Autecology of Bastard Toadflax on the Northern Mixed Grass Prairie

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Report DREC 16-1111

The autecology of Bastard Toadflax, *Comandra umbellata*, is one of the prairie plant species included in a long ecological study conducted at the NDSU Dickinson Research Extension Center during 67 growing seasons from 1946 to 2012 that quantitatively describes the changes in growth and development during the annual growing season life history and the changes in abundance through time as affected by management treatments for the intended purpose of the development and establishment of scientific standards for proper management of native rangelands of the Northern Plains. The introduction to this study can be found in report DREC 16-1093 (Manske 2016).

Bastard Toadflax, *Comandra umbellata* (L.) Nutt., is a member of the sandalwood family, Santalaceae, syn.: *Commandra pallida* A. DC., and is a native, perennial, dicot, herb that is a root hemiparasite; it uses underground suckers (haustorium) to obtain water, minerals, and essential elements from the roots of other plants. The first North Dakota record is Bolley 1891. Annual aerial growth has few to several stiff erect clustered stems 10-20 cm (3.9-7.9 in) tall, usually unbranched, there are a few with branches, arising from an extensive shallow to deep horizontal rhizome system. Stem leaves are alternate, thick, smooth, pale green, linear to lanceolate to elliptic or ovate 1-3 cm (0.4-1.2 in) long, 0.6-1.3 cm (0.25-0.5 in) wide, with short petioles below, sessile above along the full length of the stem, blades have pinnate venation. The root system consists of numerous slender, 1-5 mm thick, long, woody rhizomes that can form loose colonies. A fibrous root system develops at nodes of rhizomes. Numerous specialized root like organs (haustoria) grow from the fibrous root system that penetrate the roots of host plants from which nutrients are obtained. Regeneration is very limited by vegetative and sexual reproduction. Vegetative growth is by annual sprouts from the crown bases on rhizomes and by sprouts from the rhizome system. Inflorescence has many small solitary flowers, 5 mm wide, each terminal on a pedicel, forming a cluster in a corymb. Flowers do not have petals, but have 5 whitish sepals that appear during late May to late June. Pollination is by small bees, flies, and other insects. Fruit is a fleshy, oily, drupe containing one large seed and are claimed to be eatable with a sweet taste when immature. Aerial parts are not usually eaten by livestock and are top killed by fire. Damage to aerial stems activates regrowth shoots from the crown and sprouts develop on the rhizome system. This summary information on growth development and regeneration of bastard toadflax was based on the works of Stevens 1963, Zaczkowski 1972, Great Plains Flora Association 1986, and Larson and Johnson 2007.

Procedures

The 1955-1962 Study

Bastard Toadflax plant growth in height was determined by measuring ungrazed stems from ground level to top of leaf or to the tip of the inflorescence of an average of 10 plants of each species at approximately 7 to 10 day intervals during the growing seasons of 1955 to 1962 from early May until early September. Dates of first flower (anthesis) were recorded as observed. These growth in height and flower data were reported in Goetz 1963.

The 1969-1971 Study

The range of flowering time of Bastard Toadflax was determined by recording daily observations of plants at anthesis on several prairie habitat type collection locations distributed throughout 4,569 square miles of southwestern North Dakota. The daily observed flowering plant data collected during the growing seasons of 1969 to 1971 from April to August were reported as flower sample periods with 7 to 8 day duration in Zaczkowski 1972.

The 1984-1985 Study

Bastard Toadflax plant growth in height was determined by measuring stems from ground level to top of stem or leaf or to the tip of the inflorescence of 12 ungrazed specimens randomly selected on each of the three replications of grazed sandy, shallow, silty, and clayey ecological sites biweekly during June, July, and August of the growing seasons of 1984 and 1985. Phenological growth stage of each specimen was recorded as vegetative, budding, anthesis, seed developing, seed shedding, or mature. Percentage of stem dryness of each specimen was recorded as 0, 0-2, 2-25, 25-50, 50-75, 75-98, or 100 percent dry. Mean stem weight was determined by clipping at ground level 25 specimens at typical phenological growth stages at biweekly sample dates on separate grazed areas of the sandy, shallow, silty, and clayey ecological sites. Clipped stems at each sample site were placed in separate labeled paper bags of known weight, oven dried at 62° C (144° F), and weighed in grams.

