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HABITAT AND DISTRIBUTION OF *CRYPTANTHA CRINITA* GREENE (BORAGINACEAE)

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ABSTRACT

Cryptantha crinita Greene (silky cryptantha) is a rare native annual plant previously known solely from alluvial soils of the northern Sacramento Valley in California. It has been considered a lowland species (85–300 m) associated with creekbeds. Several recent collections (1990–2004) made in upland habitats at 850–1200 m show that the species is more common and has a wider ecological amplitude than previously thought. Although the habitats of the upland and valley sites differ, they are both characterized by a sparse vegetative cover which appears to be a key factor for establishment and growth of *C. crinita*.

Key Words: breccia, California, *Cryptantha crinita*, Ishi Wilderness, Tuscan formation.

Cryptantha crinita Greene is a rare annual native plant (List 1B, CNPS 2001) of northern California. Discovery of a disjunct upland population in 2003 prompted several site visits and a review of herbarium specimens by the authors. This investigation has demonstrated that the species is more common and has a wider geographic distribution and ecological amplitude than previously documented. Field botanists and botanical surveyors should change their perception of potential habitat for *C. crinita* to include Tuscan mudflow and other rocky upland sites with little competing vegetation.

Before 1990, the species was known from only 22 occurrences in Shasta and Tehama counties. All of these populations were found in alluvial soils of ephemeral creekbeds or permanent creekbanks on the floor of the northern Sacramento Valley at elevations of 90–290 m. At least 40% of these valley populations are threatened by residential development, gravel mining, cattle grazing, or recreation (Lis 1994). The remaining populations may be impermanent due to the dynamic and unstable nature of their ephemeral streambed habitat.

On April 25, 1990, the first upland population of *C. crinita* was discovered at 850 m elevation (*Dean W. Taylor 10684*, *UC1584585*). Located north of South Cow Creek near Shingletown, CA (40°22′55.8″N, 122°09′20.7″W), the population was found growing on volcanic soil in an opening surrounded by chaparral and ponderosa pine. Due to the unusual habitat and distance from other occurrences this population was considered an anomalous product of a long-distance dispersal event.

Since Taylor's initial upland discovery, several other populations have been found in upland habitats away from riparian zones. The location and habitat of these recently discovered populations challenge the notion that ephemeral creekbeds of the northern Sacramento Valley are the exclusive or primary habitat of the species. The populations from Tehama and Shasta counties (Table 1) are all in upland habitats away from the riparian zone.

As a result of the confirmed upland occurrences the known range of *C. crinita* has increased southward by 10 km and eastward by 34 km into the extreme eastern edge of the Cascade foothills. The uppermost known elevation has increased from 290 m to 1200 m, an increase of 910 m. Furthermore, the discovery of the species in upland habitats of open gray pine and blue oak woodland, coupled with montane chaparral habitat at the Shingletown site, indicates that it has a wider ecological amplitude than previously believed. All of these recently discovered upland populations were found on obviously volcanic substrates, particularly Tuscan mudflow. Thus, the species' upland distribution may be limited to such substrates or to habitats with little competing vegetation regardless of substrate.

Given this new range and ecological information, it is clear that much of the intervening area with potential habitat has not been surveyed for *C. crinita*. This property is mostly private land, national forest, wilderness, or game refuge (including the Lassen National Forest, Ishi Wilderness, Tehama Game Refuge, and Dye Creek Preserve) with rough terrain and poor access.

TABLE 1. SUMMARY OF UPLAND *CRYPTANTHA CRINITA* SITES IN CHRONOLOGICAL ORDER.

