

**28-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:
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Cover: *Oenothera coloradensis* trends on three WAFB creeks (1984, 1986-2015)

ABSTRACT

Annual census of Colorado butterfly plant (*Oenothera coloradensis* (Rydberg) W.L. Wagner & Hoch) was initiated in 1986 and conducted consecutively for 28 years from 1988-2015 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. WAFB also has one of the most hydrologically complex settings for the species, and is among the few populations or population segments that is not under agricultural management. As such, monitoring provides a gauge of success in maintaining the population and a long-term dataset for understanding species' trends throughout its range. The most recent census tally of 3,409 flowering plants is 48.4% below average, possibly linked to the unfavorable germination conditions in the spring of 2012 despite the favorable bolting conditions in the spring of 2015.

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INTRODUCTION

Status

Colorado butterfly plant (*Oenothera coloradensis* (Rydb.) 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 first recognized as a distinct taxon by Rydberg (1904) based on a specimen collected in 1895 near Fort Collins, Colorado, and was listed as Threatened under the Endangered Species Act in 2000 (USDI FWS 2000). 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.

Current evaluations of Colorado butterfly plant status are presented in the Recovery Outline (USDI FWS 2010) and the Five-year Review (USDI FWS 2012). The latter represents the most current compiled information on the species, including all available species trend data and results of monitoring it on WAFB in particular.

Recent taxonomic research elevated Colorado butterfly plant from a subspecies to a full species (Wagner et al. 2013) based on genetic analysis (Kraeos 2011). This was preceded by earlier research in the Evening Primrose family (Onagraceae) documenting that the evening primrose genus (*Oenothera*) is monophyletic only by subsuming two smaller genera, butterfly plant (*Gaura*) and stenosphon (*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 recovering taxa at lower taxonomic levels. These published taxonomic changes will also appear in an upcoming volume of the *Flora of North America*, were 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.

Life history

Colorado butterfly plant was first 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, plants appear as a stemless 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 through the growing season 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 following spring germination, vegetative plants grow for one more season, and then flower in the third year (Heidel 2009).

There are typically four seeds per capsule, encased in a hard but permeable seed coat, which 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), suggesting 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 representing one, two, or three populations on the three confluent streams. They are referred to in this report as one population because the species' distribution is confluent on two of three streams, and there is high likelihood of genetic exchange via lepidopteran pollination vectors traveling between streams. Yet, they are referred to as three subpopulations because they are discrete and have three fundamentally different hydrological conditions and other habitat differences. Furthermore, seeds are dispersed primarily around the base of the parent plant (Floyd 1995a) and are thus limited to the same creek, though seeds float on water and might be transported greater distances in flood 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 coordinate 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

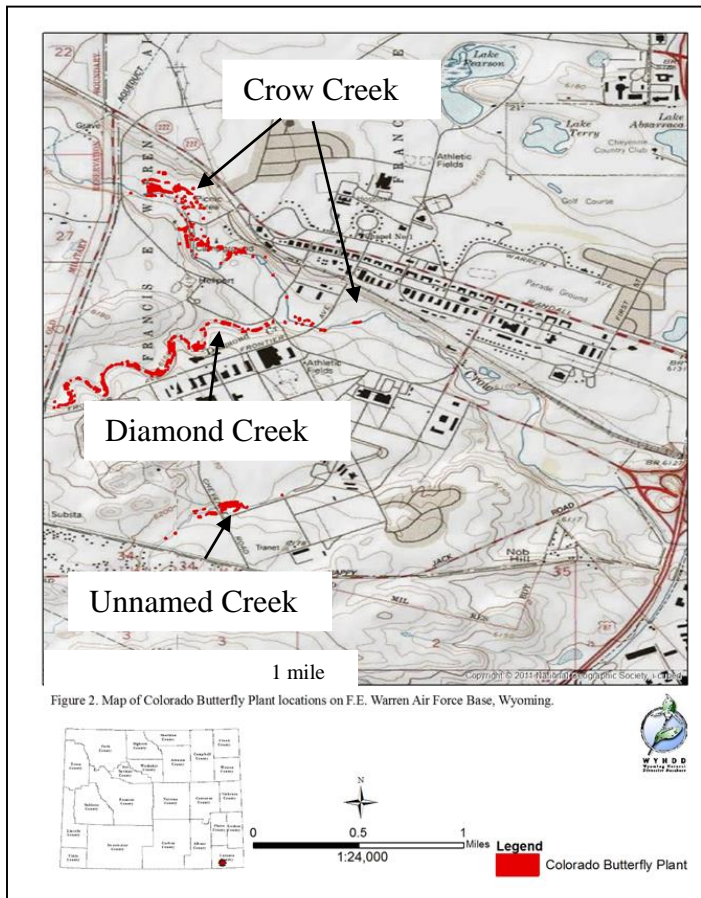
The study area is located on F.E. Warren Air Force Base (WAFB) immediately west of Cheyenne (41° 07'N 104° 52'W) in Laramie County, Wyoming. Colorado butterfly plant occupies riparian habitat along three confluent creeks including Crow Creek, Diamond Creek, and an unnamed, ephemeral creek (hereafter 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 discontinuous and the cumulative occupied habitat (2002-2014) is about 5 ha (12.4 ac). The creeks are low-gradient drainages at 1862-1887 m (6110-6190 ft) elevation with a

relief of ca 5.7 m per km (ca 30 ft per mile). All of the following study area information pertains to Colorado butterfly plant occupied habitat unless otherwise stated, including the upper end of Crow Creek, all of Diamond Creek, and the upper end of Unnamed Creek as present within WAFB boundaries (marked in red on Figure 1). In the middle of occupied habitat on Crow Creek is the FamCamp recreation area, with camping and picnic shelters that represent the only developments besides roads in WAFB occupied riparian zones.

