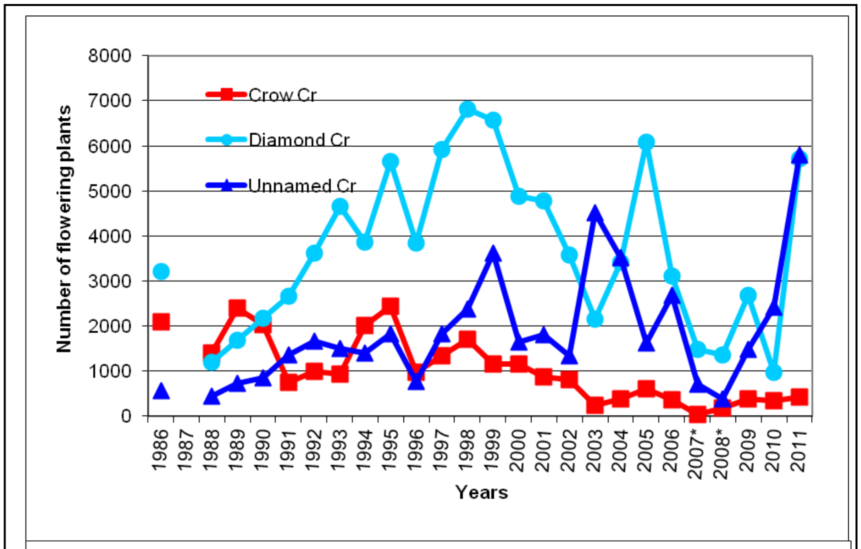
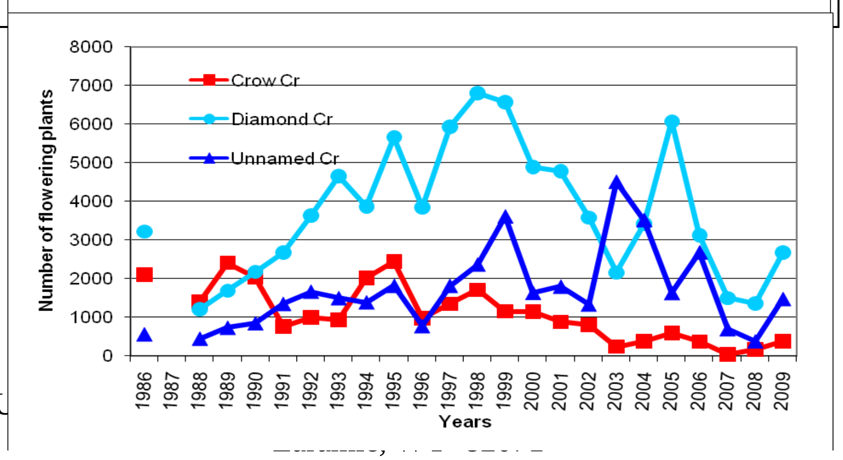
24-YEAR POPULATION TRENDS
OF COLORADO BUTTERFLY PLANT
(GAURA NEOMEXICANA SSP. *COLORADENSIS;* ONAGRACEAE),
A SHORT-LIVED RIPARIAN SPECIES ON
F.E. WARREN AIR FORCE BASE,
LARAMIE COUNTY, WYOMING





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ABSTRACT

Annual census of Colorado butterfly plant (*Gaura neomexicana* Woot. ssp. *coloradensis* (Rydb.) Raven & Gregory) was initiated in 1986 and conducted consecutively for 24 years from 1988-2011 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 ESA. This Colorado butterfly plant monitoring also provides the only long-term dataset for reference throughout its range. The 2011 census results continued the overall rebound in population numbers from record lows in 2007-2008 associated with an herbivory outbreak by the apple flea beetle (*Altica foliaceae*). Total 2011 population numbers on WAFB exceed the previous peak reported in 1999.

