Holocene vegetation and climate change on the Colorado Great Plains, USA, and the invasion of Colorado piñon (Pinus edulis)

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INTRODUCTION

The study of long-term vegetation change during the late Quaternary has been instrumental in understanding the modern geographical distributions of species, as well as the timing and location of corridors for movement of plant species during the post-glacial period. Many studies have involved pollen sequences from lakes and bogs, but in arid regions of western North America, where lakes are rare, analysis of plant remains from packrat (Neotoma sp.) middens is critical for

ABSTRACT

Aim To reconstruct the last c. 7000 years of vegetation and climate change in an unusual region of modern Great Plains grassland and scarp woodland in southeast Colorado (USA), and to determine the late Holocene biogeography of Colorado piñon (Pinus edulis) at its easternmost extent, using a series of radiocarbon-dated packrat (Neotoma sp.) middens.

Location The West Carrizo Canyon drains the Chaquaqua Plateau, a plateau that projects into the western extent of the southern Great Plains grasslands in south-eastern Colorado, USA. Elevations of the study sites are 1448 to 1525 m a.s.l. Today the plateau is mostly Juniperus scopulorum–P. edulis woodland.

Methods Plant macrofossils and pollen assemblages were analysed from 11 ¹⁴C-dated packrat middens. Ages ranged from 5990 yr BP (6839 cal. yr BP) to 280 yr BP (485 cal. yr BP).

Results The results presented here provide information on the establishment and expansion of Juniperus–P. edulis woodland at its eastern limits. The analysis of both plant macrofossils and pollen from the 11 middens documents changes in plant communities over the last 7000 years, and the establishment of P. edulis at its easternmost limit. Though very minor amounts of P. edulis pollen occur as early as the middle Holocene, plant macrofossils were only recovered in middens dating after c. 480 cal. yr BP.

Main conclusions Originally, midden research suggested a late glacial refuge to the north-east of the Carrizo Canyon site, and a middle Holocene expansion of P. edulis. Results reported here are consistent with a late Holocene expansion, here at its eastern limits, but noted elsewhere at its northern and north-eastern limits. In general, this late Holocene expansion is consistent with pollen data from sediments in Colorado and New Mexico, and suggests that P. edulis is still expanding its range at its present extremes. This has implications for further extension of its range due to changing climatic conditions in the future.

Keywords Biogeography, climate change, Colorado, Great Plains, Holocene vegetation change, packrat middens, Pinus edulis, plant macrofossils, pollen, range expansion.
understanding post-glacial biogeographies. The Holocene biogeography of Colorado piñon (*Pinus edulis* Engelmann) has interested many researchers. Using midden remains, Van Devender (1990) suggested a glacial distribution of *P. edulis* and related species in Texas and southern New Mexico, perhaps below 1770 m elevation and 31–34° N latitude, because some of the oldest piñon remains date to 43,000–11,330 yr BP from southern New Mexico (Lanner & Van Devender, 1981). The northernmost known late Pleistocene remains of *P. edulis* come from northern Arizona (near Flagstaff at c. 16,500 cal. yr BP; Cinnamon & Hevly, 1988), or western Arizona (c. 19,500 cal. yr BP; Van Devender, 1987). Betancourt (1990) thought that the high elevation of the Colorado Plateau limited its northern distribution because the species reached its upper limits in southern New Mexico between elevations of c. 1550 and 1705 m (Van Devender et al., 1984; Betancourt, 1987). *Pinus edulis* expanded rapidly into much of its modern core range by the early Holocene (Lanner & Van Devender, 1998). But during the latest Holocene, several studies suggested an expansion of *P. edulis* at its northern and north-eastern limits, by c. 800 years ago in north-eastern Utah (Dutch John Mountains; Jackson et al., 2005; Gray et al., 2006) and by c. 450 years ago in north-eastern Colorado (Owl Canyon; Betancourt et al., 1991). Cole et al. (2007, 2008) used these data to model the potential distribution of *P. edulis* in the future with respect to changing climatic conditions, suggesting continual expansion to the north, north-east and east of its present range.