Hydrology

Crow Creek is the largest of the three creeks occupied by Colorado butterfly plant on WAFB, and the other two are its tributaries. It has perennial flow, a large watershed, and several large impoundments higher up in the watershed. On WAFB it has oxbows, beaver dams, springs, and seeps. Diamond Creek is the largest tributary of Crow Creek on WAFB, with a watershed magnitudes smaller in area than Crow Creek. It has a drop-structure impoundment directly upstream from WAFB. On WAFB it is a highly meandered seasonally-flowing creek. Unnamed Creek is a very small tributary of Crow Creek on WAFB, not named 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 a relatively steep, north-facing valley slope, with open meanders covered by wet and dry meadows and with a narrow wooded segment at the mouth. Unnamed Creek riparian corridor lies in open plains with almost no valley relief, and has wet and dry meadows with small patches of shrubs.

Plant species that have been described as common in Colorado butterfly plant wet meadow habitat on WAFB and elsewhere include *Agrostis stolonifera* (redtop), *Symphotrichum 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). Botanists monitoring Colorado butterfly plant since 1986 noted certain species becoming abundant over time. Large increases in *Cirsium arvense* (Canada thistle), *Euphorbia esula* (leafy spurge), and *Salix exigua* (e.g., Marriott 1988, Marriott and Jones 1988, Fertig 2000b) occurred in the 1990's through about 2007, 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 a habitat suitability criterion for Preble's jumping mouse (Jones 2003).

Starting in 2007, *Salix exigua* stems died back, and by 2008, many stems had completely died. There has been vigorous resprouting, but resprouts have yet to return to previous heights and density. This has changed the appearance of vegetation structure on Crow Creek. In addition, a resurgence of native species cover was noted by 2009, 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). This has replaced some of the noxious weed cover, shifting the herbaceous vegetation structure particularly on Diamond and Unnamed Creeks. These native grasses and grass-like plants might be more representative of species associated with Colorado butterfly plant in pre-settlement wet meadow vegetation

conditions on the high plains than the previously named associates that have been listed in earlier monitoring reports and in species status reports.

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 Crow Creek 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 grazed by horses or any livestock 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). Trees have flourished on Crow Creek over the decades, and beaver numbers have grown as a response. In 2011, beaver dams were removed throughout Crow Creek to prevent inundation of roads and recreational facilities, but beaver activity has changed channels and water tables in places.

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 was transferred to the U.S. Air Force Base in 1947. Colorado butterfly plant was discovered on WAFB in 1981, and designation of a Colorado Butterfly Plant Research Natural Area (RNA) followed (Marriott and Jones 1988). Agricultural uses that included hay leases were curtailed at about that time. A major goal of riparian management since then has been the maintenance of the Colorado butterfly plant population through control of noxious weed species and evaluating the need to control competition. 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.

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 (1984-2014) was 39.2 cm (15.6 inches), with heaviest rainfall in May, followed by June and July (USDI NOAA 2015). The average annual temperature over this same period was 7.9 °C (46.3 °F), peaking in July.

Mean monthly temperatures and total monthly precipitation over the growing season (April-September) are represented in Figures 2 and 3 (based on USDI NOAA 2015). 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 2014 and 2015 climate conditions started out similarly cool and wet in April, but all ensuing months have been closer to or above average.

Meteorological data were compiled into datasets (Table 1) for comparing with census results. 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. Monthly climate data is compiled into annual spring, summer and growing season datasets. Climate conditions were also compiled for annual conditions, as the 12-month hydrological year of climate data starting in October prior to the year of census through the end of September (not shown here).

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

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 Water Year”)	Net 12 month precipitation	Average annual mean monthly

This compilation of precipitation and temperature data into three- and six-month blocks is a schematic representation of meteorological conditions, a visual representation of the data used in climate correlation analyses. Past analyses comparing census results and climate conditions for these multi-month periods have included Pearsons and Spearman coefficients (Laursen and Heidel 2003) and multiple regressions (Heidel 2005). In addition, climate correlations for each month of the growing season have also been calculated from residuals of best fit models (Appendix F in Heidel and Handley 2010). The 6-month conditions have been depicted to show overall trends in past monitoring reports (Figures 2 and 3). However, in this report, we split out spring conditions from summer conditions. Spring precipitation and temperature conditions have remained relatively stable over the monitoring period despite oscillations, whereas summer precipitation has declined and summer temperature has increased (Figures 2 and 3).

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). That extended drought was longer than any prior droughts since the monitoring began in 1895; since 1976 there has not been a period of drought in southeastern Wyoming longer than two years (Appendix A). The 2000-2006 drought period is evident in both average monthly temperatures and monthly precipitation over the growing season when compared with the previous 16 years; (Figures 2 and 3).

Figure 2. Growing season precipitation totals in Cheyenne, WY (1984-2015; Apr-Sept); followed by spring and summer components