The most recent census results provide additional context for evaluating the extended affects of herbivory, suggesting that the lag effect of depressed seed production during herbivory years was limited to a two-year period. The 2011 results suggest strong capacities for rebound in two of the three population segments, particularly in smaller watersheds. It is hypothesized that this is also indicative of drought-rebound capacity of these hydrological settings, ones that are particularly vulnerable to landscape change and intensive management elsewhere in the distribution of this taxon. Thus, it offers possible explanation for habitat loss patterns under natural weather cycles in combination with land use practices. The unknown frequency of herbivory outbreaks and possible shift in weather cycles could ultimately determine decadal trends on WAFB.

Citation for this report: Heidel, B. and J. Handley. 24-year population trends of Colorado butterfly plant (*Gaura neomexicana* ssp. *coloradensis;* Onagraceae), a short-lived riparian species on F.E. Warren Air Force Base. Prepared for F.E. Warren Air Force Base by the Wyoming Natural Diversity Database (University of Wyoming), Laramie, WY.

Cover: *Gaura neomexicana* ssp. *coloradensis* trends on three WAFB creeks (1986-2011)

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INTRODUCTION

Status

Colorado butterfly plant (*Gaura neomexicana* Woot. ssp. *coloradensis* (Rydb.) Raven & Gregory; syn. *Oenothera coloradensis* (Rydb.) W.L. Wagner & Hoch ssp. *coloradensis*) 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). The goal is important to the overall conservation and recovery of Colorado butterfly plant under ESA. This 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.

Recent taxonomic research in the Primrose family (Onagraceae) suggests 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 are transferred to the *Oenothera* genus. This nomenclatural revision does not change the taxonomic circumscription or taxonomic level of Colorado butterfly plant or accompanying status under ESA. This taxonomic change will appear in an upcoming volume of the *Flora of North America*, has 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.

Incidental to this monitoring study, leaf samples were collected from Colorado butterfly plant on WAFB in September 2011. They have been used for DNA sequencing to advance phyllogenetic and taxonomic research in the Primrose Family (Onagraceae) at Missouri Botanical Garden. Publications of results are in progress (Krakos pers. commun. 2012).

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 is an obligate outcrosser that 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 it 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 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.

Population biology

The three creeks occupied by Colorado butterfly plant on WAFB have variously been referred to as corresponding to one, two, or three populations. They are referred to in this report as one population because of the proximity of occupied habitat, confluence of the three creeks, and likelihood of genetic exchange with lepidopteran pollination vectors traveling between creeks. 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 in high-water conditions.

Genetic variation in Colorado butterfly plant on WAFB reveals high similarity between plants on the three creeks 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 creek, 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 the Unnamed Creek) (Figure 1). The three creeks include 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 (30 ft per mile) per km.

