Journal of Arid Environments 72 (2008) 1562–1572

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Patterns of mast production in pinyon and juniper woodlands along a precipitation gradient in central New Mexico (Sevilleta National Wildlife Refuge)

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ARTICLE INFO

Article history:
Received 29 September 2006
Received in revised form
5 December 2007
Accepted 27 February 2008
Available online 18 April 2008

Keywords:
Arid ecosystems
Juniper monosperma
Pinus edulis
Quercus turbinella
Sevilleta LTER

ABSTRACT

This paper reports on an 8-year continuing project with the Sevilleta Long-Term Ecological Research program (LTER) in central New Mexico aimed at the study of dynamics of woodland ecosystems. The study of mast production was conducted at six experimental woodland sites situated across an elevational gradient of 1500–2000 m in proximity to permanent meteorological stations. The dominant woody species were *Juniper monosperma*, *Pinus edulis*, and *Quercus turbinella*. Functioning of arid ecosystems of the Southwest undergoes seasonal, annual and multidecadal fluctuations which link to corresponding dynamics of available moisture. Results of the 1997–2004 study show a gradual decrease in mast production of all three species at all six sites, due to a continuing drought in this period. Mast production in a given year is determined to a considerable extent by available moisture during the entire growth year, from the previous spring to the current summer. The areas of oak–pinyon–juniper woodlands with higher elevation and highest precipitation generally have the highest yield of juniper berries, pinyon nuts and acorns. The severe drought of 2001–2003 has been accompanied by a mass dying of mature pinyon pines and loss of foliage in junipers. According to our observations, there is no correlation between mast production and amount of precipitation in the current year's monsoon period (June–September). A high correlation between acorn production and non-monsoonal precipitation (October–May) was established, but no such correlation was found for juniper berries and pinyon nuts. Weather conditions (wind, temperature, and moisture) of late May are a critical factor determining the success of fertilization and subsequent mast production in all three species.

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1. Introduction

Arid woodlands are one of the world most widespread biomes occupying significant area of subtropical thermal belt on each of six continents (Walter, 1979). They represent the most widespread natural biome in the North American Southwest where ecosystems of this kind cover about one-third of the total area in the region (West and Young, 2000). However, despite of broad geographic range of arid woodlands, they have been little studied with respect to production, particularly fruiting mast.

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0140-1963/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.jaridenv.2008.02.021

Dominant trees in coniferous–deciduous mixed woodland ecosystems of central New Mexico include one-seed juniper (*Juniper monosperma*), Colorado pinyon pine (*Pinus edulis*), and shrub live oak (*Quercus turbinella*). Juniper berries, pinyon nuts and acorns are an essential part of total primary production in woodland ecosystems. Seeds of juniper, pinyon and oak are the only source of tree recruitment in woodlands (Chambers et al., 1999); they also serve as a vital food staple for numerous animals species (Christensen et al., 1991; Forcella, 1981; Hope and Parmenter, 2007).

The aim of this study is to determine if there is a significant correlation between mast production of three dominant tree species (juniper, pinyon pine and oak) and patterns of moisture distribution. The study began in 1997 as a part of Sevilleta LTER program, continued through 2004, and is ongoing.

2. Methods

2.1. Study area

The area of our study is located within the Sevilleta National Wildlife Refuge (NWR), Socorro County, in central New Mexico, approximately 80 km south of Albuquerque. The severe drought of the 1950s had considerable impact on tree density and age structure of woodland ecosystems at the Sevilleta NWR. Significant numbers of juniper trees and many pinyon pines died during the drought. The area was a sheep and cattle ranch in the past, and the signs of intensive grazing are still noticeable. Following transfer of the Sevilleta lands to the US Department of the Interior, Fish and Wildlife Service in 1974, the land received the status of National Wildlife Refuge, and since then has been managed in its natural state.

In an arid environment of the Southwest, water is the most significant abiotic driver of ecosystem functioning. The climatic conditions in the Sevilleta area are characterized by two major patterns (Milne et al., 2003): (a) a multi-decadal variability in precipitation associated with approximately 50-year cycles of the Pacific Decadal Oscillation, and (b) annual dynamics in moisture influenced mostly by 3- to 4-year El Niño Southern Oscillation. There is also a seasonal pattern: non-monsoon precipitation of October–May, and monsoon rains of June–September. The summer monsoon brings about 60% of total precipitation (Sevilleta LTER web site: www.sev.lternet.edu).

This general climatic pattern varies significantly from year to year, resulting in high variability of seasonal and annual water inputs. During the period of study, the Sevilleta area and the rest of the southwestern US were under the influence of severe drought, that has characteristics of the drought of the 1950s.

In order to account for diversity of the Sevilleta woodland ecosystem with respect to mast production, we chose six research sites which differed in their location, elevation and composition of dominant woody species. The presence of a meteorological station nearby was a main selection criterion. Six permanent plots of 1 ha each was chosen in the vicinity of local meteorological station (Fig. 1). The six plots represented a range of woodland sites across the elevation/precipitation gradient: (a) oak–pinyon–juniper woodland, Cerro Montoso site (CM), 1971 m, (b) pinyon–juniper woodland, West Mesa

