Aliso: A Journal of Systematic and Floristic Botany

Volume 24 | Issue 1 Article 7

2007

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Aliso 24, pp. 97–104

REASSESSMENT OF *YUCCA BREVIFOLIA* AND RECOGNITION OF *Y. JAEGERIANA* AS A DISTINCT SPECIES

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ABSTRACT

A brief historical account of the Joshua tree (*Yucca brevifolia,* Agavaceae) is presented. The geographical distribution, morphological and pollinator differences between subsp. *brevifolia* and subsp. *jaegeriana* are examined and the latter is raised to specific rank. The fossil *Protoyucca* and its possible relationship to the Joshua trees are considered together with implications as to the possible origin of the genus.

Key words: Agavaceae, botanical history, Great Basin, pollination, *Protoyucca, Tegeticula, Yucca*.

INTRODUCTION

The Joshua tree (*Yucca brevifolia* Engelm.) is one of the more commonly recognized plants of the Mojave Desert region of the southwestern United States. The earliest known written record of Joshua tree is an entry in Lieutenant J. C. Frémont's report (1845) to Colonel J. J. Abert, dated 14 April 1844. On his second expedition, Frémont and his party left the Tulare [San Joaquin] Valley, crossed the [Tehachapi] mountains by way of Oak Creek Pass (Johnson 1927) [now Willow Springs Road] and, following the route taken by Francisco Garcés in May, 1776, entered the Great Basin [Antelope Valley], where he was ''struck by the sudden appearance of yucca trees which gave a strange and southern character to the country . . . their stiff and ungraceful form makes them to the traveler the most repulsive tree in the vegetable kingdom . . .'' (Frémont 1845). Frémont was born in Georgia and was familiar with the yuccas of the Southeast. In his diary Garcés made no mention of a plant that might be interpreted as a Joshua tree (Coues 1900). Except for the presence of wind machines, the pass today appears much as it did when Frémont saw it over 160 years ago. *Yucca brevifolia* occurs at elevations below the summit of the pass, often with valley oak (*Quercus lobata* Née), an association not previously reported.

It has been claimed that Frémont was the first to use the term ''Great Basin'' (Williamson 1853) and as reported by Jackson (1970), it was Frémont's vital geographic discovery. The credit for the discovery may go to C. H. ''Kit'' Carson, who was Frémont's guide on his second expedition. On 17 January 1844, Frémont wrote that Carson had gone to search for beaver cuttings; ''the absence of such signs was to him a sure indication that the water had no outlet from the great basin.'' The map accompanying Frémont's report (1845) shows a long arching line extending from the Blue Mountains of Oregon to the present Antelope Valley labeled ''Great Basin.'' The Great Basin is shown more realistically on the map accompanying the Williamson report (1853). Lieutenant R. S. Williamson of the Corps of Topographical Engineers, who was then surveying for a practical railway route from the Mississippi to the Pacific, followed the same course taken earlier by Frémont and entered the Great Basin by way of what is shown on his map as Tejon Pass. The present pass of that name was then known as Cañada de las Uvas. In Williamson's report is a colored lithograph prepared from sketches by Charles Koppel, the expedition's assistant civil engineer and artist, showing Joshua trees (Fig. 1). This may be the earliest illustration of *Y. brevifolia.* Williamson noted that the vegetation in the valley was remarkable, consisting entirely of the straight trunks of yuccas that grew very thickly in several places, making passage by the wagons difficult. He also reported that the leaves of the *Yucca* were about as strong and as sharp as a bayonet and that it was commonly called the *bayonet tree.*

According to Norris and Webb (1990), during the early Miocene the sea invaded the western portion of the Antelope Valley for a short time, leaving shallow marine sediments. Historically, the largest individuals of *Y. brevifolia* were found growing there in the rich valley soil, supplied with abundant underground water (Fig. 2, 3). It has been reported that the largest Joshua tree was intentionally fired and that it burned for three days. Now the largest known specimens are growing in a remote area of Joshua Tree National Park.

TAXONOMY

George Engelmann described *Yucca brevifolia* in 1871 from a specimen collected on 15 March 1854 by

Fig. 1. Possibly the first published illustration of *Yucca brevifolia.* Described in Williamson (1853 [1855]: 214 ff.) as ''Valley in the slope of the Great Basin'' [Antelope Valley].