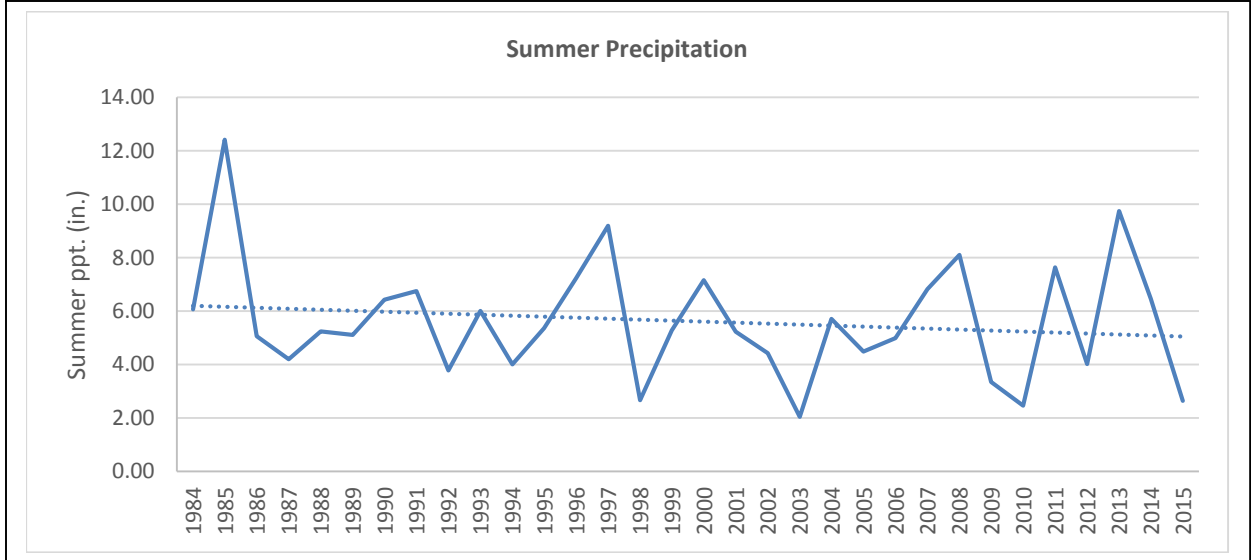
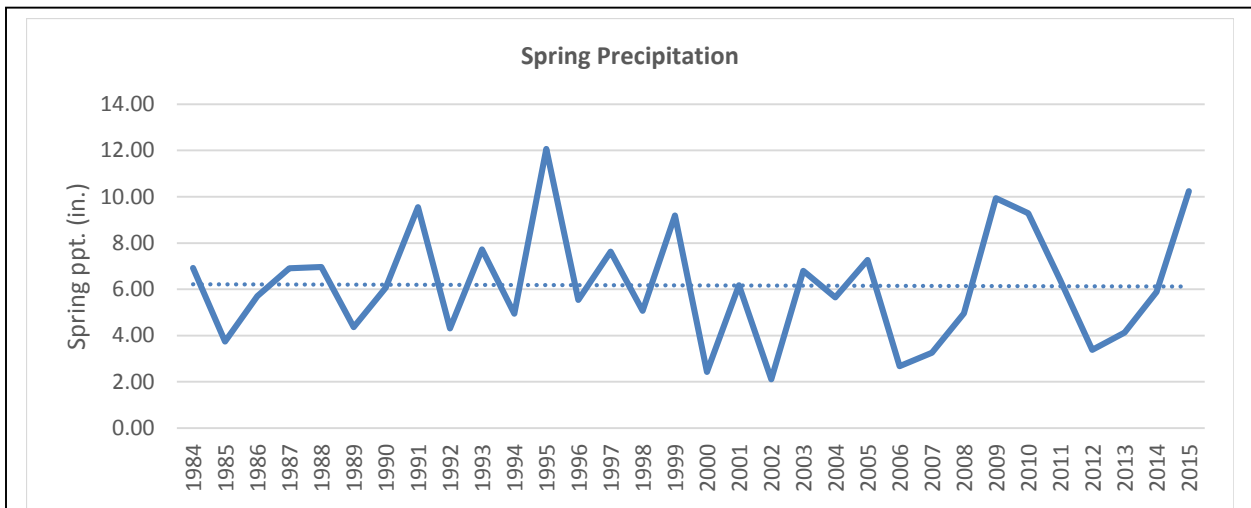
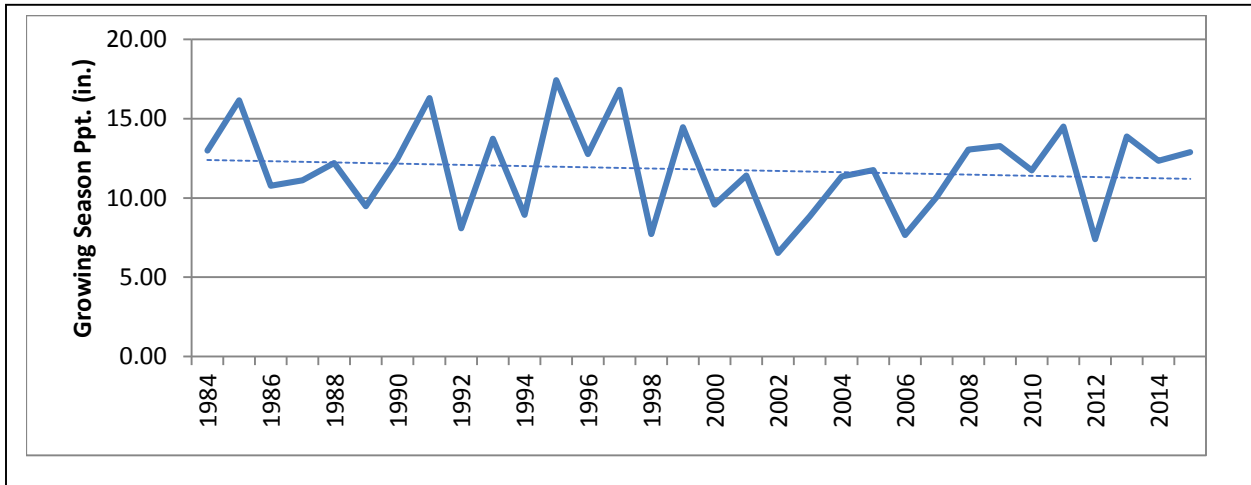
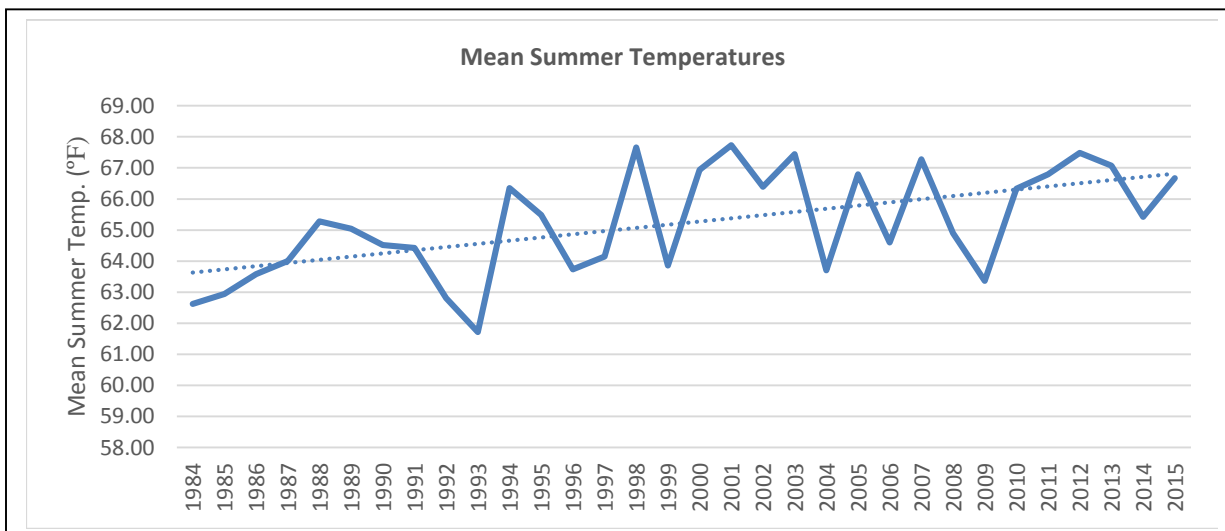
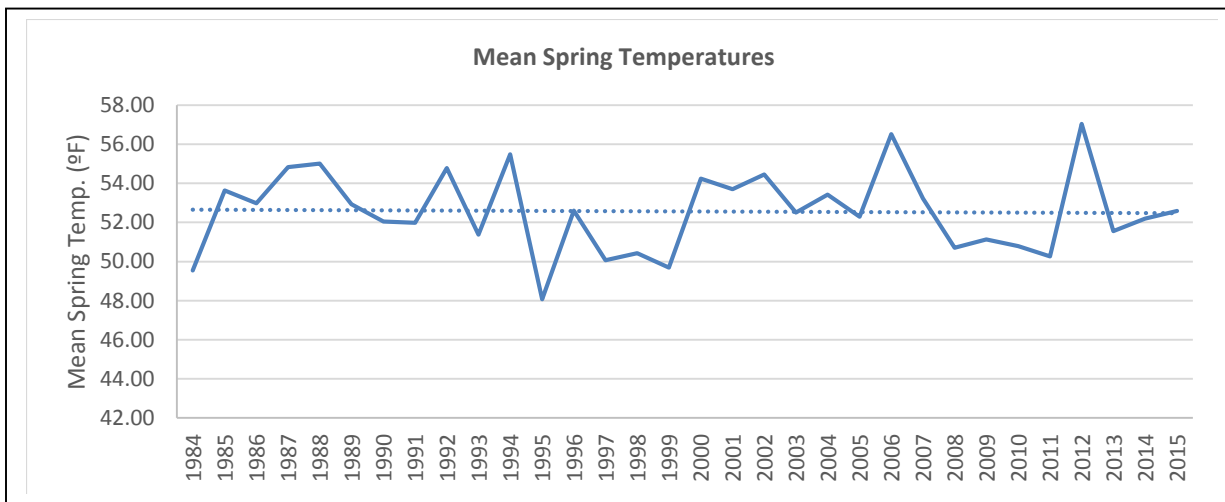
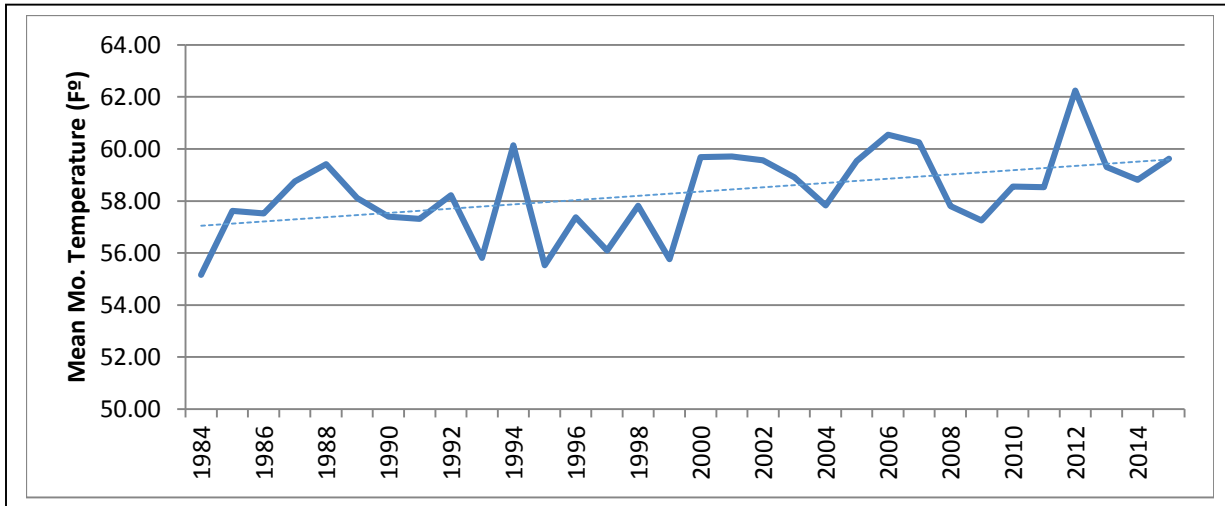