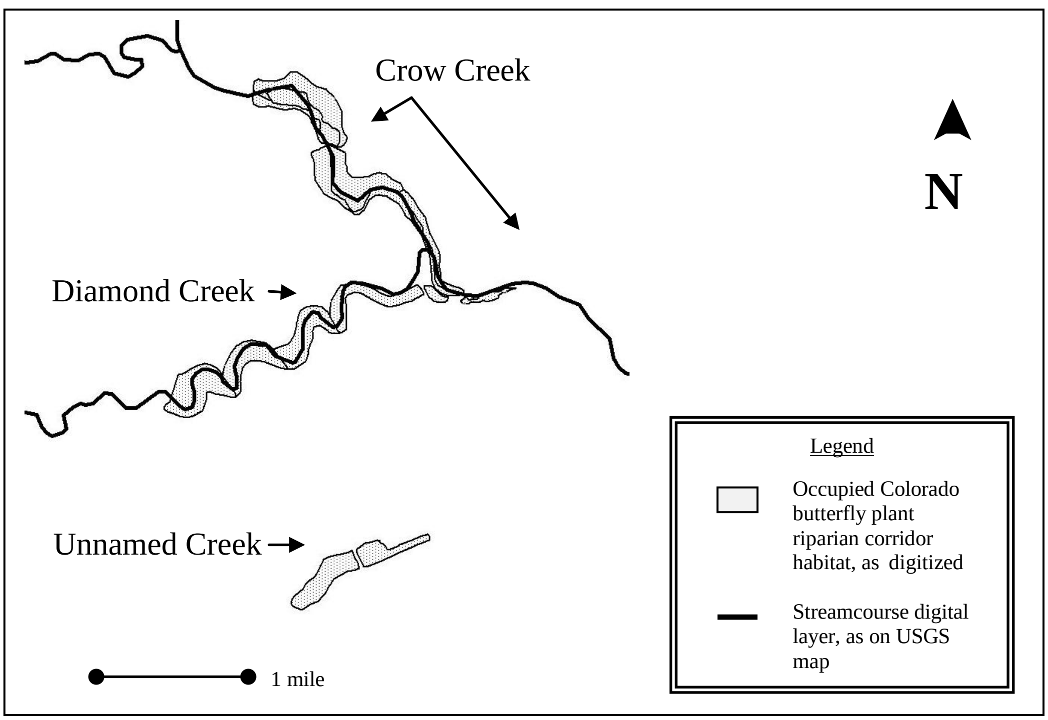
Hydrology

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 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.

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), with coarse soils that 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).

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



[1] Based on GIS themes for streamcourses and riparian corridor habitat occupied by Colorado butterfly plant

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), *Symphyotrichon 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 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 going back to the establishment of 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 except 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. There has been research into Canada thistle control (Floyd 1995b), other management response research (Munk 1999, Munk et al. 2002, Burgess 2003, Burgess et al. 2005), biocontrol agents, and goats brought in to graze in predetermined areas (2008, 2009, 2010) early in the growing season. In 2011, beaver dams were removed throughout Crow Creek.

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 2011). 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 for comparison with Colorado butterfly plant trend results (USDI NOAA 2012). Several of the strongest correlations are between trend results and temperature conditions two years prior to census (Heidel et al. 2010), suggesting that climate exerts a strong influence on early stages of life history. Thus, the climate dataset developed for characterizing study period climate covers 1984-2011. For an overview of climate conditions,

Figure 2. Growing season precipitation totals in Cheyenne, WY (1984-2011; Apr-Sept)