In this study we extend the analysis of the biogeography of Colorado piñon (*P. edulis*) using a sequence of radiocarbon-dated packrat middens collected from scarps in south-eastern Colorado at its present eastern limit to determine: (1) the local history of vegetation change in an unusual region of modern Great Plains grassland and scarp woodlands; and (2) the immigration history of a peninsular stand of *P. edulis* on the Chaquaqua Plateau. This study is important as a primary analysis of late Holocene vegetation change from the Colorado Great Plains, an arid region where organic preservation in rare sedimentary basins is poor. It is also important in our understanding of the latest Holocene expansion of Colorado piñon at its present eastern extent.

**STUDY AREA**

**Local setting**

West Carrizo Canyon (Fig. 1) drains the Chaquaqua Plateau in the far west of the southern Great Plains (Fenneman, 1931;
The plateau was partially formed during the Sierra Grande uplift (Duce, 1924), while the general regional flow direction reflects proximity to the northward-propagating Rio Grande Rift (Leonard, 2002). The mesas of the plateau were formed when late Tertiary basalt flows capped underlying Tertiary alluvial deposits (Trimble, 1980). Subsequent erosion of the basalt dissected and exposed large sections of underlying bedrock, forming the canyons and escarpments that define the boundaries of this section (Fenneman, 1931; Scott, 1968). The more resistant Dakota Sandstone (Cretaceous) forms the rimrock of West Carrizo Canyon, and strongly determines the topography above the canyon rim. The underlying Purgatoire Shale (Jurassic) is much less resistant and often erodes from under the Dakota Sandstone, forming rock shelters and fractures where numerous Neotoma middens occur. Undercutting of the Dakota Sandstone frequently occurs, limiting the age of available rock shelters for midden accumulation.

**Regional climate**

The climate of the Great Plains is characterized by cold, dry winters and hot, generally dry summers. Annual precipitation averages below 500 mm year⁻¹ (Fenneman, 1931; Weaver & Albertson, 1956) but increases eastward (Harrington & Harman, 1991). Most precipitation falls between May and September. Winter climate is dominated by strong westerlies, which are the strongest in the winter when the polar front moves southward. These airmasses carry moisture from the Pacific Ocean, the majority of which is lost by orographic precipitation along the North American Cordillera, causing the development of a rain shadow effect that encompasses much of the Great Plains, especially in the west. Summer climate patterns develop as the predominant westerlies shift northward with retreat of the polar front (Higgins et al., 1997), coupled with increasing strength of the Bermuda High (Harrington & Harman, 1991). Thus, portions of Colorado, New Mexico, western Oklahoma and northern Texas experience June/July precipitation as the Arizona Monsoon develops, with moist air drawn into the region by the establishment of a thermally induced trough in the desert south-western USA (Tang & Reiter, 1984; Rowson & Colucci, 1992).

**Local climate**

The Kim, Colorado, station (1597 m a.s.l.), c. 28 km north-west of West Carrizo Canyon, documents local climate conditions (Fig. 2). July is the warmest month (average maximum 31.9°C and minimum 15.3°C), while December and January are the coldest months (average maximum 8.8°C and minimum –8.5°C) (WRCC, 2008). Total annual precipitation is 419 mm; December is the snowiest month (average 198 mm, with 1110 mm for the entire year), but July is the wettest month (68.1 mm), with 43% of annual precipitation occurring during June–August. West Carrizo Canyon sits on the edge of two prominent precipitation maxima. It is on the western edge of the late spring (May) precipitation maximum – characteristic of the western Great Plains – and on the eastern edge of the late summer Arizona monsoon maximum (Mock, 1996).

**Vegetation**

The West Carrizo Canyon area is dominated by mixed prairie vegetation (Weaver & Albertson, 1956; Coupland, 1979). Dominant taxa above the canyon include buffalo grass (Buchloe dactyloides), blue grama (Bouteloua gracilis), side oats grama (Bouteloua curtipendula), three awn (Aristida spp.), squirrel-tail (Sitanion hysterix), western wheatgrass (Agropyron smithii), cholla (Opuntia acanthocarpa), prickly pear (Opuntia phaeacantha) and members of the Asteraceae and Fabaceae. Locally, Buchloe dactyloides and Bouteloua gracilis dominate with one or both Opuntia species (Feiler, 1994).