Figure 3. Growing season monthly temperature means in Cheyenne, WY (1984-2015; Apr-Sept), followed by spring and summer means



Characterization of WAFB climate conditions and their influence on Colorado butterfly plant are complicated by extreme short-term weather events. For example, 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 three creeks are not equally affected by flood events due to watershed and streamflow differences.

There are also localized weather events associated with storm cells that can affect parts of the population differently. 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 Creek, 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 WAFB and in Cheyenne.

METHODS

Field census methods

Complete annual census of flowering Colorado butterfly plant was initiated by Hollis Marriott through Wyoming Natural Diversity Database (WYNDD; Marriott 1988) to gauge overall population trends under the RNA objectives and more recent WAFB goals of maintaining Colorado butterfly plant numbers (WAFB 2001, WEST 2001, Grunau et al. 2004, GET CITATIONS FOR MORE RECENT WAFB MNGMT PLANS). An annual census, timed during or after peak flowering in August or early September, was conducted each year between 1988-2015. The 2015 census was conducted by Bonnie Heidel, Joy Handley, Mark Andersen (WYNDD) and Dorothy Tuthill (Biodiversity Institute) on 6, 7 and 10 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. Colorado butterfly plant is semelparous (only flowering once and dying), and is conspicuous only at the flowering stage, so tally of flowering plants is an appropriate gauge of population size (analogous to breeding bird surveys, even more so if the birds had just one brood). Non-reproductive plants are referred to as vegetative plants, and they were not censused.