Fig. 2. *Yucca brevifolia.* Fifteen miles east of Lancaster, California, 9 Jul 1925. Photograph by Ernest Braunton. Postcard.

John Bigelow along the north bank of the Mojave River just southwest of Barstow in San Bernardino County, California (Reveal 1977). According to the collector, the species grew on sandy and gravelly plains west of the Colorado [River], California, where he found ''whole forests . . . on the Mohave creek [River]'' (Torrey 1856). Bigelow's collection was divided into three ''specimens'' according to Reveal (1977); one sheet at New York Botanical Garden, one at the Smithsonian, Washington D.C., and one at the Academy of Natural Sciences at Philadelphia. McKelvey (1938) designated the specimen at the Smithsonian as the type, wholly without justification according to Reveal. Reveal ignored her typification, and without explanation designated the sheet at New York as the holotype.

In 1935 McKelvey described *Y. brevifolia* var. *jaegeriana.* She designated as the type *McKelvey 2732,* collected on 30 April 1932 in the vicinity of the Shadow Mountains, San Bernardino County, California (specimen deposited at A). There are three Shadow Mountains in San Bernardino County (Durham 1998), none within the geographical range of McKelvey's var. *jaegeriana.* It appears that she, together with her chauffeur, were driving from the Los Angeles area to Las Vegas, Nevada, on Highway 66, now Interstate 15, and it is probable that her type was collected somewhere in the vicinity of Mountain Pass (32.40 N, 116.06 W, 1442 m) where var. *jaegeriana* is abundant.

Munz (1959) followed McKelvey (1938) and, in addition, recognized *Y. brevifolia* var. *herbertii* (J.M.Webber) Munz, based on the production of off-

Fig. 3. Two views of a large *Yucca brevifolia* (Anonymous 2000). Used by permission.

sets from underground rootstocks. Some plants exhibit offsets; production is not consistent and is not considered a reliable defining characteristic (Simpson 1975; Rowlands 1978; L. W. Lenz unpubl. data), and except for Munz (1959), and Munz (1974), later workers have not accepted var. *herbertii.* Rowlands (1978) recognized *Y. brevifolia* var. *brevifolia* and var. *jaegeriana.* In 2001, Hochstätter made the combination *Y. brevifolia* subsp. *jaegeriana* (Schott ex Torr.) Hochstätter.

Yucca jaegeriana (McKelvey) L.W.Lenz, comb. et stat. nov.

Basionym: *Yucca brevifolia* Engelm. var. *jaegeriana* McKelvey, *J. Arnold Arbor.* **16**: 269, pl. 139 (1935).

TYPE: California. San Bernardino Co. 30 April 1932, vicinity Shadow Mountains, approximately 4000 ft. *McKelvey 2732.* (A). *Yucca brevifolia* var. *wolfei* M.E.Jones, *Contr. West. Botany* **18**: 125. 1935, nomen invalid. (I.C.B.N. Art. 36.1: sine descriptione latina). *Yucca brevifolia* subsp. *jaegeriana* (McKelvey) Hochstätter, *Succulenta* (*Netherlands)* **80**(6): 267. 2001.

In order not to unsettle a well-established vernacular name I propose that the two species be distinguished as western Joshua tree (*Y. brevifolia*) and eastern Joshua tree (*Y. jaegeriana*).

VEGETATIVE CHARACTERS

Yucca brevifolia s.s. is arborescent with a distinct trunk and, usually, stout branches (Fig. 4); *Y. jaegeriana* is generally smaller and branched from near the base, the branches somewhat slender (Fig. 5). The two possess dissimilar patterns of branching, *Y. brevifolia* having pseudodichotomous (monopodial) branching; *Y. jaegeriana,* until flowering, has true dichotomous branching (Simpson 1975; Rowlands 1978). The species differ in leaf length; *Y. brevifolia* having leaves 15–35 cm long, those of *Y. jaegeriana* 10–20 cm. Leaf length is variable, depending at least in part on environmental conditions.