On the canyon slope in the deeper, coarser soils the community is dominated by taller grasses such as Aristida spp., switchgrass (Panicum virgatum and Panicum obtusum), Sitanion hysterix, and shrubs such as mountain mahogany (Cercocarpus montanum), wavy-leaf oak (Quercus undulata), hackberry (Celtis reticulata), skunkbrush (Rhus trilobata), Opuntia phaeacantha, Opuntia polycantha, Spanish bayonet (Yucca glauca), Asteraceae and Fabaceae.

Where perennial water occurs in the canyon bottom, cottonwood (Populus sargentii) and willows (Salix spp.) dominate, with cattail (Typha latifolia), bulrush (Scirpus spp.) and sedge (Carex spp.). On drier portions of the bottomland are grasses and shrubs, primarily Quercus and Cercocarpus.

Scarp woodlands occur locally, with juniper (both Juniperus scopulorum and Juniperus monosperma) and Colorado piñon (Pinus edulis) or ponderosa pine (Pinus ponderosa). Ponderosa pine is never a major component, but occurs in relatively rare pockets on extremely rocky outcrops. Primarily, Juniperus dominates these scarp woodlands with a minor *P. edulis* component. In general, these woodlands diminish away from
the canyon edge, either out on the level plains or down into the canyon proper.

**MATERIALS AND METHODS**

Middens were collected from locations within a 3-km section of West Carrizo Canyon (Fig. 1). Elevations of the middens are c. 1448–1525 m a.s.l. Because of the non-resistant rock type, midden preservation is sporadic, so all accessible indurated middens were collected. Modern vegetation is similar at each site.

In the laboratory, midden samples were prepared for analysis by removing the outer weathering rind, reducing the possibility of contamination with modern plant and pollen material. The samples were weighed and placed in distilled water until they were completely disaggregated, then screened using a US standard no. 20 mesh screen. The liquid portion passing through the screen was saved and subsampled for pollen (e.g. Davis & Anderson, 1987). Plant material on the screen was air dried, sorted and identified to the lowest possible taxonomic level. Facal pellets from each sample were collected for radiometric dating.

For pollen analysis, a 15-mL subsample was centrifuged to concentrate sediment and pollen out of the liquid matrix (urine and distilled water). This reduced sample was treated with 10% HCl to remove carbonates and HF to remove silicates. Pollen was separated from the remaining sample using a heavy liquid (zinc bromide, with a specific gravity of 2.0), followed by acetolysis, staining with Safranin O and suspension in glycerol. Since *Juniperus* pollen is often over-represented in midden assemblages, pollen taxa were identified and counted to a minimum sum of 200 grains not including *Juniperus* using a 400 × light microscope. Identifications were based on the reference collection in the Laboratory of Paleoeecology (LOP), Northern Arizona University (NAU), and several published keys (Erdtman, 1952; Moore et al., 1991; Kapp et al., 2000).

Identifications of plant macrofossils were based on comparisons to reference material in the LOP and the Deaver Herbarium (NAU). Macrofossil taxa were counted and quantified on the following scale (see Van Devender et al., 1987): 

1 = rare (1 specimen); 
2 = uncommon (2–29 specimens); 
3 = common (30–99 specimens); 
4 = very common (100–200 specimens); 
5 = abundant (200 + specimens). Identification of *J. scopulorum* was based on the absence of minute serrations on the leaf scales (Adams, 1983).

All taxa from both pollen and macrofossil assemblages were identified by either species names, ‘sp.’ if the specimen could only be identified to genus, ‘spp.’ if more than one unidentifiable species occurred within one genus, and ‘cf.’ when the specimen most closely resembled a particular reference specimen. Plant family designations were used if the generic level could not be reached. All species and general designations follow McGregor et al. (1986) or Weber & Wittmann (1996).

**RESULTS**

The 17 middens were located in shelters between 1448 and 1525 m elevation along West Carrizo Creek (Fig. 1). Radiocarbon dates were obtained for 12 of the 17 middens (Table 1). Middens were selected for analysis and dating based on locality as well as relative macrofossil assemblage composition. Several middens were not analysed because their macrofossil compositions and ages were duplicated by the contents of other middens. The 11 middens reported here represent approximately 7000 years of vegetation change from the middle Holocene to the present.