The 1983-2012 Study

A long-term study on change in abundance of Bastard Toadflax was conducted during active plant growth of July and August each growing season of 1983 to 2012 (30 years) on native rangeland pastures at the Dickinson Research Extension Center ranch located near Manning, North Dakota. Effects from three management treatments were evaluated: 1) long-term nongrazing, 2) traditional seasonlong grazing, and 3) twice-over rotation grazing. Each treatment had two replications, each with data collection sites on sandy, shallow, and silty ecological sites. Each ecological site of the two grazed treatments had matching paired plots, one grazed and the other with an ungrazed exclosure. The sandy, shallow, and silty ecological sites were each replicated two times on the nongrazed treatment, three times on the seasonlong treatment, and six times on the twice-over treatment.

During the initial phase of this study, 1983 to 1986, the long-term nongrazed and seasonlong treatments were at different locations and moved to the permanent study locations in 1987. The data collected on those two treatments during 1983 to 1986 were not included in this report.

Abundance of Bastard Toadflax was determined with plant species stem density by 0.1 m^2 frame density method and with plant species basal cover by the ten-pin point frame method (Cook and Stubbendieck 1986).

The stem density method was used to count individual stems of each plant species rooted inside twenty five 0.1 m^2 quadrats placed along permanent transect lines at each sample site both inside (ungrazed) and outside (grazed) each exclosure. Stem density per 0.1 m^2 quadrat, relative stem density, percent frequency, relative percent frequency, and importance value were determined from the stem density data. Plant species stem density data collection was 1984, 1986 to 2012 on the twice-over treatment and was 1987 to 2012 on the long-term nongrazed and seasonlong treatments. However, stem density data was not collected during 1991, 1993 to 1997 on the sandy, shallow, and silty ecological sites of all three management treatments, stem density data was not collected during 1992 on the sandy ecological site of all three management treatments, and stem density data was not collected during 1999 on the sandy and silty ecological sites of the long-term nongrazed treatment.

The point frame method was used to collect data at 2000 points along permanent transect lines at each sample site both inside (ungrazed) and outside (grazed) each exclosure. Basal cover, relative basal cover, percent frequency, relative percent frequency, and importance value were determined from the ten-pin point frame data. Point frame data collection period was 1983 to 2012 on the twice-over treatment and was 1987 to 2012 on the long-term nongrazed and seasonlong treatments. However, point frame data was not collected during 1992 on the sandy ecological sites of all three treatments.

During some growing seasons, the point frame method or the stem density method did not document the presence of a particular plant species which will be reflected in the data summary tables as an 0.00 or as a blank spot.

The 1983-2012 study attempted to quantify the increasing or decreasing changes in individual plant species abundance during 30 growing seasons by comparing differences in the importance values of individual species during multiple year periods. Importance value is an old technique that combines relative density or relative basal cover with relative frequency producing a scale of 0 to 200 that ranks individual species abundance within a plant community relative to the individual abundance of the other species in that community during a growing season. Density importance value ranks the forbs and shrubs and basal cover importance value ranks the grasses, upland sedges, forbs, and shrubs in a community. The quantity of change in the importance values of an individual species across time indicates the magnitude of the increases or decreases in abundance of that species relative to the changes in abundance of the other species.