FLORAL AND FRUITING CHARACTERS

Some authors failed to describe the flowers of *Yucca brevifolia* and *Y. jaegeriana* (Torrey 1856; Engelmann 1871; Trelease 1892; Kearney and Peebles 1960; Rowlands 1978). Watson (1880) wrote ''segments of the narrowly campanulate perianth greenish-white, narrowly lanceolate.'' This applies to *Y. jaegeriana.* Descriptions by Jepson (1927), Munz (1935), Abrams (1940), Webber (1953), Cronquist et al. (1977), Welch (1993), and Hess and Robbins (2002) apply in part to both species. Munz (1959, 1974) described the flowers of var. *brevifolia* as, ''perianth 4–7 cm long, fleshy,

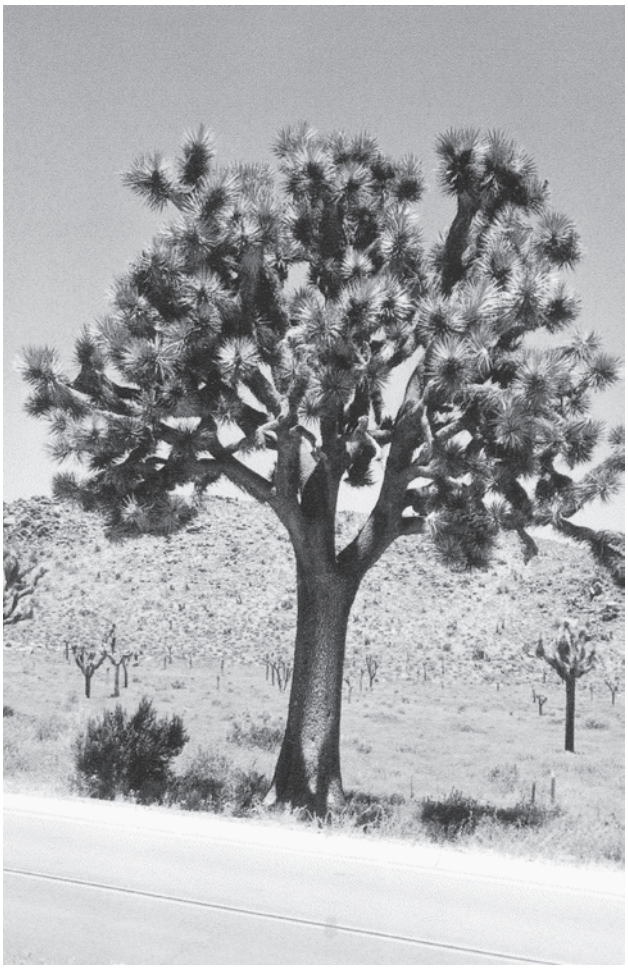

Fig. 4. *Yucca brevifolia.* Joshua Tree National Park. Photograph by author.

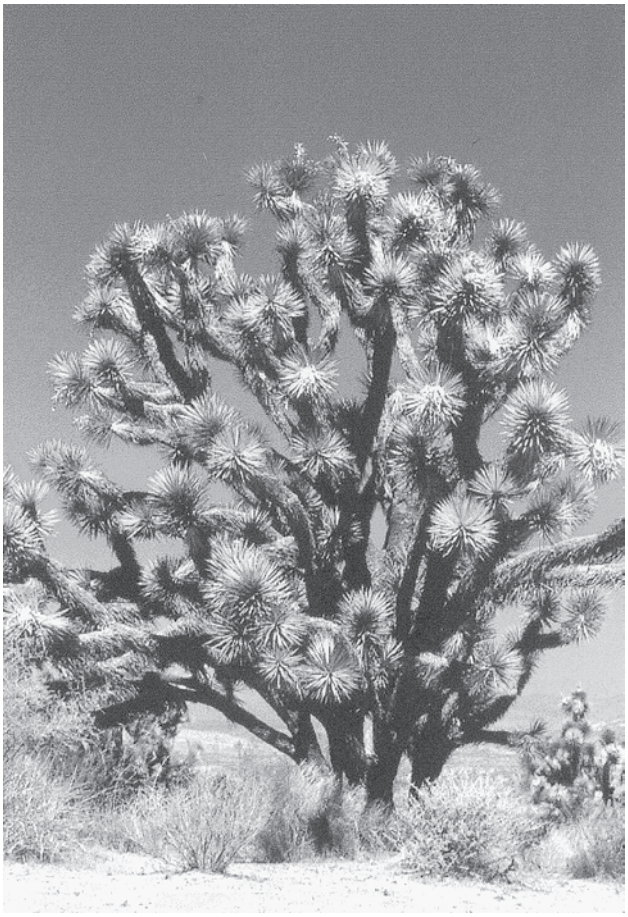

Fig. 5. *Yucca jaegeriana,* Hualapai Valley, Mohave County, Arizona. Photograph by author.