**The macrofossil and pollen records**

Thirty-one macrofossil taxa were identified to the lowest possible taxonomic level, with the relative abundance through time of the most common taxa shown in Fig. 3. Macrofossil zones were subjectively defined based on the presence or absence of *J. scopulorum*, *Portulaca cf. parvula* and *Polanisia dodecandra*. Three groups – Cactaceae, Asteraceae and *Juniperus* (exclusive of *J. scopulorum*) – are found in all middens at abundance of 3 or greater. Poaceae is also found in

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**Table 1** West Carrizo Canyon midden ages, and material dated.

<table>
<thead>
<tr>
<th>Midden (elevation)</th>
<th>Laboratory number</th>
<th>$^{14}$C age (yr BP)</th>
<th>SD ±</th>
<th>Median probability age (cal. yr BP)</th>
<th>Age up (cal. yr BP)</th>
<th>Age down (cal. yr BP)</th>
<th>Material</th>
</tr>
</thead>
<tbody>
<tr>
<td>WC 1 (1510 m)</td>
<td>Beta 59450</td>
<td>280</td>
<td>50</td>
<td>365</td>
<td>272</td>
<td>485</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 9 (1510 m)</td>
<td>Beta 59455</td>
<td>430</td>
<td>50</td>
<td>481</td>
<td>425</td>
<td>539</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 11 (1525 m)</td>
<td>Beta 59457</td>
<td>1030</td>
<td>60</td>
<td>946</td>
<td>795</td>
<td>1060</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 16 (1448 m)</td>
<td>Beta 59460</td>
<td>1260</td>
<td>80</td>
<td>1182</td>
<td>1049</td>
<td>1305</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 15 (1448 m)</td>
<td>Beta 59459</td>
<td>1320</td>
<td>60</td>
<td>1242</td>
<td>1122</td>
<td>1338</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 3 (1488 m)</td>
<td>Beta 59452</td>
<td>2230</td>
<td>90</td>
<td>2225</td>
<td>1991</td>
<td>2374</td>
<td>Neotoma pellets</td>
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<tr>
<td>WC 8 (1480 m)</td>
<td>Beta 53233</td>
<td>2820</td>
<td>60</td>
<td>2932</td>
<td>2779</td>
<td>3079</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 10 (1495 m)</td>
<td>Beta 59456</td>
<td>3620</td>
<td>60</td>
<td>3936</td>
<td>3821</td>
<td>4092</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 4 (1488 m)</td>
<td>Beta 59453</td>
<td>4290</td>
<td>70</td>
<td>4864</td>
<td>4783</td>
<td>5047</td>
<td>Neotoma pellets</td>
</tr>
<tr>
<td>WC 12 (1521 m)</td>
<td>Beta 59458</td>
<td>5340</td>
<td>80</td>
<td>6119</td>
<td>5983</td>
<td>6285</td>
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<td>100</td>
<td>6839</td>
<td>6633</td>
<td>7158</td>
<td>Neotoma pellets</td>
</tr>
</tbody>
</table>
relatively high abundance in all middens except in WC 5 (the oldest midden). *Yucca* sp. is found in moderate levels in all middens but it is absent from WC 3. Due to the relatively high abundance of these taxa throughout time, their minor absences are believed to reflect a sampling bias by the collecting packrat or the absence of these taxa within the collecting territory of the packrat, and not their absence in the local environment. A complete list of all plant macrofossils is found at the North American Plant Macrofossil Database (http://uwadmnweb.uwyo.edu/Botany/NAPMD/).

Forty-three pollen taxa were identified to the lowest taxonomic level possible; a summary of the major results is given in Fig. 4. *Juniperus* pollen is the most common pollen type in all middens. A complete list of identified pollen taxa is found in the North American Pollen Database (http://www.ncdc.noaa.gov/paleo/napd.html). Zonal boundaries are defined by macrofossil occurrence.

**Zone 1** (6839 and 6119 cal. yr BP, 5990 and 5340 yr BP)

Zone 1 represents the least diverse of all macrofossil zones; four taxa common in later zones – *P. edulis*, *Rhus* sp., *Cercocarpus* sp. and Brassicaceae – are all absent from the two middens in this interval. *Juniperus scopulorum* is common in both the 6839 and 6119 cal. yr BP middens. *Portulaca cf. parvula*, *Polanisia dodecandra* and *Chenopodium* sp. are present, but relatively uncommon in both middens. *Lithospermum* sp. is present, but rare. Euphorbiaceae, *Quercus* sp. and *Toxicodendron rydbergii* are all absent from the 6839 cal. yr BP midden, but are present, although uncommon, in the 6119 cal. yr BP midden.