Results

Bastard Toadflax resumed annual aerial growth in spring as few to several stiff, erect stems in a cluster 10-20 cm (3.9-7.9 in) tall. The small solitary flowers are terminal on a pedicel. On the fall grazed pasture of the 1955-1962 study, the earliest first flowers appeared on 19 May, the mean first flowers occurred on 1 June, and the flower period, from the 1969-1971 study, extended from late May to late June (table 1) (Goetz 1963, Zaczkowski 1972). A mean mature height of 9.4 cm (3.7 in) with an annual variance in height from 8.0 cm (3.1 in) to 11.0 cm (4.3 in) was reached during July (table 2) (Goetz 1963). The reported normal mature height in the Northern Plains ranged from 10-20 cm (3.9-7.9 in), the range of mature plant height of 8-11 cm (3.1-4.3 in) from the 1955-1962 study was at the low end or shorter than the reported range of normal height. The lower height of Bastard toadflax on the 1955-1962 study was not caused directly by the effects of grazing but was caused by low quantities of available mineral nitrogen below the threshold levels of 100 lbs/ac in the soil.

Changes in phenological growth stages from the 1984-1985 study are summarized on tables 3, 4, 5, and 6. A total of 2,023 Bastard toadflax stems were sampled during this study with, 580 stems (28.67%) from the sandy sites, 805 stems (39.79%) from the shallow sites, 314 stems (15.52%) from the silty sites, and 324 stems (16.02%) from the clayey sites. Bastard toadflax can grow on the sandy, shallow, silty, and clayey ecological sites, however, it grew the best on the shallow sites, it did not grow well on the sandy sites, and it grew poorly on the clayey and silty sites. The mean mature height reached on the 1984-1985 study was, 8.7 cm (3.4 in) on the sandy sites, 8.8 cm (3.5 in) on the shallow sites, 8.2 cm (3.2 in) on the silty sites, and 8.3 cm (3.3 in) on the clayey sites. The reduced stem heights of Bastard toadflax on the 1984-1985 study was caused by low quantities of available mineral nitrogen below the threshold levels of 100 lbs/ac that resulted from the traditional management practices conducted prior to the start of this study.

During the growing season on the grazed ecological sites, most of the Bastard toadflax aerial stems remained at early growth stages of vegetative and budding stages with, 95.7% on the sandy sites, 93.3% on the shallow sites, 92.6% on the silty sites, and 95.9% on the clayey sites. Few Bastard toadflax stems developed into mature growth stages with 4.3% on the sandy site, 6.7% on the shallow sites, 7.4% on the silty sites, and 4.1% on the clayey sites (tables 3, 4, 5, and 6).

Mean Bastard toadflax stem weights were not significantly different on the four ecological sites. Stem weights were heaviest on the clayey and shallow sites at 0.31 g and 0.29 g, respectively, medium on the sandy sites at 0.22 g, and lightest on the silty sites 0.12 g (tables 3, 4, 5, and 6).

Plant species composition in rangeland ecosystems is variable during a growing season and dynamic among growing seasons. Patterns in the changes in individual plant species abundance was followed for 30 growing seasons during the 1983-2012 study. The number of documented Bastard toadflax stems on the sandy and silty ecological sites of the three management treatments was insufficient to describe abundance patterns and were not included in this report.

On the shallow site of the nongrazed treatment, Bastard toadflax was present during 57.9% and 11.5% of the years that density and basal cover data were collected, with a mean 0.67 stems/m^2 density and a mean 0.01% basal cover during the total 30 year period, respectively. During the early period (1983-1992), Bastard toadflax was present on the shallow site during 40.0% and 16.7% of the years, with a mean 0.40 stems/m^2 density and a mean 0.008% basal cover. During the later period (1998-2012), Bastard toadflax was present on the shallow site 64.3% and 13.3% of the years, with a mean 0.77 stems/m^2 density and a mean 0.013% basal cover, respectively. Both the stem density and basal cover increased on the nongrazed treatment over time (tables 7, 8, and 9).