Colorado butterfly plant census data were recorded separately by creek 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

were observed to be relatively stable over time (Floyd 1995a, and WYNDD observations). Hand-drawn boundaries of distribution were marked onto digital orthophoto prints and digitized in 1999. Starting in 2002, Global Positioning System (GPS) coordinates 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 (2002-2014).

During census, a Trimble GPS receiver JUNO 3B was loaded with the 2014 digitized population mapping that represented all past locations, whether mapped as polygons or points., and copies of the population patterns were printed as well. These were valuable aids in determining at a glance whether plants were inside/outside the population boundaries that had been established over the years. Census tallies were assigned to the corresponding polygons or points. Intervening habitats between them were surveyed for outlying plants that may be mapped as a boundary extension of an existing polygon if located within 5 m of previously-recorded plants, or else as a new area of occupancy. GPS coordinates were recorded for all prospective boundary changes, new locations or unresolved questions. These methods build upon population census of Colorado butterfly plant on WAFB that 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, 2014; Heidel and Tuthill 2015).

Each individual plant was tallied during census, 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 people.

Starting in 2013, we started to count flowering Colorado butterfly plants that had died by the time of monitoring. These plants were partially or fully withered and brown by the time of monitoring. They are not included in the census tallies, but noted separately.

Herbivory documentation

One pre-monitoring trip was made to the WAFB population of Colorado butterfly plant on 15 July 2015 to all three creeks. The previous year's photo guide to insect herbivory (in Heidel and Tuthill 2015) was used as reference. Herbivory by flea beetles was scant and only adult flea beetles were present at one spot on Unnamed Creek having concentrated herbivory in 2015. Without larvae present in widespread herbivory, no further work was pursued.

Data analysis

Field data sheets were set up to populate spreadsheets with census data results and tallied at four spatial scales (polygon, stream reach, stream, and WAFB total). Stream reach and stream-wide results are presented in Appendix B. Polygon results are presented in master table (Appendix C) and summarized as presence/absence representation in a map (Appendix D). The actual values have been a useful reference in addressing local management questions or trend

phenomena, while the map provides an overview of the spatial pattern of trends in an ArcMap project representing all polygons over time, and whether or not they had flowering plants in 2015. The WAFB total is the tally of all stream tallies. The multi-year mean and the difference from the mean were calculated for each of the major tallies (stream-wide and WAFB total), using the most recent census numbers.

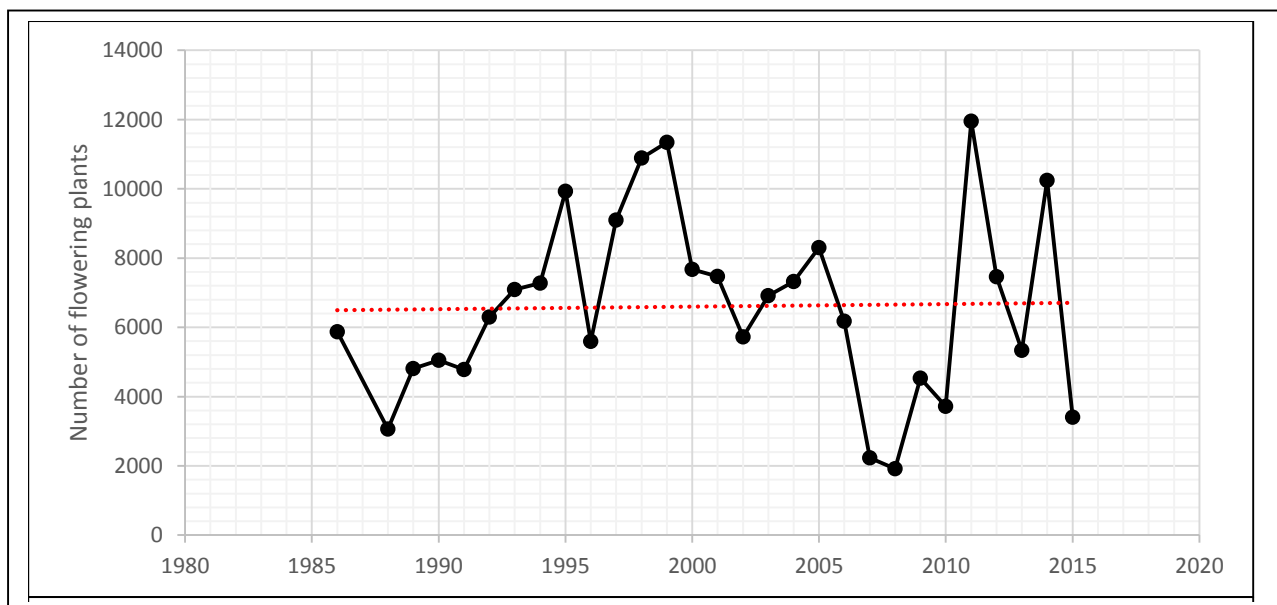
Before field data were entered, GPS coordinates were used for editing digitized boundaries of polygons and points that represent cumulative occupied habitat to ensure that data were assigned to the polygon or point representing cumulative occupied habitat over time. In 2015, there were more merged polygons (plants found between existing polygons to connect them) than outlying plants representing new polygons. The polygons that represent cumulative occupied habitat were edited to represent those that were occupied vs. unoccupied in 2015, shown in Appendix D.

