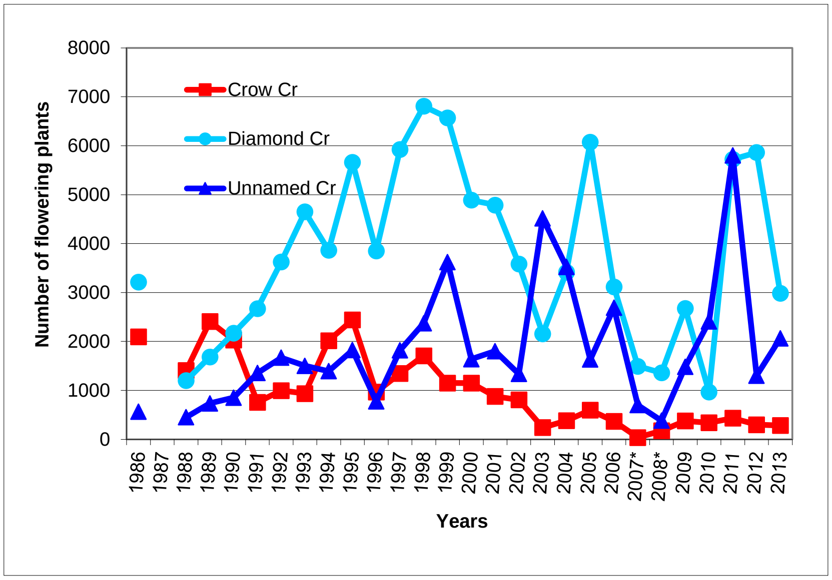

26-YEAR POPULATION TRENDS OF COLORADO BUTTERFLY PLANT *(OENOTHERA COLORADENSIS;* ONAGRACEAE), A SHORT-LIVED RIPARIAN SPECIES ON F.E. WARREN AIR FORCE BASE, LARAMIE COUNTY, WYOMING

Prepared for:
Environmental Element
Francis E. Warren Air Force Base
90 CES/CEIE, 300 Vesle Drive
F.E. Warren AFB, Wyoming 82005

Prepared by:
Bonnie Heidel and Joy Handley
Wyoming Natural Diversity Database
University of Wyoming, Dept. 3381, 1000 E. University Avenue
Laramie, WY 82071

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ABSTRACT

Annual census of Colorado butterfly plant (*Oenothera coloradensis* (Rydberg) W.L. Wagner & Hoch) was initiated in 1986 and conducted consecutively for 26 years from 1988-2013 on F.E. Warren Air Force Base (WAFB), in Laramie County, Wyoming. Colorado butterfly plant is listed as Threatened under the Endangered Species Act (ESA). WAFB has the only Colorado butterfly plant population on federal land, and it is one of the largest known populations, so its viability is important to overall conservation and recovery under the ESA. Colorado butterfly plant monitoring on the Base also provides the only long-term dataset for reference throughout its range. The 2013 census tally of 5333 plants is below average, but well above record lows in 2007-2008 when there was an herbivory outbreak, apparently by the apple flea beetle (*Altica foliaceae*). For the first time, we searched for dead flowering plants at the time of census and found 62 dead flowering plants (1.2% of total), nearly all in one stream, possibly representing incipient herbivory levels and associated mortality that are spotty. The prospect of high census numbers in 2013 did not materialize. Though the mild 2011 growing season was conducive to germination, the harsh 2012 growing season was detrimental to establishment and survival.

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Cover: *Oenothera coloradensis* trends on three WAFB creeks (1986-2013)

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INTRODUCTION

Status

Colorado butterfly plant (*Oenothera colordensis* (Rydberg) W.L. Wagner & Hoch; syn. *Gaura neomexicana* Woot. ssp. *coloradensis* (Rydb.) Raven & Gregory) is a regional endemic of the North and South Platte River watersheds on the high plains of northeastern Colorado, western Nebraska and southeastern Wyoming. It was listed as Threatened under the Endangered Species Act (USDI FWS 2000). It was first recognized as a distinct taxon by Rydberg (1904) based on a specimen collected in 1895 near Fort Collins, Colorado. The Colorado butterfly plant population on F.E. Warren Air Force Base (WAFB) is one of the three largest known populations, and the only one on federal land. The goal of WAFB is to maintain Colorado butterfly plant numbers (Warren Air Force Base 2001, Western Ecosystems Technology, Inc. 2001, Grunau et al. 2004). This goal is important to the overall conservation and recovery of Colorado butterfly plant under ESA. The monitoring study gauges Colorado butterfly plant trends on WAFB against that goal and provides a long-term population trend dataset against which other populations can be compared and understood.

Recent taxonomic research elevated Colorado butterfly plant from a subspecies to a full species (Wagner et al. 2013) based on genetics analysis (Krakos 2011). This was preceded by earlier research in the Primrose family (Onagraceae) documenting that the primrose genus (*Oenothera*) is monophylletic only by subsuming two smaller genera, butterfly plant (*Gaura*) and stenosiphon (*Stenosiphon*;Wagner et al. 2007). Species previously in the *Gaura* genus were transferred to the *Oenothera* genus. The taxonomic change does not affect status under the ESA except that elevation to full species elevates the recovery priority for Colorado butterfly plant because higher priority is placed on recovering full species than lower taxonomic levels. These published taxonomic changes will also appear in an upcoming volume of the *Flora of North America*, have been changed in the Rocky Mountain Herbarium on-line database, and will be changed at Wyoming Natural Diversity Database (WYNDD). The common name for Colorado butterfly plant is used throughout this report for the sake of clarity.

Life history

Colorado butterfly plant is reported to be a monocarpic biennial (Raven and Gregory 1972) but demographic monitoring suggests that it is a short-lived perennial (Floyd 1995a, Floyd and Ranker 1998). Colorado butterfly plant reproduces strictly by seed. Each spring, Colorado butterfly plants appear as a cluster of leaves that arise directly from the taproot and grow low to the ground as vegetative rosettes. The largest, presumably oldest, rosettes produce a flowering stalk in early June, while the rest remain as vegetative rosettes. Flowering begins in late June or early July and can continue through the rest of the growing season. Flowering plants are the most conspicuous life history stage. The mean age of plants that flower is not known but climate correlation data strongly suggest that germination generally occurs in the spring, vegetative plants grow for two years, and they flower in the third year (Heidel 2009).