On the shallow sites of the seasonlong treatment, Bastard toadflax was present on the ungrazed shallow site during 40.0% and 15.4% of the years, with a mean 0.54 stems/m^2 density and a mean 0.006% basal cover, and was present on the grazed shallow site during 70.0% and 23.1% of the years that density and basal cover data were collected, with a mean 0.98 stems/m^2 density and a mean 0.04% basal cover during the total 30 year period, respectively. During the early period (1983-1992), Bastard toadflax was present on the ungrazed shallow site during 0.0% and 0.0% of the years, and during the later period (1998-2012), Bastard toadflax was present on the ungrazed shallow site during 53.3% and 26.7% of the years, with a mean 0.71 stems/m^2 density and a mean 0.02% basal cover, respectively. Both the stem density and basal cover increased on the ungrazed shallow site of the seasonlong treatment over time. During the early period (1983-1992), Bastard toadflax was present on the grazed shallow site during 40.0% and 33.3% of the years, with a mean 1.04 stems/m^2 density and a mean 0.14% basal cover. During the later period (1998-2012), Bastard toadflax was present on the grazed shallow site during

80.0% and 26.7% of the years, with a mean 0.95 stems/m^2 density and a mean 0.01% basal cover, respectively. Both the stem density and basal cover decreased on the grazed shallow site of the seasonlong treatment over time. During the early period (1983-1992), stem density and basal cover of Bastard toadflax were greater on the grazed site than those on the ungrazed shallow site. Bastard toadflax decreased greatly during the drought year of 1988 and was not present on the seasonlong treatment for about 10 years. During the later period (1998-2012), Bastard toadflax increased in stem density and basal cover on the ungrazed shallow site, and decreased in stem density and basal cover on the grazed shallow site, resulting in greater stem density on the grazed shallow site and greater basal cover on the ungrazed shallow site of the seasonlong treatment (tables 7, 8, and 9).

On the shallow sites of the twice-over treatment, Bastard toadflax was present on the ungrazed shallow site during 68.2% and 43.3% of the years, with a mean 0.28 stems/m^2 density and a mean 0.01% basal cover, and was present on the grazed shallow site during 50.0% and 23.3% of the years that density and basal cover data were collected, with a mean 0.10 stems/m^2 density and a mean 0.01% basal cover during the total 30 year period, respectively. During the early period (1983-1992), Bastard toadflax was present on the ungrazed shallow site during 14.3% and 40.0% of the years, with a mean 0.06 stems/m^2 density and a mean 0.01% basal cover. During the later period (1998-2012), Bastard toadflax was present on the ungrazed shallow site during 93.3% and 60.0% of the years, with a mean 0.39 stems/m^2 density and a mean 0.01% basal cover, respectively. The stem density increased and the basal cover remained the same on the ungrazed shallow site of the twice-over treatment over time. During the early period (1983-1992), Bastard toadflax was present on the grazed shallow site during 28.6% and 50.0% of the years, with a mean 0.06 stems/m^2 density and a mean 0.02% basal cover. During the later period (1998-2012), Bastard toadflax was present on the grazed shallow site during 60.0% and 13.3% of the years, with a mean 0.13 stems/m^2 density and a mean 0.001% basal cover, respectively. The stem density increased slightly and the basal cover decreased on the grazed shallow site of the twice-over treatment over time. During the early period (1983-1992), Bastard toadflax stem density was the same on the ungrazed and grazed shallow sites and basal cover was greater on the grazed site than that on the ungrazed shallow site. Bastard toadflax decreased greatly during the drought year of 1988 and was not present on the twice-over treatment for about 10 years. During the later period (1998-2012), Bastard toadflax increased in stem density and remained unchanged in basal cover on the ungrazed shallow site, and increased slightly in stem density and decreased in basal cover on the grazed shallow site, resulting in greater stem density and basal cover on the ungrazed shallow site than those on the grazed shallow site of the twice-over treatment (tables 7, 8, and 9).

Bastard toadflax was present on the shallow sites of all three management treatments during the period of 1983-1988. The drought year of 1988 had low growing season precipitation at 5.30 inches (37.51% of the long-term mean) and caused the elimination of bastard toadflax from all three management treatments for the next nine years (1989-1997). Bastard toadflax reestablished itself on the shallow sites of all management treatments at various mean stem densities during the later period of 1998 to 2012. The greatest mean density at 0.95 stems/m^2 developed on the grazed shallow site of the seasonlong treatment. The second greatest mean density at 0.77 stems/m^2 developed on the shallow site of the nongrazed treatment. The third greatest mean density at 0.71 stems/m^2 developed on the ungrazed shallow site of the seasonlong treatment. The second lowest mean density at 0.39 stems/m^2 developed on the ungrazed shallow site of the twice-over treatment. And the lowest mean density at 0.13 stems/m^2 developed on the grazed shallow site of the twice-over treatment.