RESULTS

Census results

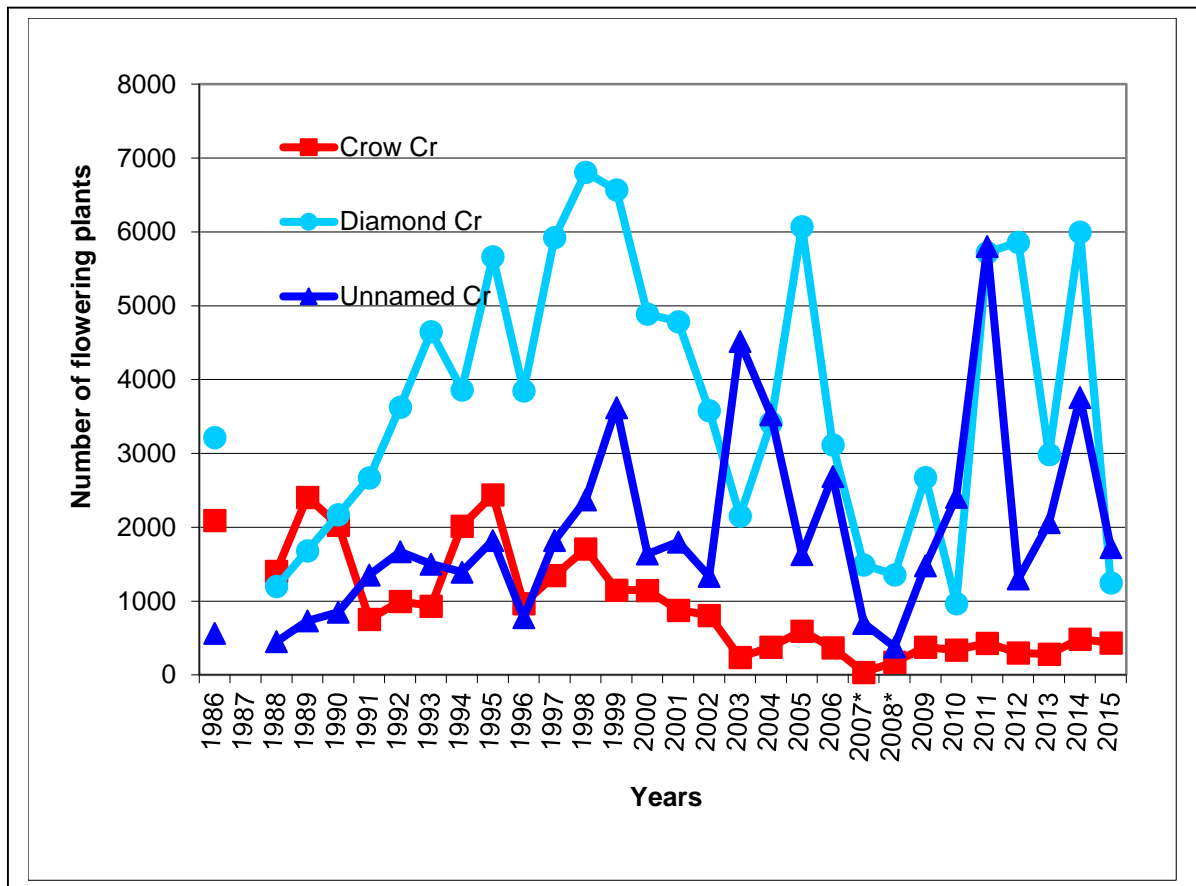
Colorado butterfly plant numbers have fluctuated greatly since 1986 (Figure 4, Table 2), but the average has not changed much over the same time period (average for first ten years = 5976; average for most recent ten years = 5698). The 25-year average is 6602 flowering plants. A regression line is superimposed on Figure 4 as preliminary indication of population trend (Figure 4). 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 consecutive period over the course of monitoring (e.g., 1988-1995, 1999-2008, 2009-2015). Fluctuation periods have ranged from 1-5 years above and below the mean.

Figure 4. Colorado butterfly plant population trends, WAFB (1986, 1988-2015)



Furthermore, very different results are also evident in comparing subpopulation numbers on any given creek. The three creeks have fundamentally different hydrology, and Colorado butterfly plant numbers on one creek tend to exhibit the same patterns compared to those on different creeks (Figure 5, Table 2). These hydrological subsets of the WAFB population may or may not represent subpopulations. The census results for each creek are subdivided further within each riparian corridor segment as presented in Appendix B, and at each polygon as presented in Appendix C to identify trends associated with local conditions. 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 2015 among all polygons over time. The spatial distribution of Colorado butterfly plant across WAFB has stayed much the same except during flea beetle outbreak years. There were 99 (of 160) polygons occupied in 2015, 109 polygons occupied in 2014, 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, 1988-2014)³



³ 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, 1988-2015)⁴

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	3,717
2011	432	5722	5803	11,957
2012	299	5863	1300	7,462
2013	283	2986	2064	5,333
2014	489	5998	3663	10,247
2015	435	1248	1726	3,409
Mean (1988-2015)	909	3751	1969	6,602

⁴ In a complete population census, there is no statistical margin of error, and the human error factors have been described (Heidel and Tuthill 2015) and addressed in a formalized framework.

Regression lines have not been superimposed on subpopulation trends. Crow Creek is still in decline compared to the first decade. Diamond Creek and Unnamed Creek numbers have generally risen to compensate for the Crow Creek decline, but both of them have been oscillating, more so in the latter half of the monitoring period compared to the first half. It is postulated that their flux is driven in large part by spring germination conditions, however favorable or unfavorable, and by the flea beetle outbreak event that lasted two years and has only happened once during the monitoring period.

There was only one dead plant noted during 2015 census. There have never been as many as ten dead plants noted in the years when dead plants were tallied (2013-2015). It is not clear whether these plants that started to produce flowers but died in the middle of the growing season were casualties of chance underground damage, or might reflect something else.

Historic context for results

We did not expand historic context for results, but recapitulate the resources. Select photographs taken by Robert Dorn and Robert Lichvar (1984-1986) have been scanned and the full suite of aerial photographs have been compiled. These photographs provide valuable context and future reference, as well as a window into some of the landscape changes taking place over the monitoring period years.