There are typically four seeds per capsule, encased in a hard but permeable seed coat, that can imbibe 56% of its weight in water within 24 hours (Burgess 2003). Germination is highly variable in the wild within and between years (Floyd 1995a). Seeds retain full viability in cold storage for at least five years (Burgess 2003), indicating that Colorado butterfly plant can form a seed bank. In the greenhouse, germination is promoted by the combination of cool storage and at least two or more months of moisture (Locklear pers. commun. no date, Burgess 2003, Burgess et al. 2005). The moisture-dependency of germination is demonstrated by the appearance of high numbers of new vegetative plants only 27 days after a 100-year flood event at WAFB on 1 August 1985 (Rocky Mountain Heritage Task Force 1987). This is also demonstrated by the appearance of new plants on all three creeks in 2001 (Burgess 2003) when there were high July rainfall events within what was otherwise a drought year (USDI NOAA 2005), and by high numbers of new vegetative plants on just Diamond Creek the same year when water releases entered WAFB in the latter part of summer during the reconstruction of a lowhead dam structure immediately upstream (outside of WAFB).

Population biology

The distribution of Colorado butterfly plant on WAFB has variously been referred to as corresponding to one, two, or three populations corresponding with occupied habitat on three streams. They are referred to in this report as one population because the streams are confluent and the species' distribution is confluent on two of three streams. In addition, there is high likelihood of genetic exchange via lepidopteran pollination vectors traveling between streams. Yet, they are referred to as three subpopulations or population segments because they are discrete and have three fundamentally different hydrological conditions and other habitat differences. Seeds are dispersed primarily around the base of the parent plant (Floyd 1995a) and are thus limited to the same creek, though seeds might be transported greater distances in high-water conditions.

Genetic variation in Colorado butterfly plant on WAFB reveals high similarity between plants on the three streams as indicated by cluster analysis of Inter-simple Sequence Repeat (ISSR) variation data (Brown 1999, 2000; Tuthill and Brown 2003). Individuals from the largest creek have unique alleles, with variation reduced among individuals of the intermediate-size creek and lowest among individuals on the smallest stream, as determined by principle component analysis. This is consistent with earlier gel electrophoresis indicating that Colorado butterfly plant on WAFB appears to have low levels of genetic variability, though plants on the largest creek have genetically unique components and higher genetic diversity than those on the intermediate-size creek and on the smallest creek (Floyd 1995a).

STUDY AREA

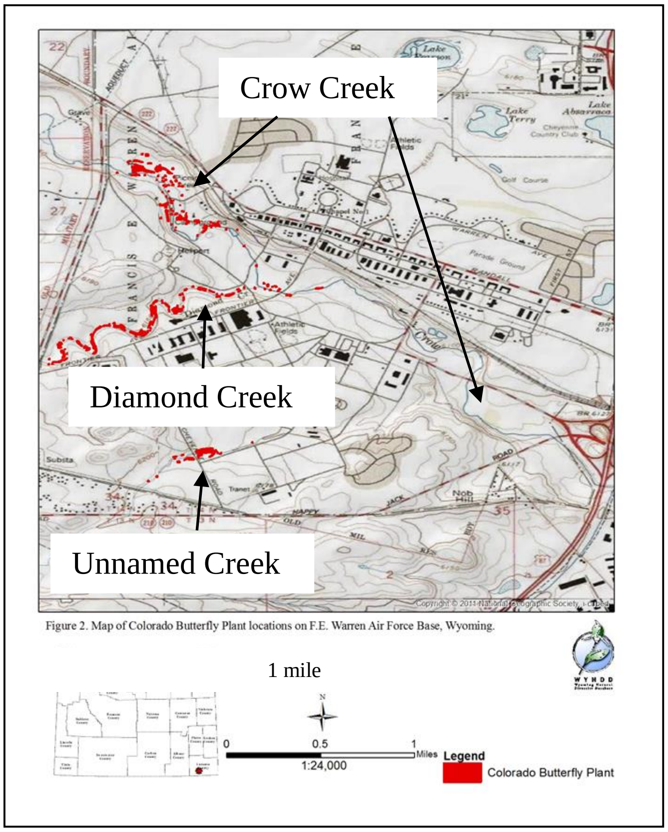
Location

The study area is located on F.E. Warren Air Force Base (WAFB) immediately west of Cheyenne (41° 07'N 104° 52'W) in Laramie County, Wyoming. Colorado butterfly plant occupies riparian habitat along three confluent creeks including Crow Creek, Diamond Creek, and an unnamed, ephemeral creek (hereafter referred to as Unnamed Creek) (Figure 1). The three creeks span approximately 4 km (2.4 miles) of riparian corridor habitat, though Colorado butterfly plant is discontinuously distributed in patches that total less than 5 ha (12.4 ac) within the occupied segments. The low-gradient creeks are at 1862-1887 m (6110-6190 ft) elevation with a relief of 5.7 m per km (30 ft per mile).

Hydrology

Crow Creek is the largest of the three creeks occupied by Colorado butterfly plant on WAFB, with perennial flow, a large watershed, and several large impoundments higher up in the watershed. It is subject to flooding, has abandoned channels, beaver dams, springs, seeps, and two tributaries on WAFB. Diamond Creek is the largest tributary of Crow Creek on WAFB, a highly meandered seasonally-flowing creek with a watershed magnitudes smaller in area than Crow Creek, and a small drop-structure impoundment directly upstream from WAFB. Unnamed Creek is a very small tributary of Crow Creek on WAFB, not shown on the USGS map, with ephemeral flow, an outflow buried below ground, and a watershed magnitudes smaller than that of Diamond Creek, largely confined to WAFB.

Figure 1. Distribution of Colorado butterfly plant habitat on F.E. Warren Air Force Base, Cheyenne, Wyoming



Soils

The three creeks on WAFB have calcareous, fine loams that include Fluvaquentic Andoaquolls of the Merden series and frigid Cumulid Enoaquolls in the Kovich series (Stevenson 1997), i.e., subirrigated mollisols (Fertig 2000a). Crow Creek soils are relatively coarse loamy sands that are nutrient-poor, while Diamond Creek and Unnamed Creek have relatively fine sandy loams that have higher nutrient, mineral and organic content (Heidel 2007). Crow Creek was reported as having higher soil temperatures than other Colorado butterfly plant settings on WAFB (Munk 1999; cited in Fertig 2000b) because its coarse soils are droughty at the surface. It was also reported as having wetter subsurface soils at 25 cm (10 in) and 50 cm (20 in) depths than other Colorado butterfly plant settings on WAFB in the high-precipitation year of 1999 (Munk 1999), which might differ drastically in low-precipitation years.

