it not been cultivated. It is important to note that the reference sites were uncultivated sites, but they were not undisturbed. The OwensValley has experienced high levels of human impacts of various types, some pre-dating European settlement, and few areas are likely to have escaped some form of anthropogenic disturbance.

Aerial photographs and survey plats were used to develop a list of potential sites. Two sets of photographs (1944 and 1968) were available. The 1944 photographs were used to identify areas under cultivation in, and those that had been abandoned by, 1944. The 1968 photographs were used to determine which of these areas had been abandoned by 1968 and which were still under cultivation. Los Angeles Department of Water and Power (LADWP) 1930/31 survey plats were used to identify active and abandoned sites in those years. These survey plats indicated areas of abandoned fields (denoted as bare land or dead crops) as well as areas in live crops. For fields abandoned before 1931, we assumed the date of purchase by LADWP was the date of abandonment. For abandonment dates between 1931 and 1968, we relied on LADWP lease and irrigation records and on the 1944 and 1968 aerial photographs. In 1970, LADWP changed water allocation policies for leases and this led to the abandonment of several fields in 1970, which were identified from 1968 aerial photographs and from the irrigation maps and lease information.

We initially selected nine areas, containing 100 potential study sites. We visited each of the 100 sites and eliminated a site if it showed evidence of additional disturbance such as heavy off-road vehicle use or farm equipment storage. We further concentrated on areas that had the widest range of abandonment dates and number of sites. This process resulted in the selection of 40 old-field and 17 reference sites for study, located in six general areas (Fig. 1). We were able to compile cultivation history for all but one of the old-field sites from LADWP lease records.

Our original intent was to select a unique reference site to be paired with each old field. In practice, this was not possible. When the sites were cleared for cultivation, most of the contiguous area of similar topography, soils, and vegetation was cleared at that site, leaving relatively little native vegetation. Adjacent areas supporting native vegetation were often used for buildings or livestock holding areas. As a result, it was impossible to find enough localized uncultivated sites to provide unique reference areas for each old-field site. The old fields did occur in clusters around the reference areas. One reference area was therefore generally used for more than one old-field site.

The vegetation in the old-field and the reference sites were sampled by use of line transects (Bonham, 1989). The number of transects varied from 10–30 per site, depending on the size of the site. Transects were 10-m long, randomly located within the site, and cover counts (by perennial species) were made at 2 mm intervals, with each 2-mm mark used as a sample point. Transects were not located near roads or in recently disturbed areas. Transect data were collected in October–November 2004 and April–May 2005. Data from an old-field and its respective reference site were collected within the same month.

2.2. Statistical methods

2.2.1. Recovery index score

The Recovery Index Score (RIS) is a similarity index that provides a first approximation of recovery of a disturbed site (McLendon et al., 1995). This estimation is an over-simplification because it assumes an exact 1:1 recovery pattern, i.e., that secondary succession will result in an exact duplication of the reference site. This is not likely to happen since no two portions of a reference area are likely to be exactly the same. However, the approach is both conceptually and computationally simple and it provides useful estimates.

A Recovery Index Score was calculated for each old-field site from the canopy data in the following manner. Canopy cover, by species, was compared between old-field and associated reference sites. The smaller values of each pair were summed, except for the species that was the dominant on the reference site. For dominant species, the entire cover value for the old-field site was included in the sum, even if this value exceeded the reference site value. The resulting sum was divided by the mean total canopy cover of the reference areas. This quotient was termed the recovery index score for that site. Because there was not a unique reference site for each disturbed site, all reference sites within a specific area were used to compare with each old-field sites in that area. If one or more of the reference sites was more similar in soils or vegetation to a particular old-field site, those particular reference sites were used in the comparison. Otherwise, the highest value for each species among all the reference sites in a particular area was the maximum allowable for that area.

Recovery rate (% per year) was estimated by determining mean annual rate of recovery (RSI/number of years since cultivation) and multiplying this number by 100. This value assumes a linear relationship between rate of secondary succession and time, which may not be accurate (Donnegan and Rebertus, 1999; Leps, 1987; Whipple and Dix, 1979). Studies of rate of successional recovery in other ecosystems give mixed results, some suggesting more rapid rates initially (Aplet et al., 1988; Myster and Pickett, 1994), some slower initial rates (West et al., 1984), and some relatively constant rates (Collins et al., 1987). Degree of aridity may also affect the rate of successional change, with the decrease in rate of