*Quercus* pollen percentages vary in opposition to Chenopodiaceae–Amaranthus (Cheno-Ams) and *Artemisia*, and to some extent with *Ambrosia* and other Asteraceae. In the oldest midden, percentages of *Artemisia* and Cheno-Ams are relatively high, while *Quercus* percentages are at the lowest for the entire record. This pattern is reversed for the 6119 cal. yr BP midden. Most other taxa show only minor fluctuations in percentages, including *Abies* and undifferentiated *Pinus*. The exception is *Yucca*, present as a palynomorph only in Zone 1. *Pinus edulis* pollen is present in minute amounts.

**Zone 2** (4864 to 2225 cal. yr BP, 4290 to 2230 yr BP)

*Quercus* sp. and *T. rydbergii* are both present in this zone. *Portulaca cf. parvula* is present in the three youngest middens, but is absent in the oldest midden. Fabaceae is present, but uncommon, in the three youngest middens. *Lithospermum* sp. is present in amounts similar to those in Zone 1, but only in the midden dating to 4864 cal. yr BP. *Cercocarpus* sp. and Euphorbiaceae also appear in only one midden, but in higher abundances than *Lithospermum*. *Chenopodium* sp. continues at the same abundance as Zone 1 until the middle of Zone 2, when it becomes absent. *Rhus* sp. is present at 4864 and 2225 cal. yr BP but is uncommon. *Polanisia dodecandra*, present in Zone 1, is absent from Zone 2.
As in Zone 1, *Quercus* pollen continues to vary in opposition to *Artemisia*, *Ambrosia*, other Asteraceae and to a lesser extent Cheno-Ams. Percentages of *Ambrosia* and other Asteraceae increase, with *Ambrosia* reaching its highest levels of the record in the 4864 cal. yr BP midden. Other Asteraceae and *Artemisia* reach peaks in this zone in the 3936 cal. yr BP midden. Cheno-Ams percentages remain low. Fluctuations in Poaceae percentages mirror those of *Quercus*, reaching the lowest percentage of the record at 3936 cal. yr BP. But *Quercus* pollen once again peaks in the midden dating to 2225 cal. yr BP, while other Asteraceae, *Artemisia* and Cheno-Ams all decline. Euphorbiaceae and *Salix* increase compared to their respective Zone 1 percentages. All coniferous pollen types remain at low percentages. *Cercocarpus* is essentially absent in the early portion of this zone, but increases significantly towards the end of the zone.

**Zone 3 (1242 and 365 cal. yr BP; 1320 and 280 yr BP)**

*Polanisia dodecandra* reappears in all Zone 3 middens. *Portulaca* cf. *parvula* is present in each midden except at 946 cal. yr BP. *Cercocarpus* sp. and Brassicaceae are present in three middens but are uncommon. *Toxicocodendron rydbergii* is represented only from the 365 cal. yr BP midden. Four taxa – *Lithospermum* sp., *Chenopodium* sp., Euphorbiaceae and *Rhus* – are present in two of the Zone 3 middens, but are uncommon or rare. *Quercus* sp. declines in the early part of this zone, but returns to common abundance in the youngest two middens. After a significant absence *J. scopulorum* reappears, but is absent in the 365 cal. yr BP midden. *Pinus edulis* makes its first appearance at 481 cal. yr BP and by 365 cal. yr BP has increased in relative abundance.

Pollen in the first two middens shows the typical covariance between *Quercus* (low percentage) and *Artemisia* and Cheno-Ams (high percentage). *Ambrosia* and other Asteraceae show brief, minor decreases in percentages between 1242 and 1182 cal. yr BP. Poaceae percentages, previously largely mirroring *Quercus*, are also relatively stable, and do not reflect the decline in *Quercus*, *Eriogonum*, Euphorbiaceae, *Salix*, Apiaceae and Cactaceae show dramatic increases in percentages in the 946 cal. yr BP midden. The two youngest middens in this zone record a return to higher percentages of *Quercus* (c. 15–20%), a decline in *Artemisia* and Cheno-Am percentages, and stable percentages of Poaceae. Coniferous pollen types fluctuate at low percentages in this zone. *Juniperus* remains the most common pollen type, with *Abies* and *P. edulis*. All three taxa show significant increases in the two youngest middens.