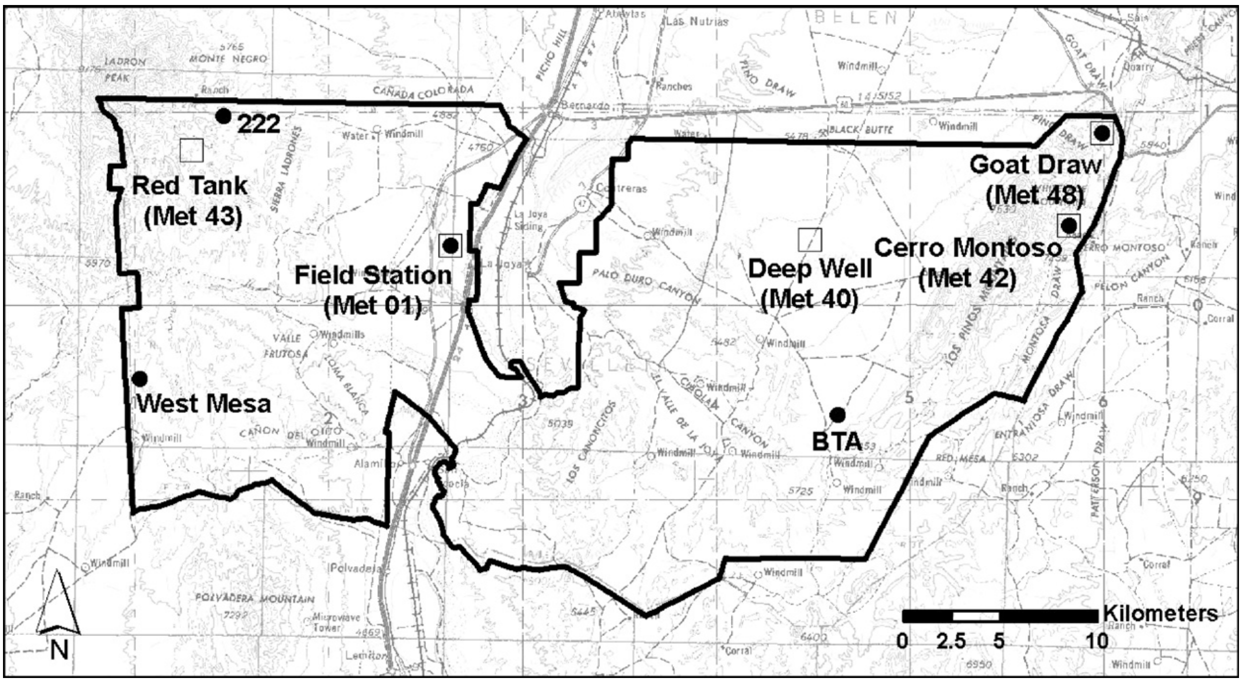

Fig. 1. Map of the Sevilleta National Wildlife Refuge with location of mast production research sites and meteorological stations (www.sev.lternet.edu).

site (WM), 1766 m, (c) oak–juniper savanna, Goat Draw site (GD), 1796 m, (d) juniper savanna, 222 site (222), 1780 m, (e) mesquite–juniper savanna, Field Station site (FS), 1469 m, and, (f) grassland with advancing juniper trees and creosote bushes, the Biome Transition Area site (BTA), 1596 m.

Two sites, Cerro Montoso and Goat Draw, were located in an intermontane valley in the Los Pinos Mountains, in the eastern part of the Sevilleta NWR. The BTA site was also located in the eastern half of the Sevilleta NWR, at the southern edge of Mackenzie Flats. The three other sites were situated in the western part of the Sevilleta NWR, on slopes of Ladron Peak: two "mesa type" sites, West Mesa and 222, and a Rio Grande valley site, the Field Station. At three of the sites (Cerro Montoso, Goat Draw and Field Station), meteorological stations were located on the study plot. Weather conditions at the BTA site were measured by the LTER Deep Well meteorological station, approximately 15 km northwest of the site. Two sites, the West Mesa and the 222 sites, were characterized by data of the Red Tank meteorological station located in between the two sites and at a similar elevation (Fig. 1).

Characteristics of average amount of precipitation for non-monsoon period, monsoon period and water year for each met station are given in Table 1. Weather data for those five meteorological stations are available at the Sevilleta's web page www.sev.lternet.edu.

2.2. Mast production sampling

All trees and shrubs within the 1 ha plot were tagged and mapped with the use of a GPS or compass. Height and two diameters (in directions of north–south and west–east) of the canopy were measured for all woody plants. Juniper and pinyon pine trees were subdivided into five age/size groups, based upon the mean canopy radius of juniper and diameter at breast height (DBH) of pinyon (Table 2). For the oak trees, the canopy surface area of all individual trees was measured.

Assessments of berry, cone and acorn production were carried out in August of each sample year when the fruits were ripening. Three different methods were developed to estimate an annual production of berries, cones/seeds and acorns.

For juniper, the percentage of twigs with berries and quantity of berries per twig were determined every year for all trees in the plot. The average twig had a length of 40 cm and trunk diameter of 12 mm. The following five categories of trees were identified: (a) with no berries, (b) less than 5% of twigs with berries, (c) 5–34% of twigs with berries (average 20%), (d) 35–65% of twigs with berries (average 50%), and (e) more than 65% of twigs with berries. The quantity of berries per twig was represented by seven categories: (I) no berries, (II) single berries, and (III) very low, (IV) low, (V) medium, (VI) high, (VII) very high quantity of berries (Table 3).

Estimates of berry production were made separately for the upper and lower halves of the crown, and for three quadrants (northwestern, northeastern and southern sectors). Each of the seven categories above was characterized by number and biomass of berries per twig (Table 3). To determine berry production per tree and per hectare, the average number of twigs on trees of different size groups was estimated. Samples of 500–800 berries from a plot were taken randomly each year to determine the percentage of well (fully)-developed and underdeveloped berries, as well as berries with the pericarp damaged by insects.

