Intraspecific competitive effects on water relations, growth and reproduction in Encelia farinosa

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Summary. An experiment was conducted to assess the importance of intraspecific competition on water relations, growth and reproductive output in Encelia farinosa, a common deciduous-leaved shrub of the Sonoran Desert. Nearest neighbor analyses in monospecific stands indicated that plants exhibited a clumped distribution. Plant size and nearest neighbor distance were positively correlated, inferring intraspecific competition. Removal experiments monitored for two years indicated that plants now without neighbors had higher leaf water potentials, higher leaf conductances, and a greater leaf area than control plants. As a consequence, growth rates and reproductive output were significantly higher in plants without neighbors. These data strongly support the notion that warm desert plants with a contagious spatial distribution compete for water.

Introduction

The strong positive relationship commonly observed between plant primary productivity and precipitation in warm deserts clearly implies that water is a significant factor limiting the productivity of both annuals and perennial shrubs (Walter 1968, McMahon and Schimpf 1980, Ehleringer and Mooney 1983). In addition to the constraints on productivity imposed by abiotic factors, attention has also been focused on potential biotic limitations. Specifically, a number of studies have examined the spatial distribution patterns of perennial shrubs for indications of competitive interactions (Woodell, Mooney and Hill 1969, Barbour 1969, Anderson 1971). A regular distribution of plants (indirect evidence of competitive interactions) has been observed, especially under low precipitation situations. In addition, studies of intraspecific nearest neighbor relationships by Yeaton and Cody (1976), Yeaton, Travis and Gilinsky (1977) and Nobel (1981) on plants in these same deserts have shown positive correlations between plant size and nearest neighbor distance. Again this is indirect evidence of competitive interactions between plants.

Fonteyn and Mahall (1978, 1981) provided additional evidence that competition for water may be occurring between desert plants. In a series of plant removal experiments, they showed that when water availability was low plant water status (leaf water potential) was affected by the presence of neighbors. Their conclusion was that interspecific competition was usually more intense than intraspecific competition.

Although ample indirect evidence exists, none of the previous studies on desert plants have unequivocally demonstrated that interplant competition (either intra- or inter-specific) is occurring, and that as a result of these interplant interactions growth, productivity and reproductive activity are reduced. The purpose of this paper is to 1) present data which inferentially demonstrate that intraspecific competition is occurring in a monospecific stand of Encelia farinosa Gray (Asteraceae), and 2) to describe an experiment conducted to measure the consequences of neighbor removal on physiological activity, growth and reproduction in E. farinosa.

E. farinosa is a drought-deciduous shrub, common to most of the Sonoran Desert of North America. Throughout most of its range, it is the dominant deciduous-leaved shrub, and in many areas it forms extensive monospecific stands. Productivity and physiological activity in this species are also positively correlated with water availability (Ehleringer, Björkman and Mooney 1976, Ehleringer and Mooney 1978, Ehleringer 1980, Ehleringer and Cook 1984). In response to reduced soil water availability, new leaves are produced with a reflective pubescence layer, which increases water use efficiency and allows the plant to maintain physiological activity later into the drought period (Smith and Nobel 1977, Ehleringer and Mooney 1978, Ehleringer 1982).

Methods and materials

This study was conducted in west central Arizona (lat. 34°57'N, long. 114°25'W, 540 m elevation) at a site approximately 9 km south of Oatman, Arizona. The vegetation for the area is typical for the Lower Colorado Valley portion of the Sonoran Desert (Shreve and Wiggins 1964). On south facing slopes and bajadas in this area, the vegetation is dominated by the subshrub Encelia farinosa. Throughout much of this area, this species forms monospecific stands. At other sites in this area, it is co-dominant with the evergreen leaved shrub Larrea divaricata and the cactus Opuntia bigelovii.

Soils and parent material at this site are volcanically derived. In general the area is rocky, with only thin soils (<20 cm) at best. Soil nutrient concentrations are low. The average soil nitrate and phosphorus concentrations were 2.2 ppm and 0.07%, respectively (soils analyzed by Utah State University Soil, Plant and Water Analysis Laboratory).

The particular site chosen for study was a south facing slope, which consisted of a monospecific stand of Encelia farinosa. The population was analyzed using nearest neigh-
In a subsampling of 205 individual plants, only 5 were less than 2 years old (based on other seedling establishment studies also at this site). Since new plant establishments had been observed in only the last two out of six years, all other shrubs were likely to have been at least 7–8 years old.

The nearest neighbor distance data clearly indicated that the distribution of individual plants was not random (Fig. 1). The vast majority of individuals were within 0.4 m of each other, and no individuals in the study area were more than 1.5 m apart. Using the Clark and Evans (1954) method for determining distribution patterns, the plants were clumped (R = 0.901, P < 0.01). A nearest neighbor analysis using the Pielou (1962) methodology also suggested that the distribution was clumped (chi-square = 429.7, P < 0.005). There were no obvious surface obstructions or topographic factors to explain the clumped distribution patterns. However, local variations in soil properties may exist that could make establishment more likely in one location than another.

When the canopy sizes of these plants were plotted as a function of distance to the nearest neighbor, it was clear that plants increased in size when they were farther apart (Fig. 2). The mean plant size increased linearly as mean distance between plants increased up to a distance of about 0.5 m. Thereafter, plant size appeared to remain constant as distance between plants increased. Since on the average plant canopies did not overlap and there was open space between the shrubs, it was concluded that if competition were occurring it was not likely to be for any aboveground resource. More likely, if competition was occurring, it was between shrubs for a belowground resource such as water and/or nutrients.

Given the inference that intraspecific competition may be occurring, an experiment was designed to measure the consequences of competition on individual plant performance. The treatment was to remove all neighbors within a 2 m radius of a shrub. From the nearest neighbor analysis, it appeared that plants were never this far apart naturally, and therefore, any potential neighbor effects would be greatly reduced.

As estimates of physiological activity, leaf conductance to water vapor and leaf water potential were measured. Previous investigations by Ehleringer and Cook (1984) have demonstrated that leaf conductance in *Encelia farinosa* is