Discussion

Bastard Toadflax, *Comandra umbellata*, is a root hemiparasitic plant that is commonly presnt but a minor component of healthy mixed grass prairie plant communities. Bastard Toadflax can grow in low productivity sandy, shallow, silty, and clayey ecological sites but does better growing in shallow ecological sites. Bastard Toadflax can fix carbon by photosynthesis and produce carbohydrates, however, it apparently has deficiencies in soil nutrient and water uptake competitiveness and must rely on root hemiparasitism of other plants. Specialized organs developed from the reduced root network (haustorium) penetrate the xylem vascular system of the host plant and acquire water, mineral nutrients, and a limited amount of organic assimilates. There are two possible mechanisms to extract these essential elements from a host plant. 1) By maintaining a more negative water potential than the host plant through a greatly elevated transpiration rate with sustained open stomata, or 2) by development of a complex active transmembrane transport system that does not depend as much on a high water potential difference and a rapid respiration rate. Bastard Toadflax has a narrow habitat productivity gradient in which it can survive. In poor productivity environments, the host plant biomass is too low to support and sustain a hemiparasitic plant population. In low to intermediate productivity environments where water and macronutrients are available at low to moderate levels, both host and hemiparasitic plants can coexist. At this level, the hemiparasitic plants can cause reductions in host plant productivity keeping competition for sunlight at tolerable levels. In high productivity environments where water and macronutrients are available at high levels, the biomass of the host plants increase which intensifies shading competition resulting in proportional reductions of hemiparasitic plant biomass and eventually causing extinction from the plant community (Fibich et al. 2010, Tesitel et al. 2010, Tesitel et al. 2015).

Annual aerial growth resumes in spring from crowns (caudexes) that develop on rhizome branches. The flower period (anthesis) occurs during late May to late June. Erect aerial stems reach maximum mature height during July, however, fewer than 8% of the stems growing in grazed prairie developed to mature phenological growth stages. Bastard Toadflax is usually not eaten by livestock and thus the effects from partial defoliation by grazing do not directly cause annual changes in stem height and abundance. The normal mature stem height of Bastard Toadflax in the Norther Plains is reported to be between 10 cm and 20 cm (4-8 in). The stem heights collected during the 1955-1962 study and the 1984-1985 study were at the short end of normal mature stem height because the soils of both studies had mineral nitrogen available at less than the threshold quantity of 100 lbs/ac which resulted from the detrimental effects caused by traditional management practices on the biogeochemical processes and the soil microbe biomass of the prairie plant communities. Bastard Toadflax is an inefficient water user causing it to be greatly affected by periods of deficient precipitation and it can be totally eliminated from plant communities following severe drought conditions. It was removed for 9 years following the 1988 drought conditions. During the later period (1998-2012), Bastard Toadflax reestablished itself and the mean stem densities increased above 0.70 stems/m^2 on the nongrazed treatment and on the ungrazed and grazed sites of the seasonlong treatment, causing some level of reduced productivity to those ecological sites. Bastard Toadflax plants appropriate water and nutrients from their host plants which results in lower production from those plants. Further reductions of productivity can lead to degradation of the ecosystem, permitting less desirable plant species to migrate into the created open spaces.

Stem height and abundance of Bastard Toadflax are affected by the level of availability of soil water and macronutrients, the placement on the productivity gradient of the plant community, and the degree of competition for sunlight by the host plants.

Acknowledgment

I am grateful to Sheri Schneider for assistance in the production of this manuscript and for development of the tables.

Table 1. First flower and flower period of Comandra umbellata, Bastard Toadflax.

	Apr	May	Jun	Jul	Aug	Sep
First Flower						
1955-1962						
Earliest		19				
Mean			1			
Flower Period						
1969-1971		X	XX XX			

First Flower data from Goetz 1963.
Flower Period Data from Zaczkowski 1972.