Unlike juniper, pinyon requires three growing seasons to form mature fruits (Jeffers, 1994). Generative female buds are formed in the fall of the first year. The following spring they develop into female strobili which are pollinated in May–June. The young brown-colored conelets grow until the end of the summer. During the second spring, the cones become green and swollen and the development of seeds begins. The seeds (nuts) ripen in August. The number of the third-year, ripened green cones is counted visually on all trees within 1 ha plot. The unit of pinyon pine mast production is a number of filled seeds per one mature tree.

During the 2 years of development, cones are subjected to predation (Forcella, 1978). First, the female stems on which young cones are formed are damaged by drilling insects (larvae of moth, *Dioryctria* sp., *Eucasma* sp., and pinyon cone beetles, *Scolytidae*). These stems, as well as juvenile cones on their tops, dry up. Some conelets are destroyed by scolytid beetles during the first summer. The following summer, green swollen cones are attacked by the larvae of *Dioryctria albovittella*, known as "pine coneworms" (Christensen and Witham, 1993; Cobb et al., 1997; Forcella, 1980), which destroy ripening nuts.

Table 1
Elevation (m) and average amount of precipitation (mm) at meteorological stations located within Sevilleta's woodland sites (1996–2004)

Ecosystem type, meteorological station	Elevation (m)	Non-monsoon (mm)	Monsoon (mm)	Water year (mm)
Oak–pinyon–juniper woodland (Cerro Montoso)	1971	160 ± 60	242 ± 84	402 ± 133
Oak–juniper savanna (Goat Draw)	1796	141 ± 105	151 ± 47	292 ± 63
Pinyon–juniper woodland, juniper savanna (Red Tank)	1766	117 ± 46	162 ± 60	279 ± 74
Biome transition area (Deep Well)	1596	101 ± 52	146 ± 32	247 ± 45
Mesquite–juniper savanna (Field Station)	1469	103 ± 58	102 ± 34	205 ± 23

Data of these five meteorological stations characterize the following woodland sites: met station 42—oak–pinyon–juniper woodland (Cerro Montoso site); met station 48—oak–juniper savanna (Goat Draw site, for the period 1998–2004); met station 43—pinyon–juniper woodland (West Mesa site) and juniper savanna (222 site); met station 40—Biome Transition Area Site; met station 1—mesquite–juniper savanna (Field Station Site).

Table 2
Size of juniper and pinyon pine trees of major age groups

	Age groups	Juniper, canopy radius (cm)	Pinyon pine, DBH (cm)
I	Seedling	⩽40	⩽2
II	Young	40–125	2–8
III	Mid-age	126–200	9–15
IV	Old	201–275	16–22
VI	Very old	⩾275	⩾22

Table 3
Relative and absolute value of juniper berry production, per twig

Relative value	Number of berries	Dry mass (g)
Single	⩽10	⩽1.0
Very low	10–50	1.0–5.0
Low	51–150	5.1–15.0
Medium	151–500	15.1–50.0
High	501–1250	50.1–125
Very high	⩾1250	⩾125

To estimate pinyon nut production, samples of 100 green ripen cones were collected randomly on 30–50 trees at each of three pinyon sites, and the ratio of filled nuts to empty nuts and percentage of cones and nuts damaged by predatory insects were calculated. Several hundred ripened cones and filled ripen seeds were measured to determine their average weight.

A different method was used to estimate acorn production. First, the canopy surface area of each oak tree was measured. The number of acorns, separately categorized as well-developed, undeveloped or damaged by larvae of *Curculionidae* beetles was counted within a frame of $31 \times 32\,cm^2$, projected onto the crown surface of each oak tree in three to five repetitions.

A comparison of production of the three woody species during the 8-year period of our study was done on the basis of fruit biomass per unit of count: well-developed undamaged berries per twig for juniper, filled seeds per mature tree for pinyon pine, and well- developed undamaged acorns per $0.1\,m^2$ of canopy surface for oak. Additionally, biomass of berries, pinyon seeds and acorns per ha was estimated in order to compare production at the six sites and its annual fluctuation over the 8 years.

2.3. Sex structure of juniper populations

Pines and oaks are monoecious species, while junipers, including one-seed juniper are dioecious (Chambers et al., 1999; Mirov, 1967). Sex ratio were estimated at six sites for all age (size) groups of juniper trees. The proportion of female trees in all sites of the Sevilleta NWR was slightly greater (53–58%) than that of male trees. Some mature female trees, during the period of study, did not produce any berries (so-called "vegetative" form of female tree), while some male trees were able to form not only male strobili but female strobili and berries as well.

3. Results

3.1. Population structure of woody species

All sites differed significantly in woody plant density and species composition. One-seed juniper was the dominant woody species among both tree and shrub species in all sites, except in the mesquite–juniper savanna and BTA (Table 4). Pinyon pine was an essential component of woody vegetation in oak–pinyon–juniper woodland site. Shrub live oak in the oak–juniper savanna and oak–pinyon–juniper woodland sites, formed an understory that covered only 6–8% of total area.

Total density of trees in woodland ecosystems of the Sevilleta is directly related to elevation: as elevation increases, so does the amount of precipitation. The correlation between precipitation amount and elevation is significant, especially that of the non-monsoon season ($r^2 = 0.66$) and the whole water year ($r^2 = 0.65$). Amount of monsoonal rain correlates with elevation to the lesser extent ($r^2 = 0.48$). Density of woody species (both trees and shrubs) increases with elevation and the amount of precipitation. The correlation of tree density with precipitation of water year was found to be the strongest ($r^2 = 0.88$), followed by non-monsoon period ($r^2 = 0.77$) and monsoon rain ($r^2 = 0.71$).