Vegetation

The Crow Creek riparian corridor lies in a broad, gentle valley and has wetland thicket dominated by *Salix exigua* (coyote willow), interrupted by small woodland bands, and wet and dry meadow openings. The Diamond Creek riparian corridor lies below an incised, north-facing slope, covered by wet and dry meadows and with a narrow wooded segment at the mouth. Unnamed Creek riparian corridor has wet and dry meadows, and small patches of shrubs.

Botanists monitoring Colorado butterfly plant since 1986 have noted large increases in *Cirsium arvense* (Canada thistle), *Euphorbia esula* (leafy spurge), and *Salix exigua* (e.g., Marriott 1988, Marriott and Jones 1988, Fertig 2000b) particularly on Crow Creek. The first two species are noxious weeds, while the third species is a native willow that has encroached on meadow habitat in the riparian corridor. In 1999-2001, noxious weeds were mapped throughout Colorado butterfly plant riparian corridor habitat (Heidel et al. 2002, Fertig and Arnett 2001, Hiemstra and Fertig 2000, Heidel and Laursen 2002). Willow cover was also mapped (Jones 2003) as habitat for Preble's jumping mouse (Jones 2003). Other species that have been described as common in Colorado butterfly plant wet meadow habitat on WAFB include *Agrostis stolonifera* (redtop), *Symphyotrichum falcatus* (white prairie aster), *Equisetum laevigatum* (smooth horsetail), *Glycyrrhiza lepidota* (wild licorice), *Poa pratensis* (Kentucky bluegrass), and *Solidago canadensis* (Canadian goldenrod); (Dorn and Lichvar 1984; Marriott 1987, Fertig 2000a).

Return of precipitation to pre-drought levels in 2009-2011 fostered a resurgence of native species cover, in which native species were identified as dominants or locally abundant along parts of riparian corridor habitat occupied by Colorado butterfly plant on WAFB, including: *Carex praegracilis* (clustered field sedge), *Muhlenbergia richardsonis* (matted muhly), *Schizachyrium scoparium* (little bluestem), *Panicum virgatum* (switchgrass), and *Spartina pectinata* (prairie cordgrass). These native grasses and grass-like plants might be more representative of pre-settlement wet meadow vegetation on the high plains than the previously named associates.

Land use history

The riparian corridor habitat on WAFB was historically open and dynamic under the influence of floods, bison-grazing, and fire (Barlow and Knight 1999). The riparian corridor habitat became a center of human activity when the Base was first established as Fort D.A. Russell in 1867, the largest cavalry post in the United States. Historic uses of riparian habitat included livestock grazing, mowing, gardening on the flats (downstream from current Colorado butterfly plant habitat), training grounds, and recreation. Tons of hay were brought in, so the rangeland may never have been heavily grazed unless near buildings and corrals (Barlow and Knight 1999). Crow Creek was highly valued as a source of good-quality water. Trees planted around the fort buildings apparently spread to the nearby Crow Creek floodplain (Barlow and Knight 1999). The fort was rededicated as Fort Francis E. Warren in 1930, in honor of Wyoming's first governor. The entire grounds, including riparian areas, were used for tank training in World War II. The Fort became an Air Force Base in 1947. Colorado butterfly plant was discovered on WAFB in 1981, and designation of a Colorado Butterfly Plant Research Natural Area followed (Marriott and Jones 1988). A major goal of riparian management since then has been the maintenance of the Colorado butterfly plant population through control of competing plant species. There has been research on Canada thistle control (Floyd 1995b) and other vegetation management (Munk 1999, Munk et al. 2002, Burgess 2003, Burgess et al. 2005), multiple introductions of biocontrol agents, and goats brought in for weed control (2008, 2009, 2010) early in the growing season. Trees have flourished on the creek over the decades, and beaver numbers have grown as a response. In 2011, beaver dams were removed throughout Crow Creek to prevent innundation of roads and recreational facilities if not maintain natural stream flow.

Climate

WAFB has a continental climate typical of the high plains. The National Oceanic and Atmospheric Association climate station closest to WAFB is at the Cheyenne Municipal Airport, located 4.3 km (2.7 miles) northeast of WAFB at the same elevation (Station 481675; USDI NOAA 2012). The average annual precipitation during recent years (1984-2005) was 39.24 cm (15.59 inches), with heaviest rainfall in May, followed by June and July (USDI NOAA 2009). The average annual temperature was 8.01 °C (46.42 °F), peaking in July.

Climate data have been compiled (USDI NOAA 2013). Mean monthly temperatures and total monthly precipitation over the growing season are represented in Figures 2 and 3. They show an overall pattern of rising growing season temperature and diminishing growing season precipitation over the monitoring period. The 2011 conditions marked an exception to overall trends, with the coolest growing temperatures this decade, accompanied by the high snowfall before the growing season and the highest growing season precipitation this decade, followed by a swing to contrasting conditions in 2012. The 2013 climate conditions started out similar with an exceptionally cool, wet April, but all ensuing months have been closer to or above average.

Climate data was compiled into datasets (Table 1) for comparing with census results as represented in Figures 2 and 3. The early part of the growing season leading up to flowering is referred to as "spring" for purposes of this report (April-June), the period when Colorado butterfly plant has vegetative growth and starts to bolt (Table 1). The later part of the growing season, referred to as "summer" in this report (July-August), is the period of Colorado butterfly plant reproduction including flowering and fruiting. The combination of spring and summer data represents general growing season climate conditions. The 12-month climate data starting in October prior to the year of census represents the annual climate conditions.