waxen, cream to greenish-white'', but he did not describe the flowers of var. *jaegeriana* or var. *herbertii.* McKelvey (1938) did not present a key for the separation of her two varieties. Failing to recognize that the flowers and fruits of her two varieties were morphologically distinct, the characteristics she attributed to var. *brevifolia* are those of her var. *jaegeriana.* Her plates LXV–LXVII, photographed in Mohave County, Arizona, are of variety *jaegeriana.* McKelvey was an astute observer and there is no convincing evidence that she ever observed the flowers or fruits of *Y. brevifolia.*

In floral characters, *Y. brevifolia* and *Y. jaegeriana* are distinct (Fig. 6). Flowers of *Y. brevifolia* are nearly globular or depressed globular, the broadly ovate, fleshy, cream-colored perianth segments are strongly incurved, and the flowers never fully expand. Flowers of *Y. jaegeriana* are narrowly campanulate, conspicuously swollen at the base, somewhat constricted above, and the narrowly oblong perianth segments are usually greenish, and recurved at their tips. The ovaries of *Y. brevifolia* are conical and taper from the base; those of *Y. jaegeriana* are lance-ovoid. Fruits of *Y. brevifolia* are ovoid to broadly ovoid (Fig. 7); those of *Y. jaegeriana* are ellipsoid (Fig. 8).

POLLINATION

It has been shown that the two taxa of the Joshua tree have different pollinators (Pellmyr and Segraves 2003). *Yucca brevifolia* is pollinated by the moth *Tegeticula synthetica* (Davis), *Yucca jaegeriana* by *T. antithetica* Pellmyr. The two moths are morphologically dissimilar from one another and from other species of *Tegeticula; T. antithetica* is distinctly smaller than *T. synthetica.* The only other *Tegeticula* species that slightly resembles *T. antithetica* is *T. maculata extranea* (Hy. Edwards) (Pellmyr and Segraves 2003). According to Davis (1967) it is the pollinator of southern populations of *Yucca whipplei* Torr. [*Hesperoyucca whipplei* (Torr.) Baker ex Trel.]. The yucca–yucca moth mutualism first reported by Riley (1872) is believed to have originated in the Eocene, ca. 40 million years ago (mya) (Pellmyr and Leebens-Mack 1999)

Fig. 6. Flowers of *Yucca brevifolia* (left) and *Y. jaegeriana* (right). Six-inch ruler.

and is a major model system for the study of coevolving species interactions (Powell 1992; Pellmyr et al. 1996; Leebens-Mack et al. 1998). *Tegeticula synthetica* and *T. antithetica* are estimated to have diverged about 10.7 (7.4–14.0) mya (Pellmyr and Segraves 2003). The two yuccas may have diverged at the same time.

GEOGRAPHY AND ECOLOGY

Except for a small area of overlap in Tikaboo Valley (Lincoln County), Nevada, the two species are allopatric. Both occur in discrete disjunct populations of variable size (Fig. 9). At present they have no effective dispersing agent (Lenz 2001).

Yucca brevifolia and *Y. jaegeriana* are not restricted to any particular vegetation type (Rowlands 1978). They are components within a broad array of plant communities from Yellow Pine Forest to Sonoran Desert (Webber 1953; Munz 1974; Rowlands 1978; Thorne et al. 1981; Van Devender 1990; Brown 1994). Except for certain southern populations of *Y. brevifolia* both species occur in areas where annual precipitation is rather evenly distributed throughout the year irrespective of total annual precipitation (Fig. 10).

KEY TO THE SPECIES

Plants ca. 6–9 (–16) m tall, arborescent with distinct trunk and monopodial branching, branches stout; leaves 15–35 cm long; corollas cream-colored, globular to depressed globular, never opening fully; perianth segments broadly ovate, tightly incurved; fruits ovoid to broadly ovoid, rounded at tips; pollinator *Tegeticula synthetica.*

CALIFORNIA, NEVADA . . . . . *Y. brevifolia*

Plants ca. 3–6 (–9) m tall, stemless or with trunks, usually branching less than 1 m above ground, the branching dichotomous until flowering, irregular thereafter; branches relatively numerous, somewhat slender; leaves 10–20 cm long; corollas greenish to cream-colored, narrowly campanulate, conspicuously expanded at bases; perianth segments narrowly oblong, tips recurving; fruits ellipsoid, tapering at tips; pollinated by *Tegeticula antithetica.*

ARIZONA, CALIFORNIA, NEVADA, UTAH . . . . . *Y. jaegeriana*

DISCUSSION

In 1990, Tidwell and Parker described *Protoyucca shadishii* from fossil material collected in Washoe County, Nevada, in a geological formation that has been dated to 14 mya (Bonham 1969). Based on close similarity of habit, root/stem/leaf relationships, as well as internal structure, the authors considered the fossil most similar to *Yucca* and found detailed leaf anatomy of *P. shadishii* similar to that of *Y. brevifolia.* Because

Fig. 7. Fruits of *Yucca brevifolia.* Six-inch ruler.