Table 4
Density of woody species in woodland sites of the Sevilleta NWR

Species	CM	GD	WM	222	FS	BTA
Trees						
Total number (per 1 ha)	788	212	305	188	10	31
Same, without seedlings	692	163	305	173	8	19
Juniper monosperma						
Total	424	175	285	188	10	31
Seedlings	9	44	n.d.	15	2	12
Mature trees	415	131	285	173	8	19
Pinus edulis						
Total	364	37	20	–	–	–
Seedlings	87	5	15	–	–	–
Mature trees	277	32	5	–	–	–
Shrubs						
Total number (per 1 ha)	166	147	n.d.	5	52	192
Same, without seedlings	166	147	n.d.	5	52	94
Quercus turbinella	115	116	n.d.	–	–	–
Cerocarpus montanus	32	12	n.d.	–	–	–
Rhus trilobata	8	19	n.d.	4	7	4
Mahonia sp.	11	–	n.d.	–	–	–
Larrea tridentate						
Seedlings	–	–	n.d.	–	–	98
Mature	–	–	n.d.	1	3	90
Prosopis glandulosa	–	–	n.d.	–	42	–
Trees and shrubs						
Total number (per 1 ha)	954	359	n.d.	192	60	223
Same, without seedlings	858	310		178	60	109
Average area to support one mature specimen (m^2)	11.6	32.3	32.8	56.2	166.7	91.7

Meaning of abbreviated names for six sites: CM—oak–pinyon–juniper woodland; GD—oak–juniper savanna; WM—pinyon–juniper woodland; 222—juniper savanna; FS—mesquite–juniper savanna; BTA—biome transition area; n.d.—no data.

The highest density of woody plants was observed at the highest elevation oak–pinyon–juniper woodland site of Cerro Montoso, and the lowest at the lowest elevation mesquite–juniper savanna site of Field Station, which was located 500 m lower. Average land area required to support one mature specimen of woody plants increases sharply as elevation and amount of precipitation decrease. This measure which we call "environmental index of woody plants holding capacity" (Table 4) is 11.6 m^2 at the oak–pinyon–juniper woodland (1971 m), then increases to 32–56 m^2 at elevation of 1800 m (oak–juniper savanna, pinyon–juniper woodland and juniper savanna sites), increases again to 91.7 m^2 at 1600 m (BTA site), and reaches 166.7 m^2 at 1469 m (mesquite–juniper site).

The severe drought of the 1950s has resulted in significant tree mortality at the Sevilleta NWR. Juniper and pinyon were most susceptible to water stress. By our estimation, 10–15% of all mature juniper trees were standing dead. The proportion of dead individuals in both juniper and pinyon populations increased at lower elevation. In 2002, a wave of mass dying began in pinyon populations of the Sevilleta NWR and by late summer of 2004, around 6–7% of old pinyon trees died. Oak trees are much more tolerant to annual moisture deficit and react to drought by shedding their foliage completely. Even though shrub live oak is an evergreen species, it is able to restore the loss of its foliage in 1–2 years.

3.2. *Dynamics of precipitation amount*

The 8-year period of the study was characterized by a gradual decrease in amount of precipitation (Fig. 2). This reflects an intensification in drought conditions in the Southwest in general. For the Sevilleta NWR area, reduced moisture was particularly obvious in relation to the monsoonal precipitation and precipitation of the whole water year. Amount of non-monsoonal precipitation also declined but at a considerably slower rate than the other two amounts. While the trend for decrease in precipitation was observed, precipitation was relatively high in 3 years: 1997, 2001 and 2004. The years 2002 and 2003 were especially dry.

At some sites, the dynamics of precipitation reflect in general the picture for the whole Sevilleta NWR (Fig. 2). At the same time, the higher elevation sites had a lower annual amplitude of differential precipitation amount, while the variation was more pronounced for lower elevation sites.