Table 1. Climate data compiled for Colorado butterfly plant climate correlation analysis

Growing Season Period	Precipitation	Temperature
April-June ("Spring")	Net spring precipitation	Average spring mean monthly
July-August ("Summer")	Net summer precipitation	Average summer mean monthly
April-August ("Growing Season")	Net spring+summer precipitation	Average spring+summer mean monthly
October-September ("Annual")	Net 12 month precipitation	Average annual mean monthly

Figure 2. Growing season precipitation totals in Cheyenne, WY (1984-2012; Apr-Sept)

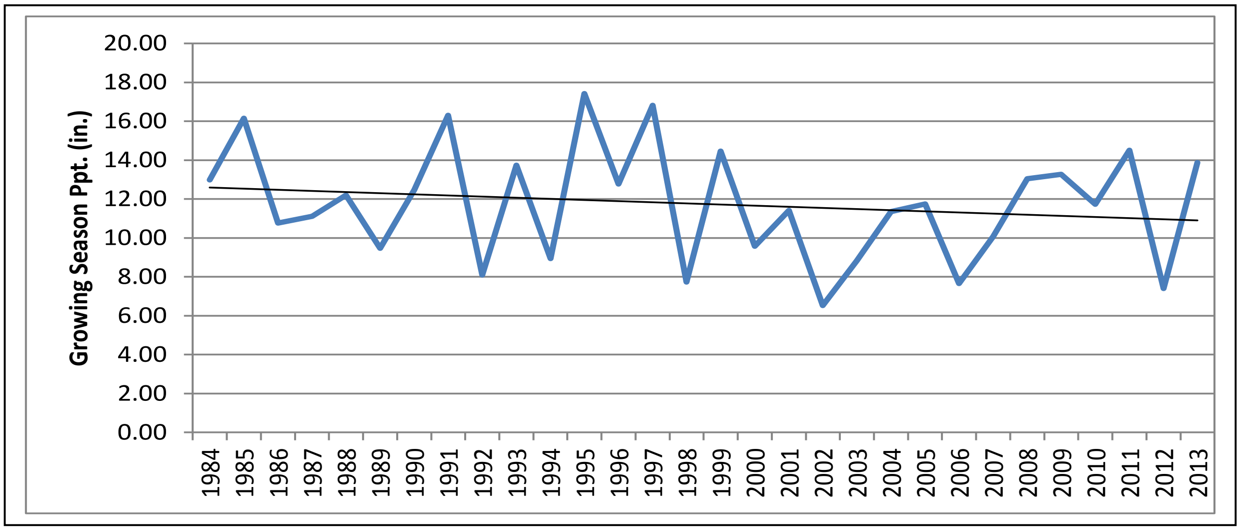
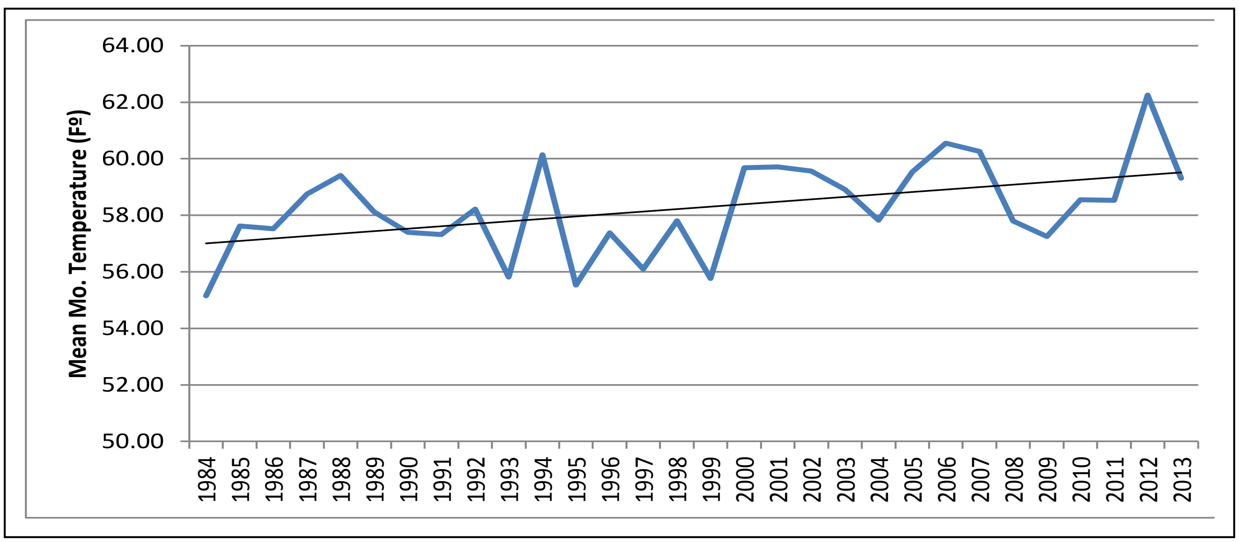


Figure 3. Growing season monthly temperature means in Cheyenne, WY (1984-2012; Apr-Sept)



Characterization of WAFB climate conditions and their influence on Colorado butterfly plant are complicated by extreme weather events. The start of Colorado butterfly plant monitoring was preceded by a flood on August 1, 1985 that was classified as a 100-year event (USDI Geological Survey 1989). In the City of Cheyenne, downstream of Colorado butterfly plant habitat, rainfall levels exceeded 17.8 cm (7 in; USDI Geological Survey 1989). Only 7.6-10.2 cm (3-4 inches) of rain fell on WAFB that day. The flood matted vegetation and deposited alluvium on Crow Creek but not on the tributaries (Rocky Mountain Heritage Task Force 1987). There was a minor spring flood in 1995, a minor but prolonged flood event in June 1999 (Munk 1999), and a minor flood event in July 2001 (Burgess et al. 2005). Summer flooding is associated with storm cell events and spring flooding is associated with high winter snowpack. Floods are described as part of the natural disturbance regime (Fertig 2001).

The monitoring period included a major drought event from 2000-2006, as indicated by the Palmer Drought Severity Index for southeastern Wyoming (Appendix A. USDI National Oceanic and Atmospheric Administration - Region 8. 2008). There has not been a period of drought in southeastern Wyoming longer than two years since 1976, and it is longer than any prior droughts since the monitoring began in 1895 (Appendix A). The 2000-2006 drought period is evident in both average monthly temperatures data over the growing season when compared with the previous 16 years; and in monthly precipitation over the growing season when compared with the previous 16 years (Figures 2 and 3).