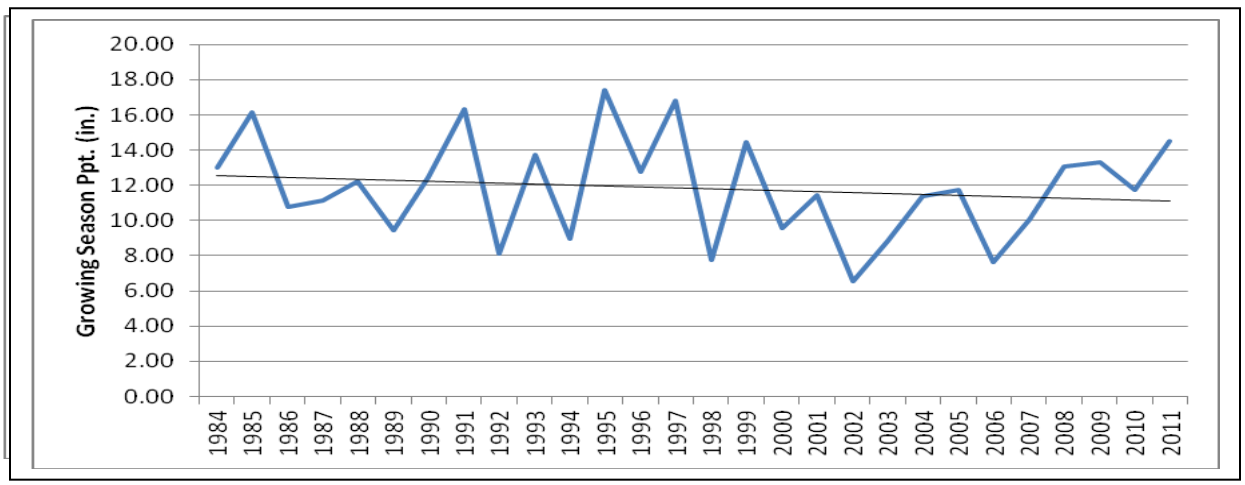
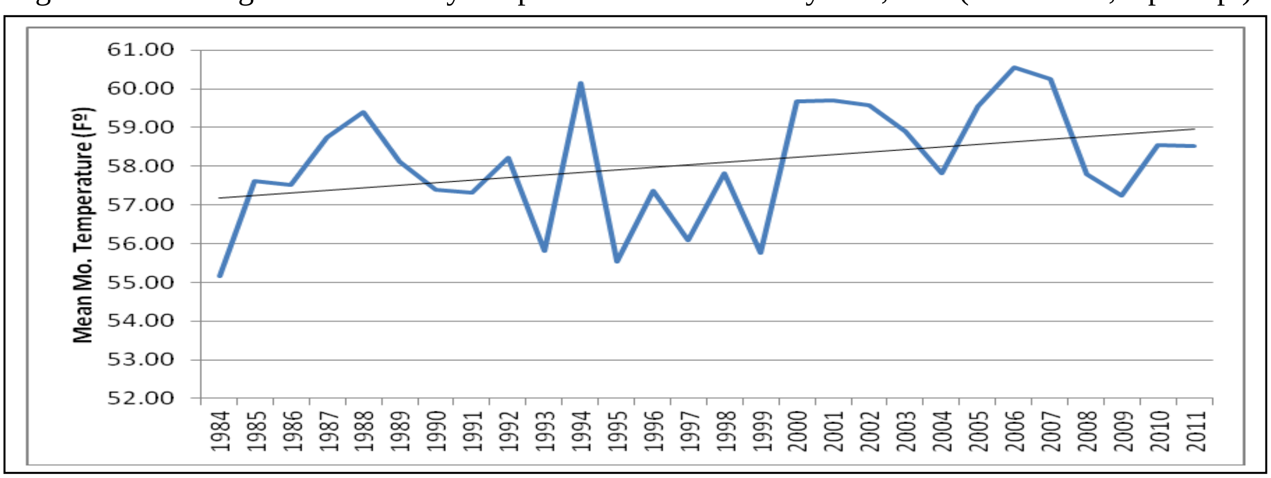


Figure 3. Growing season monthly temperature means in Cheyenne, WY (1984-2011; Apr-Sept)



mean monthly temperatures and monthly precipitation values have been compiled into a single graph with linear trend lines to graphs showing net growing season precipitation (Figure 2), and characterizing study period climate covers 1984-2011. For an overview of climate conditions, mean monthly temperature during the growing season (Figure 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 (Figures 2 and 3). It marks the fourth year in a row of mild conditions (growing season precipitation levels above the trendline, and growing season mean temperatures below the trendline).

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 particularly evident in average monthly temperatures data over the growing season when compared with the previous 16 years; more so than precipitation (Figures 2 and 3).

There were localized weather events in 2011 associated with storm cells. High levels of hail damage to Colorado butterfly plants were noted in the Unnamed Drainage subpopulation at the start of monitoring (8 August 2011), whereas plants were healthy and undamaged at the time of the previous training visit (23 July 2011). There were many broken flowering stems and branches, including some plants with no intact flowering stems remaining. Most plants in the Unnamed Drainage east of Cheyenne Road were damaged. The damage did not kill the plants, but may have prevented maturation of flowers and fruits associated with half or more of the reproductive potential that year. There was no similar damage among plants on Crow or Diamond Creeks. Close examing and conferring with Base personnel lead to the determination that the damage was caused by a severe hail event on 24 July that caused damage on the Base and in town. There was also a pummeling rainstorm on 3 August 2011 that may or may not have had any added affect. Damage was not quantified but photographs representing the damage patterns are presented in Appendix B.