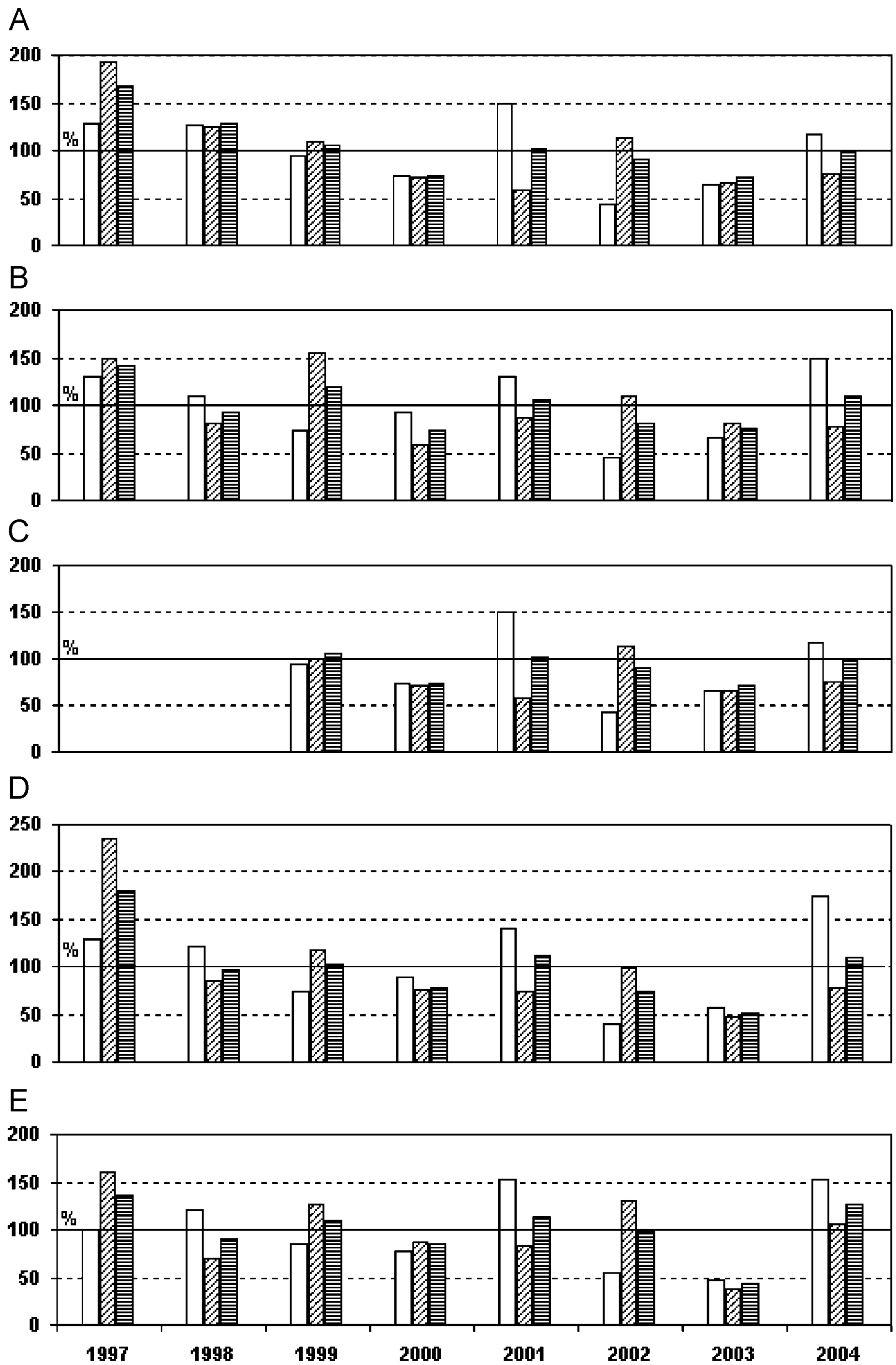

Fig. 2. Dynamics of amount of precipitation in six sites of the Sevilleta NWR (1997–2004). Precipitation amount for each site is given in percentage of average, for water years of 1997–2004. Bars represent, from left to right, non-monsoon period, monsoon period and the water year. Graphs A represents oak–pinyon–juniper woodland (Cerro Montoso site), B represents pinyon–juniper woodland (West Mesa site) and juniper savanna (222 site), C represent oak–juniper savanna (Goat Draw site), D represents mesquite–juniper savanna (Field Station site), and E represents biome transition area (BTA site).

3.3. Spatial patterns of mast production in three species

Mast production of each of the three woody species was not uniform within one habitat, and varied considerably from site to site due to differences in environmental conditions and tree age structure and sex composition. As an example of spatial heterogeneity of juniper berry production, the data for 2001 is provided (Table 5).

Table 5
Spatial patterns of juniper berry production at the Sevilleta Sites (2001)

Characteristics	CM	GD	WM	222	BTA	FS
Percent of female trees with						
No berries	28	53	22	55	14	6
Single berries	7	57	37	50	36	88
Very low production (30 berries)	19	34	33	19	39	12
Low production (100 berries)	45	7	20	22	20	–
Medium production (325 berries)	25	2	10	9	5	–
High production (600 berries)	4	–	–	–	–	–
Percent of female trees with production equal or higher than very low						
Young trees	45	21	12	7	44	–
Mid-age trees	92	26	56	20	50	–
Old trees	94	42	100	72	71	7
Percent of male trees with berries	3	5	2	7	5	29

Meaning of abbreviated names of six sites is given in Table 4. Production represents an average number of berries per twig.

In all six sites, 45–94% of all female mature juniper trees produced berries. The largest number of fruit-bearing female trees was observed in the group of old (large) junipers. The yield of berries at all sites was very low on average (30 berries per twig). The Cerro Montoso site was noticeably most productive: 70% of the trees had low to middle berry production (100–300 berries per twig).

Some male trees were able to produce single berries, and this phenomenon varied through time. In 2001, compared with previous years, the number of male trees with berries on some of the twigs was noticeably higher. The ability of one-seed juniper to produce occasionally both male and female strobili on the same twig has observed in New Mexico earlier (Johnsen, 1962).

3.4. 8-year mast production in three woody species

Fig. 3 shows fruit production of three woody species in six sites with juniper, three sites with pinyon and two sites with oak. Production figures for juniper are measured as number of well-developed undamaged berries per 1 twig, for oak, in number of well-developed undamaged acorns per 0.1 m^2 of canopy surface area, and for pinyon, in number of filled seeds per 1 mature tree.

During the 8-year study, each of the three species clearly manifested a trend for decrease in production. Though quantitative data for 1997 is available only for the 222 sites, 1997, according to our observations, was the most productive year for all six sites of the Sevilleta NWR.

The dynamics of production of each of the three species was similar at the sites where these species were found. For juniper (Fig. 3A), the peak of production in 1997 and 1998, was followed by a depression in 1999–2000. Some increase in berry production was noted in 2001 in all sites except for the FS site. The following year, in 2002, production of berries again fell to almost zero. In 2003–2004, production increased to average value in most sites, although berry production at the high-elevation CM site was nearly triple the average annual production.