There have also been localized weather events associated with storm cells. In 2011, heavy hail damage to Colorado butterfly plants was noted in the Unnamed Creek subpopulation at the start of monitoring, whereas plants were healthy and undamaged at the time of the previous training visit two weeks earlier. There were many broken flowering stems and branches, including some plants with no intact flowering stems remaining. The damage did not kill plants on the Unnamed Drainage, but may have prevented maturation of flowers and fruits associated with at least half of the reproductive potential that year. There was no similar damage among plants on Crow or Diamond Creeks. The damage was apparently caused by a severe hail event on 24 July that caused hail damage on the Base and in town.

This compilation of data into six-month blocks is based on the inference that growing season climate affects Colorado butterfly plant trends. It does not even begin to address the heterogeneity within a growing season. For example, climate conditions in the 2013 growing season were uneven, starting and ending wet but with a record dry June rainfall.

Climate may also affect the flea beetle populations, which devoured Colorado butterfly plants in 2007-08 (Heidel et al. 2011). Very little is known about flea beetle life cycle and population biology, and there were few climate conditions that were out of the ordinary in 2007 except that it was near the end of a drought cycle. In addition, there was a very early, warm spring in 2006 that may have fostered a large flea beetle hatch and proliferation in ensuing years.

METHODS

Field methods

Complete annual census of flowering Colorado butterfly plant plants was initiated in 1986 by Wyoming Natural Diversity Database (WYNDD; Marriott 1988) to gauge overall population trends under the WAFB goals of maintaining Colorado butterfly plant numbers (WAFB 2001, WEST 2001, Grunau et al. 2004). Annual census was conducted each year between 1988-2012. Census was timed during or after peak flowering in August or early September. The 2012 census was conducted by Bonnie Heidel, Joy Handley, Dorothy Tuthill and Jenna Ramunno on 5-8 August with a revisit on 14 August. At census time, plants were in full flower with fruits also present. In this report, all reproductive plants are referred to as flowering plants. Non-reproductive plants are referred to as vegetative plants.

In conducting the census, each individual was differentiated and tallied, taking care to distinguish individuals when present in high density, and to discern what constituted an individual among highly-branched stems that had been browsed close to the ground and that might be mistaken for multiple plants. In large areas of high density, the colony was partitioned into lanes using tape measures to census lane-by-lane. This ensured completeness of coverage while avoiding the error of counting any individual plant more than once, an efficient approach for two-person teams.

Colorado butterfly plant census data were recorded separately for the three creeks from the start of monitoring under assumptions that they represent different habitats if not different populations or subpopulations. The tallies were further subdivided by major riparian corridor segments beginning in 1989 to compare finer-scale spatial changes over time. More detailed documentation of distribution became part of census over the years because distribution patterns are relatively stable over time (Floyd 1995a). Hand-drawn boundaries of distribution were marked onto digital orthophoto prints and digitized in 1999. Starting in 2002, Global Positioning System (GPS) data points were collected as part of census work to map all discrete colonies as polygons or else points (for single plants or colonies less than 5 m). The collective polygon boundaries were updated to represent maximum extent over time (2002-2013).

In the field, the 2012 population map was carried into the field, representing all past polygon colonies. Intervening habitat between colonies continued to be surveyed for outlying plants that may be mapped as a boundary extension of an existing colony if they are located within 5 m of previously-recorded plants, or else as a new colony. GPS points were taken as reference for all prospective boundary changes or new colonies.

Census compilation methods

Population census of Colorado butterfly plant on WAFB has been compiled annually and trends reported on the three creeks and WAFB overall (Fertig 1993, 1995, 1996, 1997, 1998, 1999, 2000b, 2001; Marriott 1989, 1990a, 1991, 1993, Heidel and Laursen 2002, Heidel et al. 2002, Laursen and Heidel 2003, Heidel 2006a,b,c, Heidel 2007, 2008, 2009, Heidel et al. 2010, Heidel and Handley 2011, 2012, 2013). The 2013 tallies of flowering Colorado butterfly plant numbers were likewise tallied and graphed. Calculations were made of the rates of change relative to prior years and to the mean. The spatial pattern of trends was also represented by stream segment, and divided further into small polygons or points, recording presence/absence of Colorado butterfly plant in an ArcMap project representing all polygons over time, and whether or not they had flowering plants in 2013.

Viability analysis

Two-year log growth rates, or $\log(N_t/N_{t-2})$, were modeled for each subpopulation through 2009 (Heidel et al. 2010) and are in the process of being updated (Wepprich et al. in progress). Best-fit models were calculated using maximum log likelihood and information criterion statistics as summarized in Morris and Doak (2002). The results were compared to the best-fit models obtained when removing the flea-beetle outbreak years of 2007-2008.

Environmental variability and climate variability in particular are not included in the models. They would cause the observed counts to be better or worse than the predicted model values. The differences, or “residuals”, between the best-fit model values and the observed two-year growth rates indicate the influence of temperature and precipitation on growth rates. Climate correlations were calculated between residuals from the best-fit model for each Colorado butterfly plant subpopulation with climate variables (mean monthly temperature, monthly precipitation) both in the same year as a census, the year before the census, and two years prior to census using updated monthy temperature and precipitation data from Cheyenne Airport (Station 481675; USDI NOAA 2013).

In addition, the distributions of the two-year growth rates were tested for outliers that were more than two standard deviations from the average values. Outliers beyond this range could be considered catastrophes if they create a bimodal distribution of growth rate values (Morris and Doak 2002). Although the term catastrophe suffers from overuse, two standard deviations from the average growth rate can delineate a decline as being outside of the typical environmental variability.

Herbivory documentation

Colorado butterfly plant was heavily browsed by insects in 2007, an event in which every plant throughout the population had the majority of its leaf tissue eaten, and seed production was impaired or curtailed. Reduced herbivory levels were noted in 2008 and low levels in 2009. The herbivory event and flea beetle determinations are presented in Heidel et al. (2011) in which results on all three creeks exhibited declines that were over two standard deviations from the average growth rate. The insect herbivory phenomenon has unanswered questions that are important in evaluating the viability of the plant population and requires work outside of the monitoring period to evaluate.