Table 2. Autecology of Comandra umbellata, Bastard Toadflax, with growing season changes in mature height.

				Percent of Mature Height Attained					
Data Period	Minimum Annual Mature Height cm	Maximum Annual Mature Height cm	Mean Mature Height cm	Apr %	May %	Jun %	Jul %	Aug %	Sep %
1955-1962	8.0	11.0	9.4		69.1		100.0		

Data from Goetz 1963.

Table 3. Phenological growth stage changes during the growing season for Comandra umbellata, Bastard Toadflax, 1984-1985.

Site Sandy	8 Jun	23 Jun	8 Jul	23 Jul	8 Aug	23 Aug
% Population						
Veg	65.2	83.7	82.8	82.9	88.0	96.1
Bud	34.8	14.0	17.2	2.4	6.0	1.2
Anth						
Seed Dev		2.3		14.6	6.0	2.6
Seed Shed						
Mat						
Mean Height (cm)	10.2	7.0	8.7	9.1	9.3	9.9
Veg	11.3	9.5	11.2	10.7	6.6	9.2
Bud						
Anth		8.5		8.8	9.6	7.8
Seed Dev						
Seed Shed						
Mat						
% Dryness						
Veg	0.4	0.7	3.5	6.3	14.5	19.2
Bud	0.5	0.0	2.1	13.5	9.7	25.0
Anth						
Seed Dev		0.0		5.7	25.0	13.5
Seed Shed						
Mat						
Mean Weight (g)	0.10	0.22	0.25	0.22	0.30	0.21

Phenological Growth Stages: Vegetative (Veg), Budding (Bud), Anthesis (Anth), Seed Developing (Seed Dev), Seed Shedding (Seed Shed), Mature (Mat).

Table 4. Phenological growth stage changes during the growing season for Comandra umbellata, Bastard Toadflax, 1984-1985.

Site Shallow	8 Jun	23 Jun	8 Jul	23 Jul	8 Aug	23 Aug
% Population						
Veg	72.2	77.7	83.2	89.8	81.2	85.6
Bud	27.8	13.2	7.3	1.9	12.9	7.2
Anth						
Seed Dev		4.1	8.0	8.3	4.7	7.2
Seed Shed		5.0	1.5			
Mat					1.2	
Mean Height (cm)						
Veg	7.1	6.4	6.7	7.1	6.8	7.2
Bud	6.9	6.5	5.9	6.7	6.1	7.8
Anth						
Seed Dev		7.5	8.0	8.5	9.1	7.9
Seed Shed		3.4	5.5			
Mat					9.4	
% Dryness						
Veg	1.3	4.9	6.9	10.7	15.3	22.4
Bud	4.4	6.0	3.7	50.0	10.5	12.5
Anth						
Seed Dev		5.4	14.0	14.6	25.5	14.9
Seed Shed		0.0	0.0			
Mat					25.0	
Mean Weight (g)	0.34	0.28	0.22	0.28	0.27	0.32

Phenological Growth Stages: Vegetative (Veg), Budding (Bud), Anthesis (Anth), Seed Developing (Seed Dev), Seed Shedding (Seed Shed), Mature (Mat).

Table 5. Phenological growth stage changes during the growing season for Comandra umbellata, Bastard Toadflax, 1984-1985.

Site Silty	8 Jun	23 Jun	8 Jul	23 Jul	8 Aug	23 Aug
% Population						
Veg	81.6	87.2	79.7	90.6	80.4	82.5
Bud	18.4	10.3	14.1	1.9	3.9	5.0
Anth						
Seed Dev		2.6	3.1	7.5	13.7	12.5
Seed Shed						
Mat			3.1		2.0	
Mean Height (cm)						
Veg	9.5	12.3	9.2	8.9	7.9	9.4
Bud	9.1	8.4	9.3	5.1	9.5	9.3
Anth						
Seed Dev		5.8	9.6	7.7	7.2	6.6
Seed Shed						
Mat			7.8		6.5	
% Dryness						
Veg	0.5	0.7	3.9	13.8	13.6	20.5
Bud	1.0	0.0	0.7	2.0	1.0	25.0
Anth						
Seed Dev		2.0	1.0	37.5	11.9	15.4
Seed Shed						
Mat			0.0		50.0	
Mean Weight (g)	-	0.43	-	0.26	-	-

Phenological Growth Stages: Vegetative (Veg), Budding (Bud), Anthesis (Anth), Seed Developing (Seed Dev), Seed Shedding (Seed Shed), Mature (Mat).