**DISCUSSION**

**Vegetation and climate history**

**Holocene**

The Holocene vegetation history of the southern High Plains, including parts of western Kansas and Oklahoma, northern Texas and eastern New Mexico and Colorado, is not well known. Generally arid climates, a minimal number of Holocene-age basins and potential taphonomic problems with pollen assemblages have contributed to our present poor state...
of knowledge (Holliday, 1987; Grimm et al., 2001). The Strong & Hills (2005) reconstruction suggests that grasslands dominated this region from the late glacial to the present. In this context, sites such as West Carrizo Creek are important in understanding local vegetation changes there.

The available evidence suggests persistent and prolonged drought on the southern High Plains during the early Holocene, and may account for the absence of packrat middens there. Stable isotope δ13C composition of buried soils suggests temperatures 1 to 2°C lower than today from c. 11,500–8200 cal. yr BP (Nordt et al., 2007). This was accompanied in the early to middle Holocene by widespread aeolian sedimentation (Miao et al., 2007a,b) and dune formation (Holliday, 1989, 1997). Lakes dried completely between c. 7000 and 5000 cal. yr BP (Holliday, 1989), a time when soil isotopes record temperatures 1°C higher than today (Nordt et al., 2007).

Greater climate variability is suggested for the late Holocene. In eastern New Mexico, dune stabilization began after c. 5800 cal. yr BP (Holliday, 1997), with at least periodic marsh and pond redevelopment after c. 5500 cal. yr BP (Holliday, 1989), indicating generally greater effective precipitation regionally (Wanner et al., 2008). However, aeolian activity associated with drought peaked at c. 4200 and 2300 cal. yr BP, and between 1000 and 700 years ago (Miao et al., 2007b). Soil stable isotope evidence suggests cooler conditions than today c. 4800–2800 cal. yr BP, warmer conditions 2800–1000 years ago, and cooler conditions over the last 500 years (Nordt et al., 2007).

The results of macrofossil and pollen analysis from West Carrizo Canyon middens document nearly 7000 years of vegetation history for south-east Colorado. Macrofossils alone provide data relative to local environmental conditions, while pollen data can reflect both regional and local vegetation history (Davis & Anderson, 1987; Anderson & Van Devender, 1991; Pearson & Betancourt, 2002). Together these two data sets suggest that the vegetation of the West Carrizo Canyon has remained a relatively xeric, Juniperus scarp woodland since the middle Holocene. Several species of grasses, as well as cactus, Yucca and several subshrub and shrub species, including Quercus, Cercocarpus and Rhus, were common components of this woodland. Because our midden data represent relatively short glimpses of vegetation widely spaced in time, we resist the temptation to over-interpret the climatic record.

**Middle Holocene**

Within this dominantly xeric Juniperus–woodland community, the West Carrizo Canyon middens of middle Holocene age (6839–6119 cal. yr BP) include species typical of both winter and summer precipitation regimes. Summer precipitation indicators include Portulaca parvula and Polanisia dodecandra (McGregor et al., 1986; Baskin & Baskin, 1988), as well as J. scopulorum (Wells, 1970a,b; Cinnamon & Hevly, 1988; Thompson, 1990). Pollen of Quercus, primarily a summer rainfall indicator (Davis & Shafer, 1992), does not occur in the older midden, but occurs at high pollen percentage and as a macrofossil in the 6119 cal. yr BP midden. On the other hand, winter precipitation indicators, such as Chenopods and Artemisia (Hevly, 1985) are also important. The relative abundance of summer precipitation indicators during a regionally dry period might be attributed to the West Carrizo Canyon’s somewhat higher elevation than the surrounding plains, with greater orographic precipitation and lower evapotranspiration rates here than in areas to the south and east.