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 1988-2011. Census was timed during or after peak flowering in August or early September. Prior to the 2011 census, a training visit that included the U.S. Army Corps and the 2011 census team was conducted on 23 July. The 2011 census was conducted by Bonnie Heidel, Joy Handley, Dorothy Tuthill and Emma Stewart on 8, 12, 16 and 26 August. In addition, leaf samples were collected for taxonomic research in collaboration with WAFB and the U.S. Fish and Wildlife Service on 8 September. 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 genetically unique individual was 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. This ensured completeness of coverage while avoiding the error of counting any individual plant more than once, and proved to be 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, Geographic 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 (2002-2011).

In the field, the 2010 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 change to 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 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). The 2011 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 as presence/absence of Colorado butterfly plant in an ArcMap project representing those polygons that had flowering plants in 2011.

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 last three years of counts, before the flea-beetle outbreak of 2007.

Environmental variability, which is not included in the models, 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 (temperature, precipitation) both in the same year as a census, the year before the census, and two years prior using updated monthy temperature and precipitation data from Cheyenne (USDI NOAA 2012). The early half of the growing season, referred to as "spring" for purposes of this report (April-June), is the period of Colorado butterfly plant vegetative growth leading up to bolting (Table 1). The late half 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

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. The herbivory event and flea beetle determinations are presented in

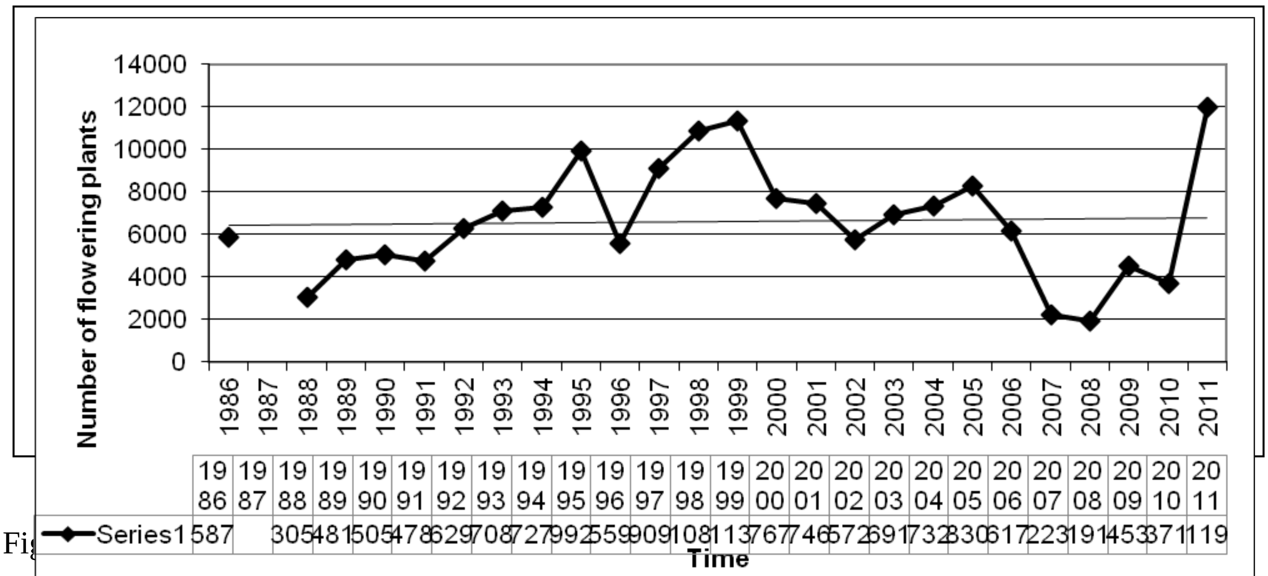
Heidel et al. (2011). In 2011, signs of herbivory were sought in advance of monitoring, in late July, but none were found.

RESULTS

Census results

In 2011, Colorado butterfly plant numbers reached the highest cumulative total of 11,957 plants on WAFB over the entire 24 years of monitoring (Figure 5). The numbers on Unnamed Creek reached their highest subpopulation totals, Diamond Creek rebounded from the 2010 drop, and Crow Creek increased modestly (Figure 6).

