1-31-1989

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SPATIAL AND TEMPORAL VARIABILITY IN PERENNIAL AND ANNUAL VEGETATION AT CHACO CANYON, NEW MEXICO

Anne C. Cully1,2 and Jack F. Cully, Jr.1,3

ABSTRACT. — Annual plant populations in northwestern New Mexico were found to be spatially and temporally highly variable. During favorable years annual plant species have patterns of dominance and diversity that are different from those of perennial species. Measurement of perennial plant diversity in plant communities is a poor predictor of productivity. Both perennial and annual components of plant communities should be considered in measurements of diversity and productivity.

The relationship between environmental diversity and animal populations is of interest to ecologists in their attempts to understand the factors that control the composition of biotic communities (Pielou 1974). Whitaker (1972) and Pielou (1974) discuss two different types of diversity. Alpha diversity is applied to small, homogeneous areas such as local plant communities or habitat types, defined by more or less natural boundaries. Beta diversity is the measurement of differences between these small, homogeneous areas within a geographic region.

Perennial plant species are often used in descriptive and quantitative studies of plant communities that include measurements of dominance and diversity. While perennial plants are the relatively more stable part of the plant community, annual plant species are a conspicuous component during years when environmental conditions are right for germination, growth, and reproduction. The fluctuation of annual plant populations has been studied in several arid and semiarid locations in the southwestern United States (Beatley 1969, Juhren et al. 1956, Patten 1978, Tevis 1958). In desert and semiarid ecosystems, annual plant production is characterized by a fascinating cycle of years of low germination interspersed with years of superabundant germination and reproduction. This production may be a significant resource for consumer populations, but it may also be overlooked by researchers because of the high degree of variability from year to year.

In this study we report on work done at Chaco Canyon, in northwestern New Mexico. Our work included measurements of perennial species to describe habitat types and their alpha diversity. In addition, we documented one superabundant year of annual plant production, followed by several consecutive years of little or no annual production. In northwestern New Mexico fluctuation in annual plant populations has been described (Jones 1972, Potter 1974, Scott 1980), but quantitative data have not been reported.

STUDY AREAS

Chaco Canyon is in the central San Juan Basin in northwestern New Mexico. The San Juan Basin is an extension of the Colorado River drainage, although the Chihuahuan Desert to the south influences the climate and the composition of the vegetation. The soils are generally derived from shale and sandstone. The vegetation is dominated by members of the Asteraceae and Chenopodiaceae, including sagebrush (Artemisia), rabbitbrush (Chrysothamnus), and various saltbushes (Atriplex) (Donart et al. 1978, Shreve 1942). As in the Great Basin to the west, winter precipitation is a significant component of the total in northwestern New Mexico, but the summer monsoonal rains from the south provide a large proportion of the rainfall during the growing season (Tuan et al. 1973). A summary of weather data at Chaco Canyon over a 20-year period, 1957–1977 (Cully

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MAJOR HABITAT TYPES

- Bench
- Flood Plain
- Pinyon-Juniper
- Wash
- Shrub Grassland

STUDY AREAS
1. Casa Chiquita
2. Pueblo Bonito
3. Wash
4. Bench
5. Pueblo Alto
6. Werito's Rincon
7. Pinyon-Juniper

Fig. 1. Map of Chaco Canyon showing the locations of the study sites and the distribution of vegetation types.

The sites at Pueblo Alto and at the mouth of Werito's Rincon were added for this study to gather additional data on annual plant productivity.

Upland Areas

The Bench.—The bench lies within the Hilaria-Bouteloua-Atriplex vegetation type (Kelley and Potter 1974). The bench (Fig. 1) is elevated above the floodplain of the Chaco Wash and is bounded on the north and south by sandstone cliffs. Soils are thin, and there is a great deal of exposed bedrock.

Pinyon-Juniper.—The woodlands of the higher elevations of Chacra Mesa are dominated by one-seed juniper (Juniperus monosperma). Pinyon pine (Pinus edulis) is subdominant.

Pueblo Alto.—Pueblo Alto is located in a shrub grassland, the Atriplex-Oryzopsis-Sporobolus vegetation type (Kelley and Potter 1974). The site is located on the mesa north of the canyon proper.