A very similar dynamics was observed for oak mast production (Fig. 3B). The major difference was a complete absence of acorn production in 2002 and 2003, whereas junipers managed to produce a low level of berries (Fig. 3A).

The dynamics of pinyon seeds production is somewhat different (Fig. 3C). Unlike juniper or oak, which exhibited a 3-year interval between three peaks of relatively high production, the production of pinyon increased slightly only in the 7th year. There was little pinyon nut production during 4 years (2000–2003). The depression in pinyon nut production was manifested not only in a sharp decrease in cone numbers, but also in an increase of the number of unfilled seeds. In 1998, the share of unfilled seeds was on average 35%, while in 1999 it was 70%, and in 2004 it was 80% at the three sites.

Thus, Fig. 3 shows a very similar pattern in dynamics of mast production of juniper and oak, with 3-year intervals dividing three peaks of berries and acorns production. The dynamics of pinyon seed production demonstrates a different picture: the peak of production in 1997–98 was followed by the 6-year depression of 1999–2004. A high production of each of the three species followed the years with above-average amount of precipitation, primarily non-monsoon and total water year precipitation.

Juniper berries dominated total biomass of the three woody species (Table 6). During the years of high production, the share of juniper berries reaches 85–98% of total fruit biomass. The biomass of acorns was second to that of juniper with 25% on average, but as high as 62% (oak–juniper savanna site, 2001). Pinyon seeds were a noticeable component of total mast production only at the oak–pinyon–juniper woodland site comprising 2–9% of total biomass of the three species.

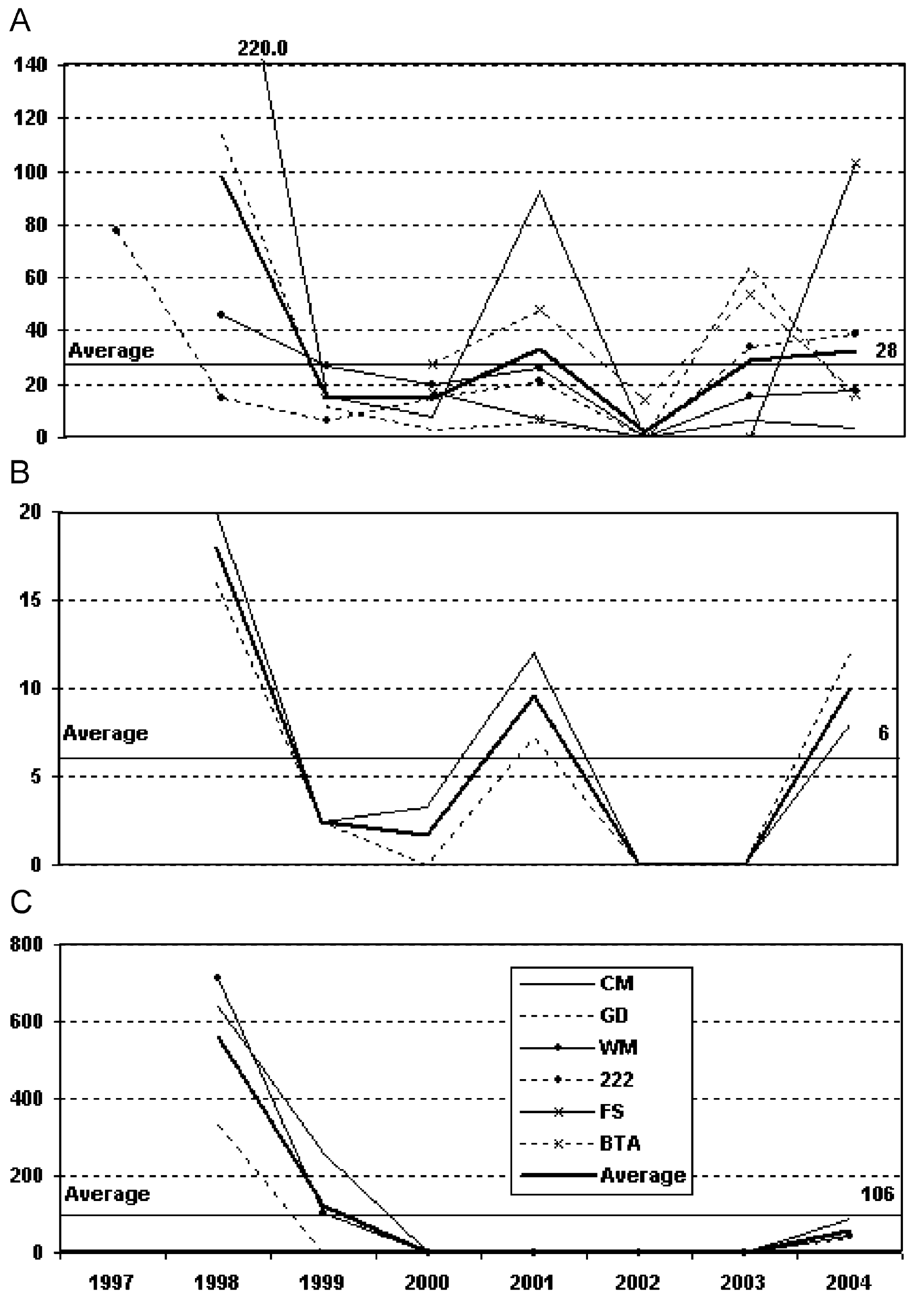

Fig. 3. Dynamics of mast production in six sites of the Sevilleta NWR (1997–2004). Graph A shows a number of well-developed undamaged juniper berries, per twig. Graph B shows a number of well-developed undamaged acorns, per 0.1 m^2 of canopy surface area. Graph C shows a number of filled pinyon seeds, per mature pine tree. Meaning of abbreviated names of six sites is given in Table 4.