**Late Holocene**

Juniperus woodland, with grasses, cacti, Yucca, Asteraceae shrubs and T. rydbergii continue to be important during the early late Holocene (4864–2225 cal. yr BP), although significant changes are apparent. Juniperus scopulorum is present in only one midden; Portulaca parvula is present, but reduced; and Polanisia dodecandra is completely absent. Additionally, the local importance of Quercus appears to have declined, but Artemisia increased in importance overall. The expansion of grasses and Artemisia (sagebrush), especially in the early part of this period, suggest that a more drought-tolerant, open Juniperus grassland and shrubland existed in the West Carrizo Canyon.

**Latest Holocene**

Both macrofossils and pollen data suggest minor adjustments in the vegetation composition during the last c. 2200 years. Though Juniperus grassland and shrubland persists, J. scopulorum becomes more common again. Cercocarpus montanum and Rhus sp. largely replace T. rydbergii along the canyon scarps, while other subshrubs (i.e. Eriogonum, Malvaceae) and herbs (i.e. members of the Brassicaceae, Fabaceae, Euphorbiaceae) increase. The wetland community also expands, including Apiaceae and the streamside shrubs willow (Salix) and alder (Alnus). These changes suggest a major shift in the composition of the riparian community of the West Carrizo Canyon, with either an increase in perennial flow of the West Carrizo Creek, a rising of the local water table, or both. Since this happens immediately prior to the local establishment of P. edulis in the record, this suggests that change in effective precipitation may have been instrumental in preparing the West Carrizo Canyon for its local establishment.

**Biogeography of Pinus edulis**

Macrofossils of P. edulis first appear in the two youngest middens (c. 481 and 272 cal. yr BP), documenting the easternmost fossil record of Colorado pine. The expansion and distribution of P. edulis has been linked to the pattern of regional air masses over continental North America and the limits of monsoonal precipitation (Neilson & Wullstein, 1983; Neilson, 1987; Lanner & Van Devender, 1998). An original model suggested northward and westward expansion from a middle–late Wisconsinan northern Chihuahuan desert.
population, effectively following the expansion of the Arizona Monsoon as the Polar Front shifted northward during and after deglaciation (Betancourt, 1987; Van Devender, 1987; Wells, 1987; Lanner & Van Devender, 1998). More recently, Cole et al. (2008) suggested that the ancestral region was a swatch of land that stretched across the Mojave Desert, across southern Nevada to the Mogollon Rim of central Arizona, into southern New Mexico and west Texas. Further, Cole & Arundel (2005) and Cole et al. (2008) suggested rapid expansion to the north and north-east after c. 11,600 years ago. Lanner (1974) and Neilson & Wullstein (1983) suggested that Colorado pinyon’s northermost distribution probably occurred during the middle Holocene. These interpretations were based on the presence of isolated stands of hybridized pinyon (Pinus monophylla and P. edulis) north and north-west of the current distribution of P. edulis. This fits well with climate models that suggested a monsoon that was more intense and spatially expanded by the early middle Holocene (COHMAP Project Members, 1988; Friedman et al., 1988).

But later work has shown that the northern extent was reached much later, during the last millennium (Betancourt et al., 1991; Gray et al., 2006; and see below). This is supported by pollen-based reconstructions from the core range demonstrating that a general expansion of the species, at least in the southern Rocky Mountains, post-dated the middle Holocene (Toney & Anderson, 2006; Anderson et al., 2008a,b; Jiménez-Moreno et al., 2008). Holmgren et al. (2007) suggested that changing insolation seasonality was the driver. Although we cannot rule out minor contamination, small quantities of pinyon-type pollen found as early as the WC12 (6119 cal. yr BP) midden provides some support for a mid-Holocene pinyon expansion, indicating that perhaps Colorado pinyon was near or moving towards the West Carrizo Canyon at that time.

Fossil evidence indicates that Colorado pinyon only recently reached its north-eastern post-glacial distribution before 400 years ago at Owl Canyon, Colorado (Davis & Anderson, 1987; Betancourt et al., 1991), and its northermost location in Dutch John Mountain, Utah (Jackson et al., 2005) by c. 800 years ago. Betancourt et al. (1991) and Lanner & Van Devender (1998) suggest the possibility of human influence in the establishment of the Owl Canyon population. Equally possible is the caching activity of the pinyon jay (Gymnorhinus cyanocephalus) or Clark’s nutcracker (Nucifraga columbiana), both known to disperse seeds over long distances (Vander Wall & Balda, 1981; Chambers et al., 1999). Because of this, a direct link to climatic factors is not definite.