1984b), showed that annual precipitation averaged 20.6 cm. The heaviest precipitation occurred during July through September, with each of these months averaging >3 cm. The balance of the rainfall was rather evenly distributed throughout the remainder of the year. The San Juan Basin can have two periods of plant productivity, one in spring if there is normal or above normal precipitation, and another more predictable period during late summer and fall in response to the monsoonal rains of late summer.

The study sites for this report are five areas used by J. Cully (1984a) in his study of the bird and rodent communities of the San Juan Basin. They were selected from Kelley and Potter's (1974) vegetation map of Chaco Canyon. The principal criteria for the choices were that each area included habitat sufficient to contain a transect 120 m wide by 1.6 km long, that the areas were different from one another, and that in combination they represented the major habitats at Chaco Canyon.
Floodplain Areas

CASA CHIQUITA AND PUEBLO BONITO.—Two study sites lie within the *Atriplex-Sarcobatus* vegetation type in the floodplain of the wash, which is dominated in the western portion of Chaco Canyon by four-wing saltbush, sand scale, and black greasewood (Kelley and Potter 1974). The sites are bordered on the south by the wash and on the north by sandstone cliffs and the bench habitat.

The wash.—The wash is the erosion channel of the Chaco River. It bisects the floodplain through the length of the canyon in the park. Riparian, woody vegetation is characteristic of the wash habitat; the inner channel is dominated by rabbitbrush (*Chrysothamnus nauseosus*), sandbar willow (*Salix exigua*), and black greasewood (*Sarcobatus vermiculatus*). Cottonwood (*Populus fremontii*), four-wing saltbush (*Atriplex canescens*), and tamarisk (*Tamarix spp.*) also occur.

WERITO'S RINCON.—This study site is at the mouth of a large rincon, or side canyon, southwest of the main canyon. According to Kelley and Potter (1974), the vegetation is similar to that on the mesa tops surrounding the Pueblo Alto study area.

Methods

Perennial plant cover was measured using the line intercept method (Canfield 1941). Cover was measured on twenty-five 10-m lines stretched in alternate directions at 62-m intervals along a 1.6-km transect in each habitat. This yielded a total of 250 m sampled in each habitat. Each perennial plant species intercepted was measured to the nearest cm. The bench, Casa Chiquita, and the wash were sampled during April 1979. Pueblo Bonito and the pinyon-juniper sites were sampled during May 1981.

To identify the species that most easily distinguish habitats, we applied discriminant function analysis to the cover data from each 10-m line segment in each habitat. The habitats were the discriminating variables, and the 29 species of plants that were encountered on three or more (of a total of 125 segments) were the predictor variables. This analysis was done on a microcomputer using SPSSPC+ Advanced Statistics (Norusis 1986).

The cover data at each transect were analyzed for species richness, or S (number of species) = $H_0$, two indices of species diversity, $1/\Sigma p_i^2 = H_1$ (Simpson 1949) and $\exp(-\Sigma p_i \ln p_i) = H_2$ (Shannon and Weaver 1949); and evenness, or J, where $J = H_2/H_0$ (Peet 1974, Pielou 1974). Hill (1973) suggests that evenness as measured above is subject to change with change in sample size, and that the ratio $H_2/H_0$ is a better ratio to describe evenness. This is partly because $H_2$ always lies between $H_0$ and $H_1$. Since J is still common in the literature, we present both measures of evenness.

Annual plant densities were sampled at the bench, Casa Chiquita, Pueblo Bonito, and Pueblo Alto in June 1979, 1980, and 1981, and at Werito’s Rincon during June 1979. At each area data were taken from twenty 1/2-$m^2$ quadrats. These were placed at 10-m intervals along 100-m tapes laid at random in a 1-ha area along the transect used to measure cover at Casa Chiquita, Pueblo Bonito, and the bench. Cover was not measured at Pueblo Alto or at the mouth of Werito’s Rincon; a transect was laid out in the same way at these two sites as at the previous sites to gather the annual data. The number of annual plants within each quadrat was counted by species. Then all vegetation was picked and saved in plastic bags to determine the aboveground biomass production. The plant material was air-dried at room temperature for a minimum of two months. Each sample was weighed to the nearest 0.1 g. Subsequently, the seeds were removed from foliage, stems, and flower parts in a seed separator and weighed separately.