Voucher information	Locality	Elevation and habitat
Dean W. Taylor 10684 (UC1584585) Shasta County 4/25/1990	40°22′55.8″N 122°09′20.7″W Shingletown area north of South Cow Creek.	850 m. On volcanic soil in an opening surrounded by chaparral and ponderosa pine.
Dean W. Taylor 13492 (JEPS90293 and *90908)* Shasta County 5/25/1993	40°35′5.7″N 121°52′6.2″W Private. Off of Ponderosa Way.	760 m. South facing gently sloping volcanic mudflow breccia bordered by forest, with vernally moist gravel.
Brian Elliott 11631 (CHSC 84666) Tehama County 5/31/2003	40°12′25.9″N, 121°46′42.8″W Lassen National Forest on the north edge of the Ishi Wilderness, on the ridges above and between Rancheria Creek and Avery Creek in the Mill Creek watershed.	900 m. On patches of exposed Tuscan mudflow, on southern exposure, in full sun with no litter. Surrounded by open gray pine and blue oak woodland with scattered *Ceanothus cordulatus*.
Brian Elliott 11633 (CHSC 84682, JEPS 105600) Tehama County 5/31/2003	40°12′7.4″N, 121°46′55.7″W Lassen National Forest on the north edge of the Ishi Wilderness, on the ridges above and between Rancheria Creek and Avery Creek in the Mill Creek watershed.	990 m. On patches of exposed Tuscan mudflow, on southern exposure, in full sun with no litter. Surrounded by open gray pine/blue oak woodland.
Brian Elliott 11634 (CHSC 84665, JEPS 105599) Tehama County 5/31/2003	40°7′2.6″N, 121°42′22.9″W Lassen National Forest, eastern edge of Ishi Wilderness, in the Deer Creek Watershed.	1100 m. On roadcut through volcanic mudflow.
Samantha Mackey Hillaire 430 Tehama County 4/10/2004	40°8′12.4″N 121°43′21.3″W Lassen National Forest, Ishi Wilderness, along the Lassen Trail, on ridge north of Big Dry Creek.	1200 m. Soil a volcanic Tuscan mudflow, with a west-facing moderate slope, in full sun with no litter. Found in an open rocky expanse with a few *Arctostaphylos* shrubs Associated annuals are *Astragalus*, *Erodium*, *Lotus*, and *Micropus*.
Brian Elliott 12537 and *12625* Tehama County 4/40/2004	40°6′ 58.2″N, 121°42′55.7″W Lassen National Forest, Ishi Wilderness, along the Moak Trail, on ridge between Big Dry Creek and Deer Creek.	1100 m. Soil a volcanic Tuscan mudflow, with general western exposure, in full sun with little litter.

HABITAT DESCRIPTION

Valley Creekbed Habitat

Although the species is rare, population growth models of *C. crinita* have demonstrated that it does possess the potential for positive population growth under favorable conditions (Mackey 1999). Quantitative description of habitat at three lowland study sites (Mackey 1999) indicates that favorable conditions for this species include sparse vegetation cover. This is consistent with field observations at both lowland and upland sites.

The three creekbed sites used in Mackey's thesis had low cover from competing annual species and little or no large woody vegetation. The abundance of annual grass stems (in stems/m^2) was measured at sites with *C. crinita*. An average of 137–140 stems/m^2 was found in 1997–1998 with a high of 293 stems/m^2, which was much less than in a long-term study of California annual grassland that measured an average of 5113–30,537 stems/m^2 in "typical" grassland sites (Heady 1958). In addition to low competition, lowland *C. crinita* sites were also characterized by alluvial soils with physical properties that provide a harsh environment and inhibit thick plant cover. The soil is rocky with little free soil between the creek cobbles. Often there is a volcanic hardpan layer underneath the riparian zone (25–50 cm below the surface) that prevents

TABLE 2. ASSOCIATES OF *CRYPTANTHA CRINITA* AT LOWLAND SITES. Nomenclature follows Hickman (1993).

Scientific name	Family	Origin	Life form
Aira caryophyllea	Poaceae	introduced	annual graminoid
Bromus hordeaceus	Poaceae	introduced	annual graminoid
Bromus madritensis subsp. *rubens*	Poaceae	introduced	annual graminoid
Bromus diandrus	Poaceae	introduced	annual graminoid
Bromus tectorum	Poaceae	introduced	annual graminoid
Cryptantha flaccida	Boraginaceae	native	annual forb
Cryptantha muricata	Boraginaceae	native	annual forb
Erodium spp.	Geraniaceae	introduced	annual/biennial forbs
Eschscholzia lobbii	Papaveraceae	native	annual forb
Lepidium nitidum	Brassicaceae	native	annual forb
Lomatium utriculatum	Apiaceae	native	perennial forb
Lotus humistratus	Fabaceae	native	annual forb
Micropus californicus	Asteraceae	native	annual forb
Petrorhagia dubia	Caryophyllaceae	native	annual forb
Plagiobothrys nothofulvus	Boraginaceae	native	perennial forb
Plantago erecta	Plantaginaceae	native	annual forb
Poa bulbosa	Poaceae	introduced	perennial graminoid
Thysanocarpus curvipes	Brassicaceae	native	annual forb
Triphysaria eriantha subsp. *eriantha*	Scrophulariaceae	native	annual forb
Vulpia myuros	Poaceae	introduced	annual graminoid

survival and growth of most large woody riparian vegetation. The soil between the gravel and cobbles is sand to loamy sand (76–90% sand) that holds little water and dries quickly after inundation. These alluvial soils contain little organic matter (<2%), and are deficient in important macronutrients, particularly phosphorus, potassium, nitrogen, and sulfur, that are readily leached from the coarse-textured soils. The soils were generally high in magnesium, containing 318–448 ppm (7 times the amount used for agricultural crops).