4. Discussion

In central New Mexico, the water regime fluctuates on decadal, annual and seasonal time scales. According to Milne et al. (2003), In central New Mexico generally, and the Sevilleta NWR in particular, above average precipitation comes in fall, winter and spring during the cool phase of El Nino Southern Oscillation (ENSO) events, with below-average precipitation during the warm phase (La Nina) periods (Milne et al., 2003). ENSO occurs with an average episodic periodicity of 3–4 years and usually lasts only one season. Summer rain comes to New Mexico with the Mexican monsoon. The monsoon moisture of June–September is over 50% of total year precipitation (51–59% for the period of 1991–2004). Unlike winter precipitation, monsoon rains come in the form of scattered thunderstorms, which do not last long, do not

Table 6
Dynamics of mast production of three woody species in six sites at the Sevilleta NWR (1997–2004, kg/ha, dry weight)

Site	Species	1997	1998	1999	2000	2001	2002	2003	2004
CM	Juniper	n.d.	1137.4	79.0	39.1	478.5	–	33.8	18.5
	Pinyon	n.d.	20.4	8.3	–	0.05	0.05	–	2.8
	Oak	n.d.	37.5	4.7	6.2	22.3	–	–	15.0
	Total	n.d.	1195.3	92.0	45.3	500.9	0.05	33.8	36.3
GD	Juniper	n.d.	232.1	23.3	5.3	11.4	–	131.2	26.3
	Pinyon	n.d.	1.3	–	–	–	–	–	0.2
	Oak	n.d.	40.7	6.4	–	18.5	–	–	30.5
	Total	n.d.	274.1	29.7	5.3	29.9	–	131.2	57.0
WM	Juniper	n.d.	190.0	110.0	81.2	109.0	–	65.4	74.0
	Pinyon	n.d.	2.4	0.3	–	–	–	–	0.1
	Total	n.d.	192.4	110.3	81.2	109.0	–	65.4	74.1
222	Juniper	210.5	39.1	16.9	40.8	57.3	–	88.6	105.6
BTA	Juniper	n.d.	n.d.	n.d.	5.1	8.9	2.6	9.9	3.0
FS	Juniper	n.d.	n.d.	n.d.	2.5	1.0	–	–	15.0

Meaning of abbreviated names of six sites is given in Table 4. Characteristics of mast production are: well-developed undamaged berries and acorns, and filled pinyon seeds.

Table 7
Climatic variables and biological responses in woodland ecosystems of the Sevilleta NWR

No.	Climatic variables	Biological responses
1	Weather conditions in last week of May and first week of June (amount of precipitation, air humidity and temperature, wind speed)	Success of pollination in trees
2	Amount of precipitation in current monsoon period (June–September)	(a) Summer growth of foliage (b) Forming of litterfall (c) Development of fruits (d) Damage of fruits by consumers
3	Amount of precipitation in monsoon period of previous year (June–September)	Development of generative buds in fall and strobili in following spring
4	Amount of precipitation in non-monsoon period (October–May)	Development of generative buds in fall and strobili in following spring
5	Annual fluctuations in precipitation	(a) Annual production of foliage (b) Annual amount of litterfall (c) Annual increment of tree-ring (d) Annual changes in mast production

penetrate deep into soil and evaporate quickly. Accordingly, we acknowledge that the ecological effects of moisture in monsoon and non-monsoon periods on Sevilleta NWR's woodlands are essentially different.

We hypothesize that the following five climatic variables (Table 7) are most significant factors for current dynamics of mast production and some other biological responses. The first factor to be analyzed is represented by weather conditions during 2 weeks of late spring (last week of May–first week of June) when pollination in juniper, oak and pinyon occurs. The weather factors during this time period that we believe to be important are wind, temperature, relative humidity and precipitation. We hypothesize that dry warm weather with prevailing strong winds are favorable for successful pollination of generative buds and results in higher mast production.

According to our observations at the Sevilleta NWR, development of both male and female generative buds occurs in each of the three species relatively synchronously during the above-mentioned 2-week period. Pollination itself lasts for about a week during which female strobili are receptive to male pollen. As such weather conditions may affect successful pollination as follows:

(a) *Air temperature:* Mean daily temperature over the Sevilleta varied during the period in the range 19.2–25.4 °C. The 3 years with relatively high mast production (1998, 2001, and 2004) were not exceptional compared to years of low mast production. The temperature during the pollination period was always relatively consistent. Therefore, this variable was not critical in dynamics of mast production.

(b) *Air relative humidity:* This parameter fluctuated more noticeably than air temperature with mean daily values ranging from 18.1% to 38.9%. In 1999, 2001 and 2004 when mast production was highest, air humidity was 10–32% lower than the long-term average for the 2-week period. In 2004, during the days when mass pollination in pinyon was observed, mean daily air humidity at the Cerro Montoso site was 44% lower than the average for the 2-week period, and 41% lower at the Goat Draw site.