Results

Perennial Plant Species Dominance

In the upland areas the dominant species on the bench were Mormon tea (*Ephedra viridis*), Bigelow’s sagebrush (*Artemisia bigelowii*), wild buckwheat (*Eriogonum spp.*), Greene’s rabbitbrush (*Chrysothamnus greenei*), galleta grass (*Hilaria jamesii*), and Indian ricegrass (*Oryzopsis hymenoides*) (Table 1). The pinyon-juniper habitat on Chaera Mesa was dominated by Bigelow’s sagebrush, mountain mahogany (*Cercocarpus montanus*), three-leaf sumac (*Rhus trilobata*), pinyon pine, one-seed juniper, and galleta grass. On the floodplain the dominant species at Casa Chiquita were broadscale (*Atriplex obovata*), black greasewood, torrey seepweed (*Sueda torrey-
Table 1. Cover and diversity at five habitats at Chaco Canyon. The values are the number of cm intercepted for each species at twenty-five 10-m lines in each habitat. \( H_0 \) = number of species; \( H_1 = 1/P_1^2; H_2 = -\Sigma P_i \ln P_i; J = H_2/H_0; \) evenness = \( H_j/H_0. \)

<table>
<thead>
<tr>
<th>Species</th>
<th>Bench</th>
<th>Casa Chiquita</th>
<th>Pueblo Bonito</th>
<th>Wash</th>
<th>Pinyon-juniper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>71</td>
<td>0</td>
</tr>
<tr>
<td>Aristida spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>17</td>
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<tr>
<td>Artemisia bigelovii</td>
<td>1195</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>665</td>
</tr>
<tr>
<td>Artemisia dracunculoides</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>190</td>
<td>0</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>573</td>
<td>51</td>
</tr>
<tr>
<td>Astragalus spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Atriplex canescens</td>
<td>64</td>
<td>187</td>
<td>3829</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Atriplex obovata</td>
<td>0</td>
<td>1808</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Boutelloua gracilis</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td></td>
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<tr>
<td>Cercocarpus montanus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>376</td>
</tr>
<tr>
<td>Chrysopsis cilius</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chrysanthemum greenei</td>
<td>200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chrysanthemum nauseosus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2953</td>
<td>100</td>
</tr>
<tr>
<td>Chrysanthemum pulchellus</td>
<td>107</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ephedra viridis</td>
<td>680</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>23</td>
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<tr>
<td>Eriogonum spp.</td>
<td>516</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Eurotia lanata</td>
<td>49</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td>Fallugia paradoxa</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>95</td>
</tr>
<tr>
<td>Gutierrezia sarothrae</td>
<td>10</td>
<td>0</td>
<td>21</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Hilaria jamesii</td>
<td>327</td>
<td>0</td>
<td>325</td>
<td>0</td>
<td>181</td>
</tr>
<tr>
<td>Juniperus monosperma</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2117</td>
<td></td>
</tr>
<tr>
<td>Lycium pallidum</td>
<td>0</td>
<td>0</td>
<td>44</td>
<td>0</td>
<td>29</td>
</tr>
<tr>
<td>Muhlenbergia pungens</td>
<td>92</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Opuntia spp.</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Oryzopsis hymenoides</td>
<td>324</td>
<td>0</td>
<td>4</td>
<td>80</td>
<td>10</td>
</tr>
<tr>
<td>Other</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td>151</td>
<td>23</td>
</tr>
<tr>
<td>Pinus edulis</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>317</td>
</tr>
<tr>
<td>Populus fremontii</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>200</td>
<td>0</td>
</tr>
<tr>
<td>Rhus trilobata</td>
<td>79</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>217</td>
</tr>
<tr>
<td>Salix spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1772</td>
<td>0</td>
</tr>
<tr>
<td>Sarcobatus vermiculatus</td>
<td>0</td>
<td>1215</td>
<td>2260</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sporobolus airoides</td>
<td>0</td>
<td>765</td>
<td>131</td>
<td>308</td>
<td>0</td>
</tr>
<tr>
<td>Sporobolus spp.</td>
<td>101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Stuea torreyana</td>
<td>0</td>
<td>286</td>
<td>202</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tamarix pentandra</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2197</td>
<td>0</td>
</tr>
<tr>
<td>Yucca spp.</td>
<td>51</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>Total cover</td>
<td>3952</td>
<td>4261</td>
<td>6816</td>
<td>8496</td>
<td>4582</td>
</tr>
<tr>
<td>% cover</td>
<td>16%</td>
<td>17%</td>
<td>27%</td>
<td>34%</td>
<td>18%</td>
</tr>
<tr>
<td>( H_0 )</td>
<td>17</td>
<td>5</td>
<td>8</td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td>( H_1 )</td>
<td>6.30</td>
<td>3.33</td>
<td>2.33</td>
<td>4.19</td>
<td>3.96</td>
</tr>
<tr>
<td>( H_2 )</td>
<td>2.18</td>
<td>1.35</td>
<td>1.07</td>
<td>1.68</td>
<td>1.97</td>
</tr>
<tr>
<td>( J )</td>
<td>0.13</td>
<td>0.27</td>
<td>0.13</td>
<td>0.17</td>
<td>0.09</td>
</tr>
<tr>
<td>Evenness</td>
<td>0.37</td>
<td>0.67</td>
<td>0.21</td>
<td>0.41</td>
<td>0.19</td>
</tr>
</tbody>
</table>