Two pre-monitoring trips to the WAFB population of Colorado butterfly plant were made to evaluate flea beetle herbivory levels, on July 3 and July 17. The early, warm spring temperatures of 2012 were basis for recommending such scouting (Heidel and Handley 2013), reinforced by warm spring temperatures of 2013. Such conditions might be conducive to early flea beetle hatch, multiple life cycles in one year, and exponential growth. We visited two colonies of Colorado butterfly plant colonies on all three creeks (Crow C-I-4, Crow C-VI-2; Diamond D-I-23, D-III-8, Unnamed U-I-5, Unnamed U-II-4) that had high numbers in 2012, searching for presence of herbivory. Three representative plants were flagged, GPS points were taken, a single lower stem leaf was collected from each plant for quantifying the level of herbivory on the leaf, and the following were measured:

Height
No. of inflorescences, total
No. of flowers currently open
No. of seed capsules (they usually persist for some weeks)
Level of leaf damage
- 0
- 1-5% reduction
- 5-25% reduction
- 26-90% reduction
- 91-100% reduction

No. of flowers currently open
No. of seed capsules
Notes

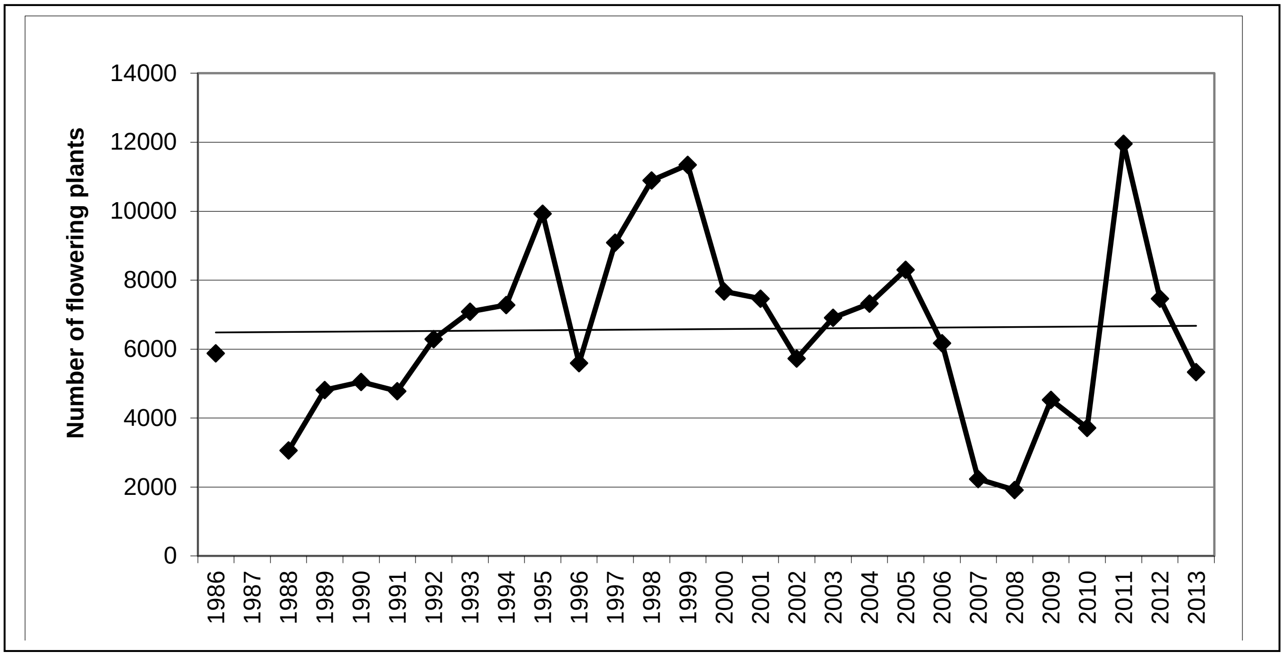
Herbivory results were tabulated and considered in furthering flea beetle research.

RESULTS

Census results

Overall Colorado butterfly plant numbers have been relatively stable since 1986 (Figure 4, Table 2). The 25-year average is 6613 flowering plants, and numbers have fluctuated 81% above the mean and 66% below. Fluctuation periods have ranged from 2-5 years above the mean and 1-5 years below.

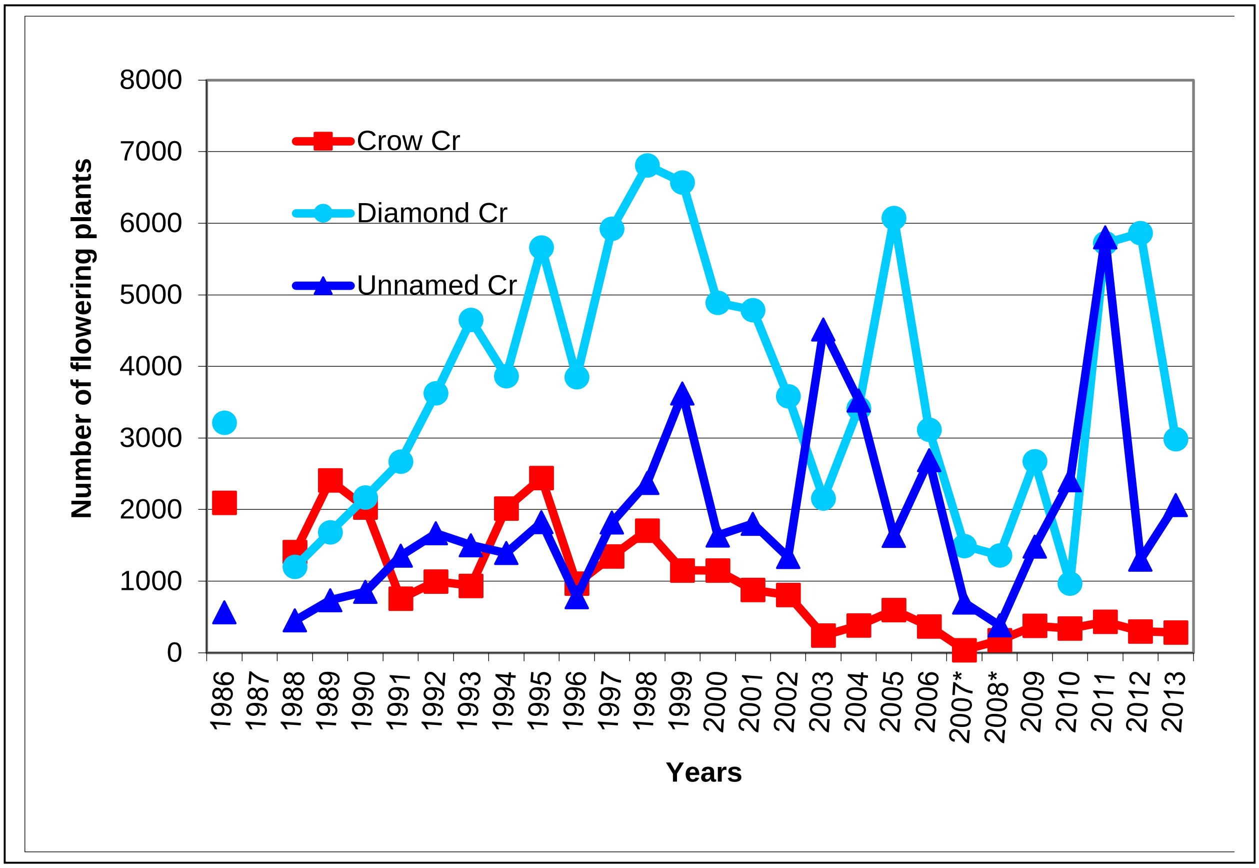
Figure 4. Colorado butterfly plant population trends, WAFB (1986, 1988-2013)