(c) *Wind speed:* Values of mean maximum wind speed for the 2-week period vary less than air humidity but more than air temperature, from 8.1 to 14.3 m/s. Constant strong winds are typical for the Sevilleta NWR all year round, including the pollination time. In certain years very strong and gusty winds provide uniform dispersion of male pollen. For instance, pollination was especially successful in 2004 when maximum wind speed during the pollination period (May 28–June 2) was 60% higher than the average at the Cerro Montoso site and 11% higher at the Goat Draw site. Thus, strong winds favor fertilization and higher mast production. It is possible that wind speed is a more important factor for pinyon pine, than for juniper, due to its pollen larger size.

(d) *Precipitation:* Rainy weather delays blossoming and hinders fertilization in all wind-pollinated plants, including the three species which are the subject of our study. At the Sevilleta NWR, mast production was successful in years when no rain was observed during the pollination period. Rainy weather and high relative air humidity was associated with a decrease in both the number of pinyon cones and the number of fertilized filled seeds. Thus, in 2003 when the amount of precipitation during the pollination period was 1.5–4 times higher and air humidity was 30–50% above average, the success of pollination in pinyon was low. The following year, 75–80% of seeds in all sites were infertile and unfilled. As a result, while an average yield of cones was reached at the Cerro Montoso site, the production of filled seeds was very low.

Thus, weather conditions during the pollination period appeared to be critical factors which determined the success of fertilization and mast production in pinyon pine, one-seed juniper, and possibly shrub live oak. According to our observations, duration of the pollination period was 5–7 days, and its success was enhanced by dry, windy, and relatively warm weather.

The success of pollination in juniper also depends to a certain degree on the number of mature male trees in the population. For instance, at the 222 sites in 2004, the yield of berries was higher in those female trees close to mature male trees with greater pollen production.

However, the forming of a sufficient number of generative buds and the successful pollination of female strobili do not necessarily result in a good crop. Developing fruits are attacked by frugivorous insects, rodents and birds. Seed predation is especially significant in pinyon, is not as strong in oak and is much less for juniper berries. Percentage of damaged pinyon cones varies widely in different years and different habitats, but in general it is much higher when the yield is low (up to 80% of cones) and much lower (1–10% of cones) in years of high production.

The second variable which, as we hypothesized, may have potentially affected mast production was the amount of precipitation in the current year monsoon period (June–September). However, the relationship observed between this factor and mast yield in all three species was negligible. Correlation with amount of precipitation during the monsoon depended to a certain degree on quality of fruits and their damage by consumers. Summer precipitation also determined such ecological responses as annual foliage production and litterfall (Table 7).

The third variable we addressed was summer monsoon moisture from the previous summer. Assuming that the amount of precipitation in the current monsoon period may affect the mast yield of the following year, we determined the correlation between production and monsoon precipitation of the previous year (Table 7). However, no significant correlation was found.

The fourth variable considered was the non-monsoon precipitation of October–May (Table 7). A significant correlation ($r = 0.70$) was observed between acorn production and this variable. But for both juniper and pinyon mast production, the correlation with non-monsoonal precipitation was negligible. However, this meteorological factor can play a certain role for all three species because in the years with high fruit production of juniper and oak (1997–1998, 2001, and 2004) and pinyon (1997–1998, and 2004), the amount of moisture in the non-monsoon period was 1.2–1.7 times higher than in years when production was low.

During the especially dry non-monsoon periods of 2002 and 2003, the production of berries was particularly low, and oak and juniper bore no fruit at all. Moreover, in 2002, all oaks at the Sevilleta completely shed their foliage by early June and no blossoming was observed. At the Goat Draw site in 2002, the number of juniper strobili was sufficient forming an average yield of berries, but very dry and hot weather during June and July interrupted further development of the strobili.

The same situation was observed in 2002 at the Cerro Montoso site: the shortage of moisture in winter and spring (2001–2002) slowed the development of strobili in 90% of male trees and 98% of female trees, resulting in zero yield of berries. Pinyon also initially formed abundant male strobili which stopped to developing and died after reaching 1 cm in length. Due to the fall–winter drought of 2001–2002, the number of female stems at the Cerro Montoso site was very low the following spring, and these dried when their length was only 1.0–1.5 cm. Therefore, due to pinyon pine's 2 year reproductive cycle, in 2003 the yield of cones was zero. Obviously, more data are needed for analyzing the role of non-monsoonal precipitation in the forming of mast production.

Relatively high correlation has been found between production of berries and acorns and actual precipitation of the whole growth year, i.e. from the previous spring to the current summer (fifth variable, Table 7). For juniper the coefficient correlation is 0.52, and for oak 0.76. For pinyon seeds, the correlation is weaker than for acorns ($r = 0.57$).

The data and analyses of this study have shown both spatial and temporal patterns in mast production of juniper, oak and pinyon pine over the 8 years of sampling and we have provided a list of factors that we believe may regulate these processes. Clearly, the addition of future years of data will help clarify and strengthen the relationship between climate dynamics and mast production, and will help in predicting the potential effects of long-term climate change on these important semi-arid woodland tree species.

Acknowledgments

We thank the US Fish and Wildlife Service for the use of the Sevilleta National Wildlife Refuge for this study, and Greg Shore and Carla Restrepo for their help in tree mapping at the studied sites, Mike Friggens for sampling juniper berries to assess their damage by insects, and Doug Moore for providing LTER meteorological data. In addition, we are grateful to Dr. Charles Greer (Indiana University) and Dr. Walter Whitford (New Mexico State University) for valuable comments on the manuscript.

Financial support for this work was provided by Sevilleta LTER Program (NSF DEB94-11976, DEB00-80529, and DEB02-17774) and the NSF Ecology of Infectious Diseases Program (NSF DEB03-26757).

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