However, invasion by P. edulis into the Dutch John Mountain, Utah, area about 800 years ago was most likely climatically driven. Expansion of P. edulis into north-eastern Utah was contemporaneous with declining expansion of J. osteosperma into northern Wyoming (Lyford et al., 2003; Jackson et al., 2005). This led Jackson et al. (2005) to suggest that a potential increase in effective growing-season moisture in the region was responsible. The first direct occurrence of P. edulis in the West Carrizo Canyon during the latest Holocene – a time of increased effective precipitation – lends direct support to a climatic explanation of northward and eastward expansion during the last millennium.

**CONCLUSIONS**

The West Carrizo Canyon record is important in: (1) providing palaeoenvironmental information from the western Great Plains, where few sites with palaeobotanical data have been recovered; (2) further documenting the utility of using both pollen and plant macrofossils in palaeo reconstructions; and, most importantly, (3) identifying the easternmost extension of an expanding front of P. edulis.

Throughout the nearly 7000-year record of the West Carrizo Canyon middens, Juniperus grassland and shrubland, with Quercus, Yucca, members of the Cactaceae, shrubs of the Asteraceae, Toxicodendron rydbergii and many other species, covered the scars of the canyon, with only modest variation. From c. 4864 to 2225 cal. yr BP, the local vegetation may have included more grasses and Artemisia than prior to this period. But the greatest vegetation change occurred during the most recent c. 2200 years, when Cercocarpus montanus largely supplanted T. rydbergii, and riparian species such as Salix and Alnus became prominent. These changes suggest important shifts in the local environment, which may have presaged the local establishment of P. edulis by c. 480 cal. yr BP.

The occurrence of expanding populations of P. edulis on three fronts – north-west, north-east and east – within the last millennium suggests at least in part a climatic cause. This was the explanation hinted by Betancourt et al. (1991) for the north-west expansion in Colorado, and advanced by Jackson et al. (2005) for the north-west expansion into the Dutch John Mountains, Utah. At least for the West Carrizo Canyon population, this may have been a result of long-term broad-scale shifts in seasonal precipitation, including continued intensification of the El Niño–Southern Oscillation (Moy et al., 2002; Menking & Anderson, 2003; Rasmussen et al., 2006) throughout the late Holocene. But it also may have been in response to long-term changes in seasonal insolation values, resulting in warmer winters and cooler summers (see Holmgren et al., 2007).

Other potential causes for the expansion include distribution by Native Americans and/or corvids, changes in local fire frequencies or declining competition from grasses and shrubs. The seed of P. edulis is an important food source, and we cannot exclude its late Holocene distribution by humans or birds. Although very sensitive to fire (Baker & Shinneman, 2004; Romme et al., 2008) we cannot comment on any changes in local fire frequency at the extremes of the present range of P. edulis, since long-term records of fire occurrence are unknown for the Colorado Great Plains. Neither do changes in competition from grasses or shrubs seem to have been a significant factor, since pollen and plant macrofossils do not show declines in those communities.

Our data are important in understanding the modern and, potentially, future distribution of P. edulis. Midden data reported and summarized here have been useful in producing
models of the potential distribution of *P. edulis* in the face of climate change and human interference with natural processes, such as fire. Cole *et al.* (2008) produced models demonstrating that potential habitat exists for *P. edulis* directly to the east and north-east of the West Carrizo Canyon study site. It is possible that not enough time has lapsed in its present expansional run to colonize all available habitat there. Their analysis also suggests that *P. edulis* could potentially expand even further east onto the plains of Nebraska, Wyoming, Kansas, Oklahoma and north-west Texas, but its further expansion there may have been limited by a combination of factors caused by high early summer rainfall leading to presumably higher fire incidence in the past. Perhaps as long as scarp habitat is available, in conjunction with a decline in fire on the Great Plains, *P. edulis* could eventually colonize these areas. Our data further demonstrate the importance of retrospective studies for projecting the reaction of species to changing climate.

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**BIOSKETCHES**

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[Correction added after online publication, 20 October 2009: in the section 'Study area', subsection 'Vegetation', paragraph 4, *Juniperus osteosperma* was corrected to *Juniperus monosperma*.]