These lowland creekbed sites are also characterized by periodic disturbance. Although the lowland creeks are ephemeral, they sporadically carry heavy torrents of water, particularly in the winter. The rushing winter water disturbs the habitat so greatly that few plants are able to become established or survive.

The physical properties of the soil, the dynamic and shifting nature of ephemeral creekbeds, and the lack of shade-providing riparian vegetation are all factors that serve to reduce competition in the lowland habitat of *C. crinita*. Some plant species, mostly annual, do manage to survive in this habitat. Table 2 lists associated species at lowland sites.

Upland Habitat

Although the upland sites differed from the valley creekbed sites in many ways, they also had similarities that make them suitable habitat for *C. crinita*. Upland populations of *C. crinita* were found on soils derived from Tuscan and Basaltic Mudflow with little soil development. These slightly acid soils are thin inceptisols. An impermeable layer under these thin, rocky Tuscan soils produces an environment in which many species, particularly woody and invasive species, are unable to grow due to water stress and low nutrient availability (Chiarucci 2003). They are very rocky to extremely rocky, medium textured and/or sandy loams that are part of the Toomes, Iron Mountain, and Supan Series. Large rocks (8–90 cm) and exposed bedrock can make up to 25% or more of the soil surface. They are well-drained to excessively well-drained soils that hold little water and become hard when dry. The soils are only an average of 20–30 cm deep, and are underlain by an impervious layer that consists of either basaltic rock or breccia of tuffaceous material cemented together (USDA Soil Conservation Service 1967, 1974). Trees and shrubs are only able to grow where cracks exist in this layer.

Because vegetation provides organic material that increases water retention, these poorly vegetated rocky and sandy soils remain too well-drained to support much additional vegetation. Humic material also tends to lower soil pH, enhancing availability of minerals in the soil to plants. Lack of available nutrients, particularly the macronutrients nitrogen, phosphorus, and potassium, has been shown to play a large role in limiting the productivity of hard volcanic soils and minimizing colonization of invasive species (Chiarucci 2003; Huenneke et al. 1990).

Another factor limiting encroachment of vegetation, most notably large woody vegetation, into the upland *C. crinita* sites is local precipitation patterns. The foothills of eastern Tehama and southeastern Shasta counties lie in a band of lower precipitation than hills of similar elevation to the north and south. This precipitation deficit

TABLE 3. ASSOCIATES OF *CRYPTANTHA CRINITA* AT UPLAND SITES. Nomenclature follows Hickman (1993).

Scientific name	Family	Origin	Life form
Astragalus pauperculus	Fabaceae	native	annual forb
Bromus madritensis subsp. *rubens*	Poaceae	introduced	annual graminoid
Bromus hordeaceus	Poaceae	introduced	annual graminoid
Bromus tectorum	Poaceae	introduced	annual graminoid
Centaurea solstitialis	Asteraceae	introduced	annual forb
Chorizanthe polygonoides var. *polygonoides*	Polygonaceae	native	annual forb
Chorizanthe stellulata	Polygonaceae	native	annual forb
Githopsis pulchella subsp. *campestris*	Campanulaceae	native	annual forb
Lotus humistratus	Fabaceae	native	annual forb
Micropus californicus	Asteraceae	native	annual forb
Petrorhagia dubia	Caryophyllaceae	native	annual forb
Polygonum bolanderi	Polygonaceae	native	perennial shrub
Taeniatherum caput-medusae	Poaceae	introduced	annual graminoid
Thysanocarpus curvipes	Brassicaceae	native	annual forb
Vulpia microstachys var. *pauciflora*	Poaceae	introduced	annual graminoid

probably results from a rain shadow effect from the Yolla Bolly Range which is located to the west of this area (A. Conlin, National Resources Conservation Service, personal communication). Foothills in the northern Sierra and southern Cascade regions typically receive an average of 125–165 cm of precipitation per year (Oregon Climate Service 1995). This level of precipitation promotes the growth of woody vegetation, in this case montane conifer forest dominated by ponderosa pine, down to approximately 600 m elevation. However, eastern Tehama and southeastern Shasta counties receive an average of only 90–125 cm of precipitation per year (Oregon Climate Service 1995). As a result, conifer forest does not become the dominant vegetation type in this area until approximately 1070 m elevation. Grass and shrubland vegetation, usually found at lower elevations, remain the main vegetation types at higher elevation than typically expected.