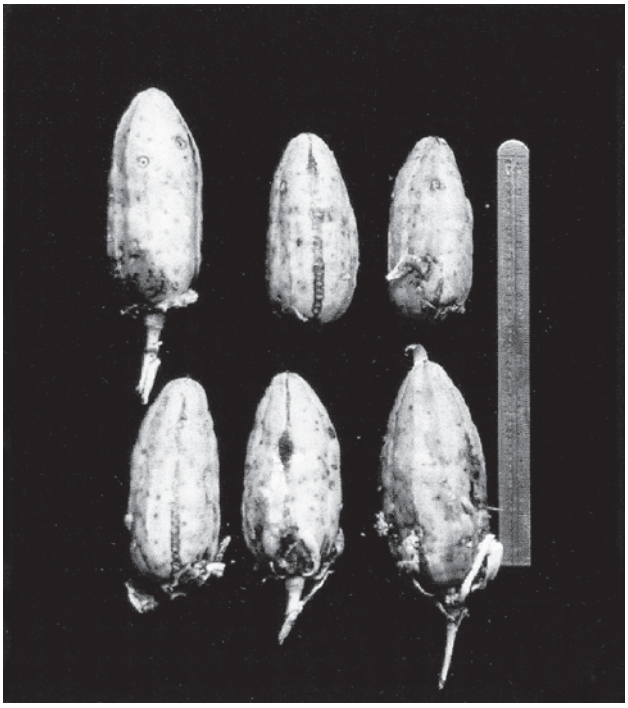

Fig. 8. Fruits of *Yucca jaegeriana.* Six-inch ruler.

Fig. 9. Geographical distribution of *Yucca brevifolia* and *Y. jaegeriana.* Redrawn from Rowlands (1978).

of differences in vascular bundles the authors established a new genus.

The Stewart Valley fossil flora of western central Nevada (dated ca. 14.1 mya) is dominated by species of modern western affinity related to those now in California, Oregon, and the Rocky Mountains; it also includes species of Madrean derivation, *Populus* L., *Rhus* L., *Sapindus* L., and *Schinus* L., indicating the occurrence of summer rain (Axelrod and Schorn 1994). It seems reasonable to presume that *P. shadishii* may have been one of the Madrean elements. In western North America, most of the Miocene epoch was characterized by climates warmer and milder than today with precipitation well distributed throughout the year (Edwards 2004).

Young plants of *Y. baccata* Torr. and *Y. schidigera* Roezl ex Ortgies, both often sympatric with Joshua trees, rapidly develop thick, carrot-like, water-storing roots; Joshua trees do not, and young plants rely upon available moisture to become established. Germinating seeds of *Y. brevifolia* may produce primary roots as much as 20 cm long before growth appears above ground (L. W. Lenz unpubl. data), and Simpson (1975) showed a 95-day-old plant with a root 58 cm long. Total and seasonal distribution of precipitation for selected sites of *Y. brevifolia* and *Y. jaegeriana* is shown in Fig. 10. Based on geographic, morphological, and anatomical evidence Simpson (1975) postulated that yucca evolved from tropical ancestors. Except for Joshua trees, arborescent yuccas are restricted to Mexico (Matuda and Lujan 1980; Serna and Ferrari 1992). Perhaps the Joshua tree's dependence on somewhat uniformly distributed precipitation for establishment is a heritage from the past and supports Simpson's (1975) view.