The expertise of prior Colorado butterfly plant researchers is also a wealth of information, and an opportunity to confirm that there have been no known flea beetle herbivory outbreaks during prior years. In 2014, Hollis Marriott visited Colorado butterfly plant on WAFB after a 22-year hiatus, and later commented:

“During the early surveys and monitoring on Warren Air Force Base, I was impressed with the Air Force’s concern for conservation and support for our work. In 1989, the Base received the Secretary of Defense Environmental Award for their efforts to protect the butterfly plant, well-deserved in my opinion, and a Research Natural Area was designated in 1990. It’s really great to see that the Base has continued to support butterfly plant protection, and to fund research and monitoring. The latter is especially important. Having people in the field every season to see what’s going on, and to learn more about butterfly plant biology is critical.” (Marriott pers. commun. by email to Heidel 2015)

Rangewide context for results

We did not compare 2015 field season results with cumulative trend data from other populations (outside of WAFB) to characterize levels of synchrony, or lack of it, between populations as we did last year (Heidel and Tuthill 2015). However, we maintained communication with biologists working at Soapstone Prairie in order to make an informal comparison of monitoring data as collected and provided by the City of Fort Collins (Crystal Strouse, Natural Areas, pers. commun. 2016), where numbers declined sharply in both 2014 and 2015. There was flea beetle outbreak at Soapstone Prairie both of these years that might portend flea beetle outbreaks elsewhere and/or may reflect a greater vulnerability of hotter, dryer settings

to insect herbivory. This points to the need for evaluating the nature and conditions that promote or hinder insect herbivory outbreaks, the impact of outbreaks on fecundity, and the life history of the flea beetle vector.

DISCUSSION

Census results

Colorado butterfly plant population numbers plummeted on both Diamond Creek and Unnamed Creek in 2015. The 2015 Colorado butterfly plant census results may reflect the importance of germination vs. bolting in population trends. The climate graphs (Figures 2 and 3) pool spring and summer data, but in general, 2015 spring conditions were cool and wet (favoring bolting) whereas 2012 spring conditions were hot and dry (unfavorable for germination). The sharp drop in flowering plant numbers may reflect the importance of germination conditions two years prior to census. Studies of Colorado butterfly plant germination (Burgess et al. 2005) indicated that germination is favored by cool, wet spring conditions. This is consistent with climate correlation studies that showed the highest correlation between census results and climate conditions of current or recent years was for spring temperature conditions two years prior (Heidel 2006b). Demographic studies (Floyd 1995a, Floyd and Ranker 1998) indicated that bolting is favored by cool, wet spring conditions. Thus, the contrasting spring conditions of 2012 and 2015 provide an uncontrolled experiment in their influence on two different stages of life history.

The dramatic contrast between 2014 and 2015 flowering levels appear to mirror the germination conditions in the springs of 2011 and 2012 (three years prior). This supports earlier hypotheses that the species trends are driven primarily by germination levels, that the species commonly has a three-year life cycle, and it is further inferred that germination levels are not closely tied to recent flowering levels but draw from a seed bank that lies dormant pending favorable conditions. By this interpretation, Diamond Creek and Unnamed Creek have future stable or increasing trends, if there are future favorable spring weather conditions and if the frequency of flea beetle outbreak events does not impact too often or too seriously.

Germination conditions on Diamond Creek and Unnamed Creek are more strongly affected by precipitation than Crow Creek, which is more strongly influenced by stream flow. If so, the swings in spring conditions would account for dramatic oscillations on Diamond Creek and Unnamed Creek during years without corresponding patterns on Crow Creek. The pattern of extreme oscillation is exaggerated by the flea beetle outbreak that preceded it, and the drought that preceded the outbreak. These series of events might account for the “yo-yo years” of Colorado butterfly plant trends on Diamond Creek and Unnamed Creek in the latter half of the monitoring period compared to the first half.

It is hypothesized that Colorado butterfly plant numbers on Crow Creek are related to climate and stream flow in tandem, so both climate and stream flow need to be favorable to foster germination and survival to flowering stage. This would help account for the pattern of species' trend differences on Crow Creek compared to its trends on the other two creeks. It appears that the Crow Creek subpopulation has higher vulnerability to drought than the other two creeks because the droughty soils and low streamflow patterns there may be compounded by

drought. The generally low stream flow levels that followed the 1999 surge in stream flow, from 2000-2009, meant that any germination event that followed 1999 flooding would have had extremely dry conditions impeding survival and regeneration despite whatever high precipitation months or seasons intervened. Such conditions might deplete the seed bank. If so, this would also mean that hydrologists are in a better position than biologists to evaluate the long-term prospects for Colorado butterfly plant numbers to rebound on Crow Creek. In the short-term, the fact that four of the past five years have had mean monthly stream flows peak at medium (20-50 cubic feet per second – cfs - monthly average) or high (50+ cfs monthly average) levels provide conditions for evaluating the hypothesis and the reversibility of downward Colorado butterfly plant trends on Crow Creek. It is appropriate to revisit USGS stream flow data (Figure 6 in Heidel and Tuthill 2015) in any future evaluation of Crow Creek trends.

Crow Creek is still in overall decline. However, recent above-average precipitation years and resulting flows (Heidel and Tuthill 2015) may recharge the water table. Recent willow dieback and biocontrol of noxious weeds may reduce competition. Recent removal of beaver dams may eliminate prolonged floods and elevated water table conditions. The presence of a seed bank, no matter how small it may be, reduces the probability of extirpation on Crow Creek. Contingent on weather and flea beetles, the species might rebuild its seed bank to maintain and eventually increase its numbers.

It is also likely that Colorado butterfly plant trends are affected by flooding events. We have no data on species' response to flooding, but it is possible that seedlings do not survive and vegetative plants might not bolt under prolonged inundation. Flooding might be a recurring event on Crow Creek but the other two creeks do not ordinarily flood. This might explain the fluke of species' trends on Diamond Creek and Unnamed Creek being completely out of synchrony in 2003. That year, a low-head dam was removed on Diamond Creek directly upstream (west of WAFB) for replacement. As a result, occupied habitat was flooded and saturated over large areas of Diamond Creek, but no other creeks, during the growing season. We recommend acquiring the history of low-head dam construction and replacement on Diamond Creek. This is all the more appropriate because Colorado butterfly plant surveys were conducted on both sides of the Round Top Road in 2015, finding it west of the road for the first time, extending the boundaries of the WAFB population onto both sides of the right-of-way. Another major population of Colorado butterfly plant lies farther upstream on Diamond Creek, separated by the low-head dam. Information on dam history and on trends of the upstream Diamond Creek population would provide context and watershed perspective for the WAFB population.