Table 6. Phenological growth stage changes during the growing season for Comandra umbellata, Bastard Toadflax, 1984-1985.

Site Clayey	8 Jun	23 Jun	8 Jul	23 Jul	8 Aug	23 Aug
% Population						
Veg	66.7	71.0	80.0	97.1	91.4	96.8
Bud	33.3	12.9	20.0		2.9	3.2
Anth						
Seed Dev		12.9		2.9	5.7	
Seed Shed		3.2				
Mat						
Mean Height (cm)						
Veg	7.3	12.9	8.7	8.1	8.6	9.3
Bud	8.2	9.5	8.8		8.1	7.2
Anth						
Seed Dev		9.1		7.5	8.3	
Seed Shed		12.5				
Mat						
% Dryness						
Veg	5.5	0.5	5.9	9.3	19.6	18.3
Bud	5.8	0.0	0.9		25.0	50.0
Anth						
Seed Dev		0.5				
Seed Shed		0.0		25.0	37.5	
Mat						
Mean Weight (g)	0.38	0.37	0.27	0.46	0.25	0.16

Phenological Growth Stages: Vegetative (Veg), Budding (Bud), Anthesis (Anth), Seed Developing (Seed Dev), Seed Shedding (Seed Shed), Mature (Mat).

Table 7. Autecology of Comandra umbellata, Bastard toadflax, with growing season changes in density importance value, 1983-2012.					
Ecological Site Year Period	Nongrazed	Seasonlong		Twice-over	
		Ungrazed	Grazed	Ungrazed	Grazed
Sandy					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					
Shallow					
1983-1987	8.54	0.00	12.61	0.23	0.53
1988-1992	0.52	0.00	4.10	0.00	0.17
1993-1998	7.10	0.00	13.45	0.49	0.00
1999-2003	1.77	0.43	6.75	0.94	0.71
2004-2009	4.67	5.79	2.74	1.17	0.94
2010-2012	1.51	1.36	0.41	1.07	0.55
Silty					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					

Table 8. Autecology of Comandra umbellata, Bastard toadflax, with growing season changes in basal cover importance value, 1983-2012.					
Ecological Site Year Period	Nongrazed	Seasonlong		Twice-over	
		Ungrazed	Grazed	Ungrazed	Grazed
Sandy					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					
Shallow					
1983-1987	0.46	0.00	3.02	0.13	0.25
1988-1992	0.00	0.00	0.58	0.09	0.04
1993-1998	0.00	0.00	0.00	0.02	0.00
1999-2003	0.23	0.03	0.19	0.16	0.04
2004-2009	0.10	0.41	0.02	0.11	0.00
2010-2012	0.00	0.00	0.00	0.00	0.00
Silty					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					

Table 9. Autecology of Comandra umbellata, Bastard toadflax, with growing season changes in density, 1983-2012.					
Ecological Site Year Period	Nongrazed	Seasonlong		Twice-over	
		Ungrazed	Grazed	Ungrazed	Grazed
Sandy					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					
Shallow					
1983-1987	0.18	0.00	0.25	0.01	0.01
1988-1992	0.01	0.00	0.07	0.00	0.00
1993-1998	0.14	0.00	0.19	0.03	0.00
1999-2003	0.08	0.00	0.18	0.05	0.02
2004-2009	0.08	0.17	0.17	0.04	0.01
2010-2012	0.05	0.02	0.00	0.03	0.01
Silty					
1983-1987	Few Plants Present				
1988-1992					
1993-1998					
1999-2003					
2004-2009					
2010-2012					

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