However, the regression line is not a statistical representation of trend as best determined by population viability analysis. Moreover, results provide multi-year fluctuations that differ for any given five- or ten-year period over the course of monitoring (e.g., 1988-1997, 1998-2007, 2008-2013). Furthermore, very different results are also evident in comparing overall subpopulation numbers on any given creek (Figure 5, Table 2).

The three creeks have habitat that functions hydrologically different, and locales on the same creek tend to exhibit the same patterns more than locales on different creeks. The census results for each creek are divided further within each riparian corridor segment as presented in the Appendix B table, and at each polygon as presented in the Appendix C table. The results of mapping all Colorado butterfly plant locales are presented in Appendix D superimposed on digital orthophotographs. The latter represents each locale where Colorado butterfly plant was present or absent in 2013 among all polygons over time. The spatial distribution of Colorado butterfly plant across WAFB stayed much the same over time, with 105 polygons occupied in 2013, 106 polygons occupied in 2012, 109 polygons in 2011 and 101 in 2010, but only 35 polygons occupied in 2007.

Figure 5. Colorado butterfly plant subpopulation trends by creek, WAFB (1986, 1988-2013)[1]



[1] Refer to the study area map – Figure 1 (p. 4) for Colorado butterfly plant distribution on three WAFB creeks. Crow Creek has the most extensive habitat of the three creeks, and the most numerous discrete places (points or polygons) where Colorado butterfly plant has ever occurred.

Table 2. Colorado butterfly plant flowering plant numbers on F.E. Warren Air Force Base (1986, 1988-2013)

Year	Crow Cr	Diamond Cr	Unnamed Cr	WAFB (Total)
1986	2,095	3,216	565	5,876
1987	No data	No data	No data	No data
1988	1,406	1,201	452	3,059
1989	2,408	1,684	734	4,813
1990	2,030	2,171	851	5,052
1991	756	2,673	1,354	4,783
1992	997	3,627	1,669	6,293
1993	935	4,650	1,503	7,088
1994	2,017	3,865	1,393	7,275
1995	2,441	5,664	1,822	9,927
1996	967	3,850	777	5,594
1997	1,348	5,926	1,820	9,094
1998	1,708	6,809	2,372	10,889
1999	1,152	6,571	3,621	11,344
2000	1,148	4,890	1,638	7,676
2001	878	4,788	1,801	7,467
2002	808	3,582	1,336	5,726
2003	240	2,155	4,517	6,912
2004	381	3,416	3,525	7,322
2005	597	6,074	1,632	8,303
2006	369	3,116	2,690	6,175
2007	38	1,492	700	2,230
2008	175	1,360	381	1,916
2009	377	2,674	1,480	4,531
2010	339	969	2409	3717
2011	432	5722	5803	11,957
2012	299	5863	1300	7,462
2013	**283**	**2986**	**2064**	**5333**
Mean (1988-2013)	943	3761	1909	6613
2010 vs. 2009	-10.1%	-63.8%	+62.8%	-18.0%
2011 vs. 2010	+127.4%	+590.5%	+240.9	+321.7%
2012 vs. 2011	-30.8%	+2.5%	-77.6%	-37.6%
2013 vs. 2012	-5.3%	-49.1%	58.8%	-28.5%

Viability analysis

When using the 1988-2009 data, Crow Creek was best modeled by a theta-logistic model: $\log(N_t/N_{t-2}) = A+B*(N_{t-2})^C$. Diamond Creek was best modeled by the "no-theta" model: $\log(N_t/N_{t-2}) = A+B*(N_{t-2})+C*(N_{t-1})$. Unnamed Creek was best modeled by a Ricker model: $\log(N_t/N_{t-2}) = A+B*(N_{t-2})$. These three models all take into account density dependence, because the two-year growth rate is a function of the population count from two years earlier (N_{t-2}), or one year earlier (N_{t-1}). One surprise was that the Crow Creek subpopulation was no longer best modeled as having density-independent growth rates, as it was in the 2007 and 2008 analyses. The best-fit model parameters and selection statistics for count data ending in 2006, 2007, 2008, and 2009 show how the best-fit models changed with each year's successive count (Appendix D). This indicates that the decline in 2007 was severe enough to change the model to density dependent compared to 1988-2006 as density-independent regulation of the growth rates. More detailed discussion of growth rate contrasts between creeks and over time is re-examined in work underway (Wepprich et al. in progress).

Environmental variables in concert with climate may play a linked role in these population trends. Correlations between climate variables of temperature and precipitation may be compared in two ways. One could correlate the climate variables with the 2-year growth rates, but this only takes into account whether the growth rate is above or below average. Correlating the climate variables with the residuals from the best-fit model for each subpopulation will take into account whether climate variables are correlated with deviations from the growth predicted by the models. Appendix F and Appendix G in Heidel et al. (2010) indicated that best-fit models were influenced by climate variables in different ways between creeks.

Standard deviation for Colorado butterfly plant growth rates on all three creeks was graphed (Heidel et al. 2010, Appendix H) and indicated that all three creeks had negative outlier values in 2007 or 2008 but in no other years. More detailed analysis of standard deviation between subpopulations over time is under consideration.