ana), and alkali sacaton (Sporobolus airoides). Pueblo Bonito was similar to Casa Chiquita, except that broadscale was missing and four-wing saltbush was much more important than at Casa Chiquita. Black greasewood and seepweed were also important at Pueblo Bonito. Galleta grass was absent at Casa Chiquita but contributed 2% cover at Pueblo Bonito. The wash was dominated by rabbitbrush, tamarisk, sandbar willow, and big sagebrush. Shrubs and forbs were the primary components of the vegetation at all study sites sampled for perennial vegetation.

In the discriminant function analysis, there were 12 species important in discriminating between the habitats (Table 2). The list includes many of the species listed above as dominants plus Artemisia dracunculoides. Although galleta, wild buckwheat, mountain mahogany, three-leaf sumac, Torrey seepweed, big sagebrush, and sandbar willow were all subdominant in one or more habitats,
they were not used by the DFA. This may be partly due to the high probability level required for inclusion with 27 variables (P < .002; 0.05/27). Figure 2 shows the relationships of the observations from each habitat on canonical variables (discriminant function axes) 1 and 2. Casa Chiquita and Pueblo Bonito are similar to each other. The bench and pinyon-juniper habitats are also very similar; in fact, they are almost completely overlapping on canonical axes 1 and 2. (They are separated on axis 4 where juniper is an important variable.) The wash habitat was distinct from the others with a small area of overlap on canonical axes 1 and 2.

One value of the DFA is the ability to show which habitats are most similar to each other and, by a jackknife procedure, to show how accurately the habitats can be distinguished on the basis of the predictor variables. The jackknife procedure takes each of the observations used to derive the discriminant functions and tests, a posteriori, the accuracy with which the cases are attributed to the correct groups; it is a test of the accuracy of the discriminant functions to discriminate between groups.

At all habitats the DFA correctly assigned 80% or more of the samples. At the bench two samples were misclassified to pinyon-juniper, and at the pinyon-juniper two were misclassified to the bench. These two habitats are broadly overlapping on DF axes 1 and 2.

![Graph of canonical variables](image)

**Fig. 2.** Relationship of each habitat based on discriminant function analysis of perennial vegetation on the first two discriminant function axes (canonical variables), which account for 65% of the vegetative variance. A = bench, B = Casa Chiquita, C = Pueblo Bonito, D = wash, and E = pinyon-juniper.
Table 3. Results of the discriminant function analysis bootstrap analysis to determine the accuracy of classifying cover samples to their correct habitats. See text for explanation.

<table>
<thead>
<tr>
<th>Group</th>
<th>% correct</th>
<th>Bench</th>
<th>Casa Chiquita</th>
<th>Pueblo Bonito</th>
<th>Wash</th>
<th>Pinyon-Juniper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bench</td>
<td>92</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Casa Chiquita</td>
<td>80</td>
<td>0</td>
<td>20</td>
<td>4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Pueblo Bonito</td>
<td>88</td>
<td>0</td>
<td>1</td>
<td>22</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Wash</td>
<td>80</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td>Pinyon-Juniper</td>
<td>92</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>21</td>
<td>28</td>
<td>20</td>
<td>31</td>
<td></td>
</tr>
</tbody>
</table>