ACKNOWLEDGMENTS

I would like to thank Travis Columbus, Richard Felger, James Henrickson, Robert Thorne, and an anonymous reviewer for valuable suggestions for the im-

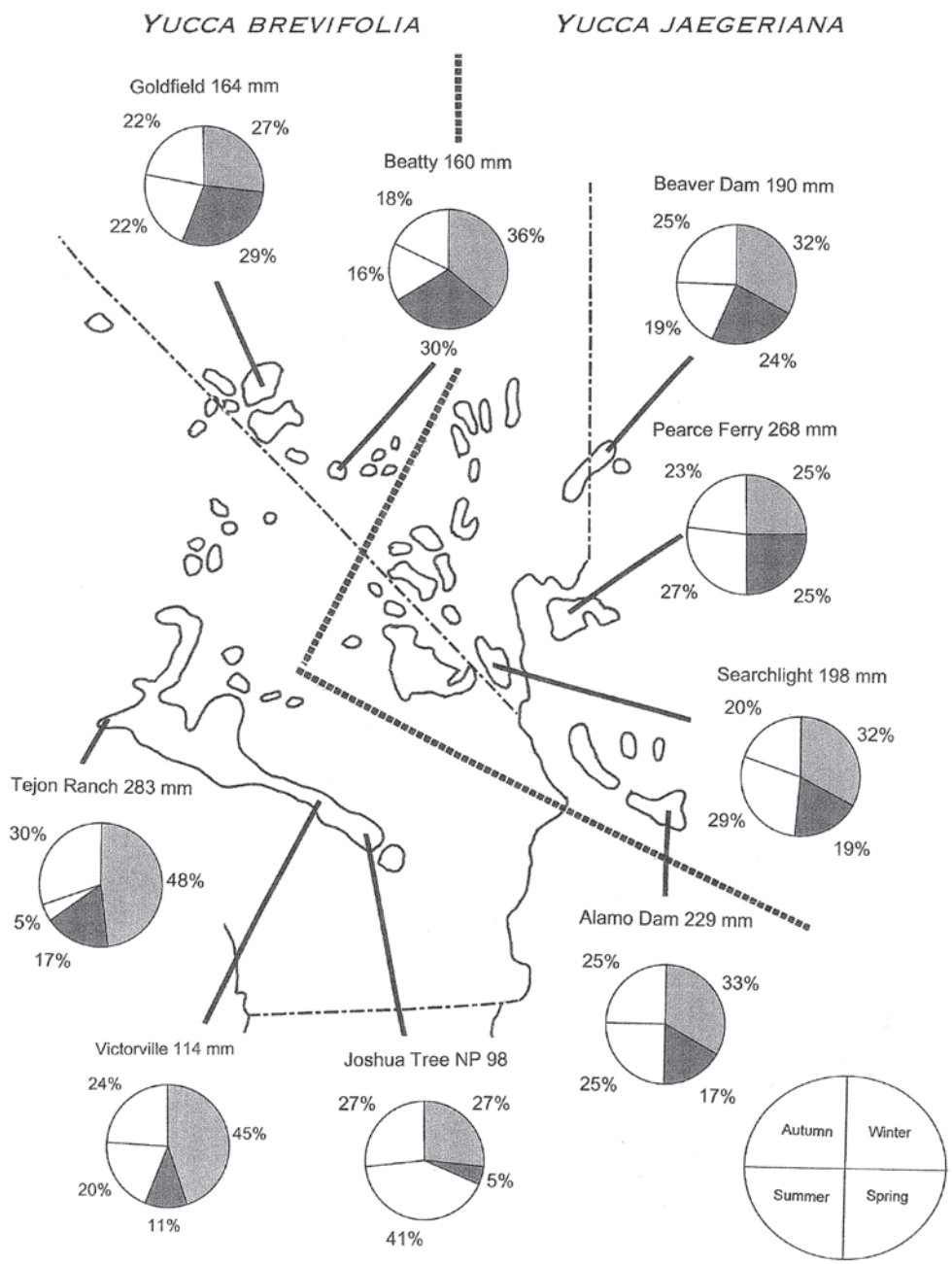

Fig. 10. Total annual and seasonal distribution of precipitation for selected sites of *Yucca brevifolia* and *Y. jaegeriana.* (Winter: Dec–Feb; Spring: Mar–May; Summer: Jun–Aug; Fall: Sep–Nov). The number of years for which precipitation records are available varies. Data from the Western Regional Climate Center, Desert Research Institute, Reno, Nevada (*http://wrcc.dri.edu*).

provement of the manuscript. As I bring to a close my active botanical career I wish to convey my deep-felt thanks to Jim Henrickson and to dedicate this contribution to him. Over many years he has provided encouragement and support in countless ways; a true friend and commendable colleague.

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