Figure 4. Colorado butterfly plant population trends, WAFB (1986, 1988-2011)



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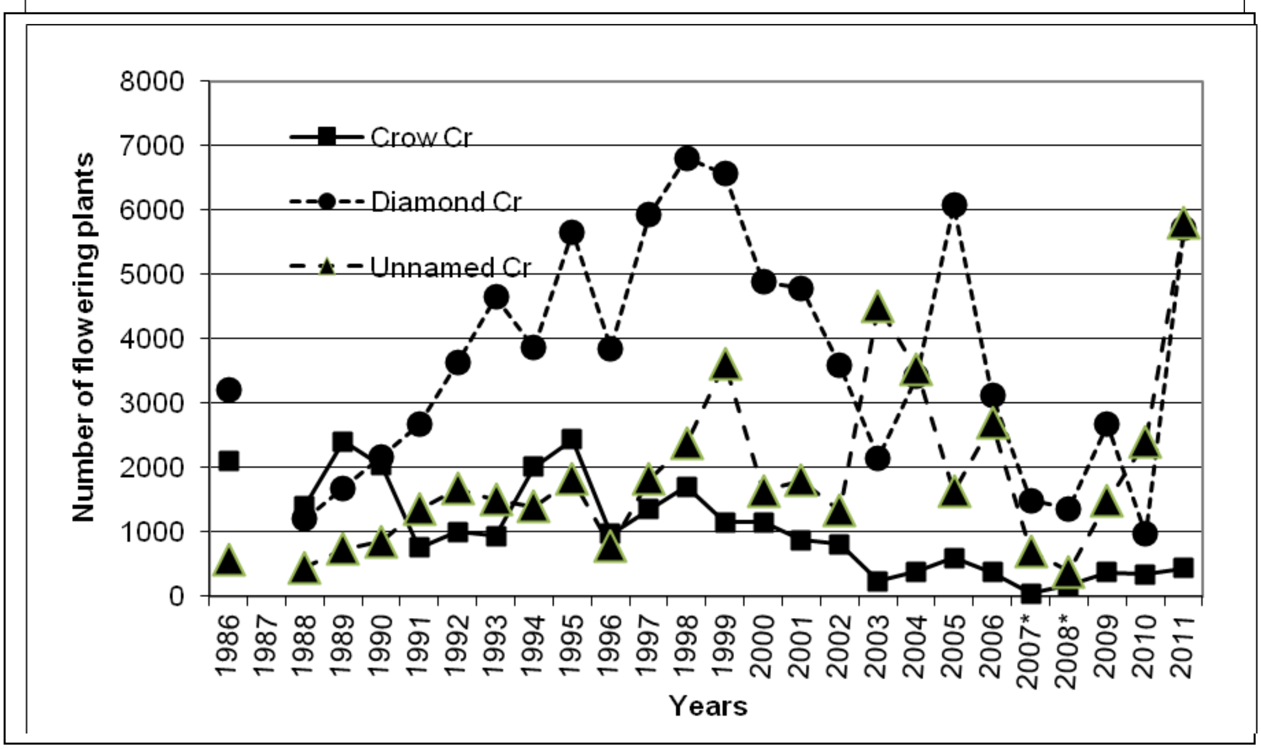

Table 2. Colorado butterfly plant flowering plant numbers by stream on F.E. Warren Air Force Base (1986, 1988-2010)

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**
2010 vs. 2009	89.9%	36.9%	162.7%	82.0%
2011 vs. 2010	127.4%	590.55	240.95	321.7%
2011 vs. mean (1988-2011)	43.3%	154.4%	300.1%	180.3%

The Colorado butterfly plant census results are divided further within each riparian corridor segment as presented in the Appendix C table, and within each polygon as presented in the Appendix D table. The results of mapping all Colorado butterfly plant colonies are presented in Appendix E superimposed on digital orthophotographs. The latter represents each locale where Colorado butterfly plant was present or absent in 2011 among all polygons over time. The spatial distribution of Colorado butterfly plant across WAFB stayed much the same between 2010 and 2011, with 109 polygons occupied in 2011, compared to 101 polygons in 2010 and 107 in 2009, but only 35 polygons occupied in 2007.