(Fig. 2). They are also similar in species composition, species richness, and cover (Table 1). Casa Chiquita and Pueblo Bonito were classified by Kelley and Potter (1974) as belonging to the same habitat type; thus, it is not surprising that four samples from Casa Chiquita were misclassified to Pueblo Bonito and one from Pueblo Bonito was misclassified to Casa Chiquita. The perennial vegetation at Pueblo Bonito was more variable than that at Casa Chiquita, and two samples were misclassified to the pinyon-juniper, which shared four species with Pueblo Bonito. The wash was the most variable habitat on DF axes 1 and 2 and had three samples misclassified to pinyon-juniper and two to Pueblo Bonito.

Perennial Plant Species Diversity and Cover

The bench had the second highest species richness and the highest diversity according to the two diversity indices (Table 1). It also had the lowest cover of the five habitats. The pinyon-juniper habitat was similar to the bench in its high species diversity, particularly richness, and low cover values. On the floodplain, Casa Chiquita had considerably lower diversity than the bench, but cover that was similar in value. Pueblo Bonito had similar diversity to Casa Chiquita, but much higher cover. The wash had similar cover, but greater diversity.

Annual Plant Species Density and Diversity

At all five areas sampled for annual plant densities the total densities were considerably higher in 1979 than in the following two years (Table 4). Annual species richness was also higher during 1979, with most species occurring only in that year. The densities varied considerably from site to site, the floodplain sites producing higher annual densities than the upland locations.

The annual species composition at Werito’s Rincon was different from the other sites (Table 4, Fig. 3). In 1979 pinnate tansy-mustard (Descurainia pinennis) was the dominant annual in terms of density at all sampling locations except Werito’s Rincon. There, stickleaf (Mentzelia spp.) was the most abundant.

Biomass Measures

At the floodplain sites of Casa Chiquita and Pueblo Bonito the high annual plant densities were accompanied by high biomass in 1979 (Table 5, Fig. 4). At Werito’s Rincon, in spite of densities similar to those at Casa Chiquita, the total biomass and seed biomass were much lower in 1979. The differences between these study areas in biomass may have been related to the differences in species composition of the annual populations at the two sites or to local differences in soil conditions and water availability. Overall, the flood plain sites were more productive than the upland sites during 1979. Biomass was drastically reduced at Casa Chiquita and Pueblo Bonito in 1980. However, at the upland sites of Pueblo Alto and the bench, total plant biomass and seed biomass were higher than in 1979. The biomass figures include grasses, a component of the perennial vegetation whose growth and reproduction may not be affected by winter-spring moisture until later in the same year or the following year. Biomass was low at all sites in 1981.

Discussion

Because perennial plant species are relatively stable components of the plant community, measurements of their characteristics
provide information that can be used to distinguish one habitat type from another. The results of this study indicate that the wash, the floodplain, the bench, and the mesa tops are distinct habitat types. Individual species distribution may overlap habitat types, but each type is distinguished either by the presence of species unique to that habitat or by the greater dominance of particular species over others.

One of the most conspicuous characteristics of annual plant productivity is the variability from year to year. Juhren et al. (1956) found that different constellations of annual species germinate under specific combinations of temperature and rainfall at Joshua Tree National Monument in southern California. During some years only a few individuals occurred. Likewise, in Nevada, Beatley (1969) observed that biomass of annual species fluctuated both spatially and temporally, depending on local conditions.

At Chaco Canyon annual spring plant densities fluctuated drastically from year to year during the period 1979–1981. We believe that the dramatic abundance of annuals in 1979 was due to late winter and spring precipitation that fell at Chaco Canyon in 1978–1979. During December and January mean monthly temperatures were low (Fig. 5), resulting in low water loss from soil and low evapotranspiration rates. These climatic conditions were favorable for the germination and growth of annuals to reproductive maturity. Conditions were particularly favorable for pinnate tansy mustard, which, we believe (based on densities), accounts for most of the increase in total biomass and seed biomass on the study plots. However, perennial grasses also contributed to the total. Different climatic conditions produce different dominant species in the annual plant populations from year to year, and there are years when annual species are rare or absent. Another characteristic of annual production is spatial variability. Within a limited geographic area such as Chaco Canyon, the abundance and species composition of annual plant populations differ from habitat to habitat during the same growing season. Patten (1978) noted similar differences in productivity in annual plants in different microhabitats within a Sonoran Desert shrub community. During the winter and spring of 1978–1979 the climatic conditions were probably the overriding factors in the abundance of annuals throughout Chaco Canyon. The differences
Fig. 3. Total plant and seed biomass at five sites at Chaco Canyon during three years.

in the species composition and the productivity between habitat types were probably a result of local characteristics of soil and physiography.