Herbivory documentation

Field inspection of herbivory levels in July revealed that insect herbivory levels were absent or low (1-5% leaf area) on sampled Crow Creek and Diamond Creek plants, while becoming moderate (6-25%) though remaining local on some Unnamed Drainage plant leaves (and stems) by late July. By contrast, herbivory patterns were ubiquitous and high on all drainages in 2007-2008. No inflorescences were damaged by insects. Wildlife herbivory was noted by asterisk (*) and failure to relocate plants was marked by two asterisks.

Table 3. Attributes of Colorado butterfly plants checked for insect herbivory

Creek	Crow Creek		Diamond Creek		Unnamed Drainage	
Date	7/3/2013	7/17/2013	7/3/2013	7/17/2013	7/3/2013	7/17/2013
Height, av. (cm)	57 (44-71.5)	55.7 * **(29-73)	49.5 (27-65.5)	59 (18-79)	43.3 (21-62)	44.2 (24-60)*
No. of inflor.	1	5 * **	3.7	7	7	9.8
No. of flowers	0.3	2* **	0.5	2.2*	0.7	0.7
Insect herbivory	0 or Trace (1-5%)	0 or Trace (1-5%)	Trace (1-5%)	Trace (1-5%)	Trace (1-5%)	6-25%
Notes	Moderate wildlife browse by late July		Light wildlife browse by late July		Light wildlife browse by late July	

Observations and preliminary herbivory results indicate that leaf herbivory conditions on Colorado butterfly plant develop in the middle of summer, that inflorescence damage was not associated with leaf herbivory in 2013, and that the contrasts between adjoining plants may be as great as any contrasts between creeks. There were places of localized insect herbivory, as found in the remnant of an old exclosure on Unnamed Creek, where herbivory levels were so extreme that a couple plants were nearly dead by the late July visit.

DISCUSSION

Census results

Overall population numbers dipped below average in 2013. This possibly reflects lag effect of adverse climate conditions in the 2012 growing season that were some of the most severe on record when taking both net precpitation and mean monthly temperature into account, or the adverse climate conditions in the relatively hot and dry 2013 growing season that had very similar conditoions to 2012 except for heavy rains arriving in June. The census numbers for Colorado butterfly in 2013 demonstrate a prolonged, dramatic divergence in trends between Diamond and Unnamed creeks, and it is hypothesized that this reflects the dependency on on inflow for Diamond Creek compared to on groundwater for Unnamed Creek. The Unnamed Creek is one of the few places where Colorado butterfly plant is still persists in a headwater position, and offers insight into possible habitat loss patterns that took place historically outside of the Base.

A year ago, we posited that the cool, moist climate conditions of 2011 were probably conducive to germination and might be anticipated to foster high Colorado butterfly plant numbers in 2013. However, it seems as though harsh intervening climate conditions curtailed the rebound. If the bolting activity on Diamond Creek delayed bolting rather than killing plants, then the moist conditions in 2014 should be conducive to rebound on this creek in particular.

The 25-year monitoring period encompased a drought event, but the biggest decline in population numbers was not during the drought but immediately after it with the flea beetle outbreak. It is not known to whether drought or its culmination had the greatest influence on the flea beetle, and whether by direct or indirect means. The only other climate conditions that appeared to differ dramatically in or preceding 2007 was an exceptionally early, warm spring in 2006. It was the warmest spring on record over the course of monitoring, until the more recent spring of 2012.

Flea beetles are not on the same cycle or cue to the same environmental drivers as Colorado butterfly plant. The early, warm spring temperatures of 2012 and of 2013 might have been conducive to flea beetle hatch so early (pre-monitoring) visits to Colorado butterfly plant were conducted in 2013 and are highly recommended in 2014 to check for flea beetle activity (outlined in Heidel et al. 2011). XXIf found, then collections are to be made to confirm the herbivory vector(s). It might also be an opportunity to study the food preferences of the *Altica foliaceae* adult and the relationship between *Altica foliaceae* life cycle and climate in tandem research.

Viability results

The relative extinction risks for Colorado butterfly plant on WAFB, calculated through 2009 are being updated in Population Viability Analysis (PVA; Wepprich et al. in progress). They will also be recalculated using different hypothetical frequencies and durations of insect herbivory outbreaks to evaluate one-time vs. recurring outbreaks of different frequency. Two lines of evidence have been presented (Heidel et al. 2011) that the herbivory outbreak is outside the range of natural variation:

1. Change in best-fit models for two of the three creek trends when comparing 1988-2006 data vs. 1988-2009 data.
2. The two-year growth rate for all three creeks fell outside (below) two standard deviations from the average for 2007 or 2008. This supports the observations that the 2007 herbivory event did not have precedent during the 22-year period. Growth rate modeling, correlations between climate and the "residuals" of best-fit models, and testing the distribution of growth rates through 2010 are being redone.

Three analyses and re-evaluations are underway. Extirpation of the Colorado butterfly plant subpopulation on Crow Creek was thought to be imminent within 50 years based on the rate of decline through 2007 (Wepprich 2008a, b). The departure from a density-dependent best-fit model shows the severity of the 2007 crash. The return to density-dependent conditions for the subpopulation is a positive change, though the net outcome remains to be determined. Preliminary analysis suggests that Colorado butterfly plant viability on WAFB is not contingent on the Crow Creek subpopulation numbers from strictly PVA criteria, even though it may have genetic or other properties that make it indispensible.

Herbivory results

It is hypothesized that leaf herbivory on Colorado butterfly plant is density-dependent at low, possibly incipient levels. The preliminary measurements used in 2013 showed much difference in leaf herbivory between plants and uneven distribution that results. Future focus on the vector is the priority, along with a chronicling of the outbreak phenomenon if such an event were to repeat. For this purpose, one or more July visits are recommended to collect larvae as needed for rearing to make positive identifications, and to check in advance of monitoring for outbreak.

Population viability of Colorado butterfly plant on WAFB is also being re-evaluated with recurrent insect herbivory events to determine the net effects on viability. Despite an apparent capacity for population rebound, recurrence of flea beetle outbreaks at increased frequency could change viability.

2014 Monitoring plans

We will continue make advance visits to collect flea beetle larvae on Colorado butterfly plant and check if there is an outbreak event. We will continue seeking out and censusing dead flowering plants, a phenomenon that had not been addressed prior to 2013 monitoring. It introduces a possible source of error in using census results to run PVA. We will also replicate census work in 2014 (i.e., conduct it twice by different teams), in order to calculate an error rate that also tempers PVA work.

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