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 through 2011 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 being re-examined through 2011 in work underway (Wepprich et al. in progress).

DISCUSSION

Census results

The peak census numbers for Colorado butterfly in 2011 demonstrate a dramatic rebound from the lowest population numbers only three years earlier. It is consistent with 2011 being the mildest spring in recent years and suggests but does not prove that there is a seed bank that increases the capability of this taxon to respond to favorable climate conditions.

The hail event of 2011 underscores the lessons and reminders provided over the course of long-term monitoring that there is always the potential for new deviations no matter how well patterns have been documented and projected for Colorado butterfly plant on WAFB. It is ironic that the subpopulation segment with peak numbers in 2011 was precisely the one to be battered by hail. One of the things to watch for in 2012 is whether there are any signs that plants damaged in 2011 have survived in 2012, i.e., whether the mechanism that triggers senescence in this semeloparous taxon after flowering is linked to fruit production and maturation, and was thus disabled to give individual plants a second chance to produce fruits in the following year.

Early (pre-monitoring) visits to Colorado butterfly plant might be pursued in 2012 to check for survival of hail-damaged plants, as well as events like insect herbivory. If the latter is seen at or before the start of monitoring, it is recommended that the food preferences of the *Altica foliaceae* adult and the relationship between *Altica foliaceae* life cycle and climate be pursued in tandem research. The 23-year monitoring period encompased a drought event, but the biggest decline in population numbers was not during the drought but immediately after it. The 2000-2006 drought was longer than any on record since the start of weather station records in 1895. It is not known to whether drought or its culmination had the greatest influence, by direct or indirect means.

The sharp increase in Colorado butterfly plant numbers on Diamond Creek in 2011 was accompanied by a visible expansion of its spatial distribution to occupation of broad bands of habitat compared with the narrow bands in 2010. Diamond Creek is fed by groundwater early in the growing season, and in turn feeds the surrounding water table later in the growing season. If the flow rates on Diamond Creek were cut back late in the growing season, then establishment of seedlings might be impeded or prevented with increased distance from the stream. This could have much the same affect as increased or reduced seed production by increasing or reducing the extent of conditions suitable for germination and establishment. This year-to-year different in extent of suitable habitat on Diamond Creek is a likely factor in its relatively high subpopulation number oscillations between years.

Even greater than the 2011 contribution in Colorado butterfly plant population numbers on Diamond Creek was the contribution in population numbers on Unnamed Creek. The gentle, headwater stream habitat as found on Unnamed Creek is the least common habitat for the species elsewhere in its range. If these settings have the greatest rebound potential after drought, and if recovery from drought were a critical overall viability factor, then the absence of such population segments in other populations could impede their overall viability.

Viability analysis

The relative extinction risks for Colorado butterfly plant on WAFB, calculated through 2009 are being updated through 2011 (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. The event was also synchronous with dieback on *Salix exigua*, and overlapped with introduction of goats (2008, 2009, 2010) in dynamic habitat conditions. 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 there may be properties that make it indispensible by other criteria.

Population viability of Colorado butterfly plant on WAFB is also being re-evaluated with recurrent insect herbivory events to determine the net affects on viability. The 2011 results demonstrate strong rebound capacities in two of the three population segments, particularly in the two smaller watersheds. It is hypothesized that this is also indicative of drought-rebound capacity of these hydrological settings, ones that are especially vulnerable to landscape change and intensive management elsewhere in the distribution of this taxon. Thus, it offers possible explanation for habitat loss patterns under natural weather cycles. The unknown frequency of herbivory outbreaks and possible shift in weather cycles could ultimately determine decadal trends.

In summary, 2011 results suggest strong capacities for rebound in two of the three population segments, favoring the population segments in the smaller watersheds. The unknown frequency of herbivory outbreaks and possible shift in weather cycles could ultimately determine decadal trends. It is possible that herbivory events are related to drought events. If this were the case, then 2011 results are all the more significant as evidence of potentially compensating rebound upon resumption of mild conditions.

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