**SUMMARY**

We measured attributes of both perennial and annual plant species in four habitat types at Chaco Canyon. These habitat types were found to be distinct, based on perennial species representation and/or relative dominance of perennial species. Diversity based on perennial species was higher on the bench and in the wash, and the lowest by all measures of diversity at Pueblo Bonito.

**Table 5. Vegetation biomass of annual plants and grasses at five locations (g/m²).**

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Mean</th>
<th>SE</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Casa Chiquita</td>
<td>1979</td>
<td>98.8</td>
<td>12.63</td>
<td>21.8</td>
<td>2.52</td>
</tr>
<tr>
<td></td>
<td>1980</td>
<td>28.6</td>
<td>6.93</td>
<td>4.6</td>
<td>1.12</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>3.8</td>
<td>0.97</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pueblo Bonito</td>
<td>1979</td>
<td>126.8</td>
<td>9.65</td>
<td>20.56</td>
<td>1.82</td>
</tr>
<tr>
<td></td>
<td>1980</td>
<td>24.26</td>
<td>5.02</td>
<td>2.9</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>26.18</td>
<td>4.26</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Bench</td>
<td>1979</td>
<td>5.52</td>
<td>0.58</td>
<td>0.74</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>1980</td>
<td>13.46</td>
<td>2.12</td>
<td>1.98</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>5.08</td>
<td>0.74</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pueblo Alto</td>
<td>1979</td>
<td>32.50</td>
<td>2.27</td>
<td>5.44</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>1980</td>
<td>57.46</td>
<td>4.51</td>
<td>8.54</td>
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</tr>
<tr>
<td></td>
<td>1981</td>
<td>15.94</td>
<td>1.29</td>
<td>4.72</td>
<td>0.45</td>
</tr>
<tr>
<td>Werito’s Rincon</td>
<td>1979</td>
<td>42.34</td>
<td>2.91</td>
<td>4.72</td>
<td>0.45</td>
</tr>
</tbody>
</table>

*We collected biomass samples from only 10 plots at Casa Chiquita in 1979.

Fig. 4. Total density and density of dominant annual species from five sites at Chaco Canyon in 1979.
At Chaco Canyon annual plant species are an important component of the plant community even though their appearance is highly variable both spatially and temporally. Annual plant species occurred in all habitat types in varying densities and profoundly affected the aboveground biomass from place to place and from year to year. Annual plant species density, diversity, and biomass were high on the floodplain sites during 1979 but low during the other two years. Annual plants on the bench had the lowest production measured during 1979, when the floodplain sites were producing at their peak. Annual plant density at Pueblo Alto and Werito’s Rincon was also high during 1979; however, the greatest
biomass at Pueblo Alto was measured in 1980, during the year following the wet winter
spring of 1978–1979. This apparently reflects the development of grasses that responded to
the wet period more slowly than annual plants. Thus, while the floodplain habitats
were the most productive during exceptionally wet years, the upland habitats appeared
to be more productive during drier years or during years when precipitation arrived during
another season.

Measurements of perennial plant diversity are poor predictors of productivity. Those
habitats with the highest perennial alpha diversity may be the poorest in terms of plant
productivity. The bench, characterized by high perennial diversity, was low in annual
diversity and productivity during 1979. On the other hand, the Pueblo Bonito study area
was characterized by low perennial plant diversity, but annual plant species were diverse
and productivity was high during the favorable year of 1979. Our study indicates that
during favorable years, annual plant species have patterns of dominance and diversity that are
separate from those of perennial species. Both perennial and annual components
should be considered in measurements of diversity and productivity within plant com-

ACKNOWLEDGMENTS

The Division of Cultural Research, National Park Service, Santa Fe, New Mexico, provided funding for the fieldwork portion of
this project. Glen Lanier helped gather the annual plant productivity information during
Division of Cultural Research, National Park Service, provided the illustrations.

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