The 2015 population numbers were low but the lowest numbers over the 28-year were associated with a flea beetle outbreak. It is not known whether drought or its culmination had influence on the flea beetle outbreak, whether by direct or indirect means (i.e., dryness vs. growing season length). It is noteworthy that severe flea beetle outbreak was reported in 2014 and in 2015 at Soapstone Prairie (Crystal Strouse, pers. commun. to Heidel) even though flea beetles numbers were low on WAFB during these same years. Back in 2007, flea beetle outbreak was reported across the species' distribution. There has been speculation about the conditions leading up to flea beetle outbreak (e.g., Heidel and Tuthill 2015, Heidel et al. 2011). Soapstone Prairie is about 1000 ft lower elevation so is apt to have warmer, drier conditions than

WAFB. The contrasting pair of sites may shed light on the environmental conditions and effects associated with flea beetle life history and outbreak.

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 an extended drought cycle. In addition, there was a very early, warm spring in 2006. We do not know which, if either, of these conditions may have fostered the large flea beetle hatch and proliferation in ensuing years.

What is needed to assess the potential impacts of flea beetle herbivory on Colorado butterfly plant? The first thing is to measure the direct impacts on the species by sampling of individual plants during an outbreak year. During the 2007 outbreak, it appeared that flowering was severely impacted, reducing over half of the live leaf area. It was not clear if seed production was even possible. Unless this herbivory reduced fecundity, then long-term effects on a semelparous species are limited. Seeds fall off shortly after they mature, so seed production is staggered through the latter part of the growing season and repeated sampling would be needed to measure flea beetle effects on fecundity.

The population of Colorado butterfly plant reached its lowest numbers on WAFB in 2008, the year following the visible signs of flea beetle herbivory. It was postulated that either flea beetles have an influence on the underground parts of the species manifest in the following year, or else that vegetative plants are susceptible to it. These two possibilities warrant investigation in the event of an outbreak on WAFB.

The only other climate conditions that appeared to differ dramatically in the outbreak year of 2007 or immediately preceding it was an exceptionally early, warm spring in 2006. The 2014 flea beetle outbreak at Soapstone Prairie in Colorado (but nowhere else) may indicate that there is a life history threshold (e.g., if the growing season was some number of weeks longer for flea beetles than elsewhere) or some other critical factor leading up to exponential increase of flea beetle numbers.

The flea beetle larvae are the voracious herbivores. Identification can only be made with adults and it is recommended that the scouting be moved up earlier to collect larvae on Colorado butterfly plants, checking as early as the start of bolting (late June and early July). If high levels of herbivory are found, then larvae responsible for it need to be captured and reared for identification. In the future, if any plants have heavy herbivory, no matter how many or few, it is recommended that pin markers be laid out to track the fate of individual plants. It was inferred, but not proven, that heavily browsed plants have greatly reduced flowering and seed production. The impacts on fecundity remain to be determined. This would require visits about every two weeks through the duration of the growing season to evaluate seed production on a sample of plants. Also in the future, any high levels of herbivory on the flowering plants needs concerted investigation of nonflowering plants to determine if they are simultaneously attacked. Finally, if any high levels of herbivory are found, then it remains to be investigated where flea beetles are present and how they affect flowering plant numbers in the following year.

Finally, if larvae are identified to species, then the food preferences of the *Altica* spp. adult and the relationship between life cycle and climate warrant investigation. The need for more information about flea beetles and their potential effect on Colorado butterfly plant can hardly be over-emphasized.

The 2014 and 2015 results at WAFB further support the hypothesis that leaf herbivory on Colorado butterfly plant is present at low, incipient levels. Future focus on the vector is the priority, along with a chronicling of the outbreak phenomenon if such an event were to repeat. It would be appropriate to re-evaluate population viability of Colorado butterfly plant on WAFB with a scenario of insect herbivory outbreak events at different frequencies. Despite an apparent capacity for population rebound, recurrence of flea beetle outbreaks could change viability if it impacts fecundity.

To summarize, the population trend of this short-lived perennial at WAFB is buffered by a seed bank, differential germination conditions on the three streams, and ecosystem resilience despite drought, flood and flea beetle outbreak. The relative stability of spring temperatures bodes well. They are tempered by the prospect of greater extremes in spring temperatures and by more frequent flea beetle outbreaks posing risks to future Colorado butterfly plant population stability in spite of good management practices.

2016 Monitoring plans

The core Colorado butterfly plant monitoring work on WAFB will start in early August 2016. We will prepare a geo-referenced checklist of past management issues and questions that have been raised over the years in occupied habitat. We will ensure that all appropriate parties have the most current GIS layers representing Colorado butterfly plant distribution.

We will continue making advance visits to collect flea beetle larvae on Colorado butterfly plant and check if there is an outbreak event, making those visits as early as late June. The Unnamed Creek has been the most reliable place to find flea beetles and signs of herbivory outbreaks. In the case of heavy herbivory, we will collect larvae for rearing and identification. We will monitor fecundity of browsed plants. If the heavy herbivory is widespread, we will evaluate the presence and level of herbivory on nonflowering plants and their fate in the following year.

We will continue censusing any dead flowering plants, a phenomenon that had not been addressed prior to 2013 monitoring. It may or may not be important in understanding trend. There are also unexplained patterns of deformed Colorado butterfly plant seeds (Figure 8 in Heidel and Tuthill 2015) that may or may not reflect a pathogen.

We reiterate willingness to contribute to any status reviews by the U.S. Fish and Wildlife Service and promote closer communication, if not research coordination or collaboration, with others who are working on Colorado butterfly plant, including biologists working at Soapstone Prairie. It may have been possible to pursue flea beetle research in 2014 and 2015 there if such collaboration had been in place, and arrangements might still be set up to work there in 2016 if agreed upon by all parties. We will distribute copies of this report along with the invitation.

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