Cryptantha crinita shares its upland habitat with many other species. Species commonly associated with *C. crinita* at the upland sites in Tehama County are listed in Table 3. Similar to the lowland sites, most of the associates are annuals. Some associates, particularly the brome grasses and *Centaurea solstitialis*, are highly competitive invasive species.

As a result of its affinity for ephemeral creekbed habitats, botanists and land managers have assumed that *C. crinita* is a disturbance-loving species. One difference between the upland sites and lowland creekbed sites, however, is the lack of a regular disturbance regime at the upland sites. Thus, rather than being a disturbance-loving species, *C. crinita* may instead merely tolerate disturbance that reduces competition from other species. While the upland populations inhabit much more stable habitats compared to their lowland counterparts, both habitats are characterized by low density of other species, and therefore low levels of competition.

DISCUSSION

Several factors led to the perception that *C. crinita* grows only in lowland creekbed habitats with alluvial soil. First, the type locality for the species was found in the valley, and no upland populations were found in the ensuing 95 years. Second, small annual *Cryptantha* spp. are difficult to identify in the field, and neither the lowland nor upland populations stand out to the casual or even trained observer. Third, the upland habitat has relatively poor access, often compounded by the presence of copious poison oak. Finally, since much of the land in question has been set aside as wilderness and wildlife preserve, there have been only a few state or federal projects in the area, and therefore the area has not been subject to much botanical scrutiny.

The first documented upland site (Taylor 10684) was hypothesized to be the result of a long-distance dispersal event. The subsequent discovery of several upland populations in separate watersheds since Taylor's 1990 discovery makes this hypothesis less tenable. It is unlikely that several *upslope* dispersal events have taken place in separate watersheds, particularly since no upslope dispersal mechanism is known. A more likely scenario is that the upland sites are the primary habitat for the species, and the lowland sites, long thought to be the typical habitat of the species, are the result of long-distance dispersal events. Several observations support this alternative view. First, the upland populations have greater population size and area, providing a more copious and reliable seed source than the lowland populations. Although no quantitative population census or mapping has been performed, field observations have led to subjective estimates of upland populations as numbering in the thousands of individuals on 100 to several hundred acres. Valley floor populations are believed to number in the hundreds of individuals on approximately 10 acres. Second, the upland populations grow in more stable habitats and are more likely to persist through time. Finally, a downstream dispersal mechanism is known (the single nutlets within a hairy calyx are known to float, Mackey 1999), while no upstream or upslope dispersal mechanism is known.

The upland populations create a more coherent overall view of population dynamics for the species. Lowland creekbed populations establish, expand, contract, or are extirpated as they are disturbed by erosion and flooding, or as gravelbars stabilize and competition makes the habitat unsuitable for *C. crinita*. A source of new seeds for the unstable and ephemeral creekbed occurrences is provided by the more stable upland populations. Seeds are washed downstream from the upland populations and come to rest in the alluvial soils of the valley bottoms. Although this habitat differs in many ways from the upland sites, lack of vegetative cover allows *C. crinita* to establish and survive in the lowland sites at least temporarily.

Even with the discovery of additional larger populations in the uplands, it is clear that *C. crinita* is a rare species. It remains limited to relatively few occurrences in a small geographical range within Shasta and Tehama counties of northern California. These new discoveries do indicate that the species is more plentiful than previously thought, and has a wider ecological amplitude as well. Additional populations may exist in the intervening areas between lowland populations and the recently discovered upland sites. However, the presence of several highly competitive introduced species such as *Bromus madritensis* subsp. *rubens*, *B. tectorum*, *Centaurea solstitialis*, and *Taeniatherum caput-medusae* associated with *C. crinita* in upland habitats may pose a threat from increased competition.

Potential for Further Research

The distribution and population dynamics of *C. crinita* present an ideal opportunity for population genetic analysis. If the lowland populations are a result of long-distance dispersal events from upland populations, then lowland populations should have less genetic variability and should be a genetic subset of the upland populations.

On a final historical note, it seems fitting that these upland populations have only recently been discovered, since this is the same remote country where Ishi, the last free-living Stone Age Native American, was able to hide and survive until 1908.

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