Vegetation and vascular flora of tallgrass prairie and wetlands, Black Squirrel Creek drainage, Colorado: Perspectives from the 1940's and 2011

Sylvia Kelso¹

Leah Fugere²

Miroslav Kummel²

Sebastian Tsocanos²

¹ Department of Biology

Carter Herbarium

Colorado College

Colorado Springs, CO 80903

tkelso@coloradocollege.edu

² Environmental Program

Colorado College

Colorado Springs, CO 80903

mkummel@coloradocollege.edu

Abstract: We examined a tallgrass prairie-wetland complex of the Black Squirrel Creek drainage in south-central Colorado to compare the current grassland composition to its documentation by Robert Livingston in the early 1940's. Livingston then considered these grasslands as analogous to Midwestern tallgrass prairie with respect to dominant grasses and forbs. Using Livingston's methodology, we assessed an area near his original plots to determine whether the dominant grass species had changed in their contributions to cover or their frequency. We found an almost identical suite of species to that identified in the 1940's still occurs, with modest differences in frequency and relative contribution to cover by the key grass species. We also characterized wetland habitats occurring within the grassland matrix, documented the vascular flora of mesic and hydric habitats, and analyzed the extent to which it contains species of conservation concern, Midwest prairie elements, or montane species typically occurring regionally at higher elevations. The tallgrass communities here differ from others in Colorado and the Midwest in having a lesser presence of Andropogon gerardii, and a dominant presence of S. heterolepis, along with xeric or montane species that include Bouteloua gracilis, Calamovilfa longifolia and Muhlenbergia montana. Although the structure of the extant vegetation remains similar to what existed in the 1940's and continues to be supported by ample groundwater, these grasslands are now reduced in extent. The vegetation mosaic of tallgrass prairie and wetlands continues to hold a rich flora with numerous elements of phytogeographic and conservation interest.

Introduction

Over the past century, Colorado prairie have changed and diminished as urban, suburban and exurban development expanded and fire suppression, ingression of exotic species, and overgrazing altered grassland components. Prairie vegetation overall, and tallgrass communities in particular, now elicit special conservation focus amid widespread concerns about the accelerating loss, fragmentation, and degradation of prairies throughout the Midwest and West (Nicholson and Hulett 1969; Samson and Knopf 1996; Bachand 2001; Colorado Natural Heritage Program 2005; Rondeau et al. 2011). In the early 1940's, ecologist Robert Livingston undertook a detailed study of tallgrass prairie in south-central Colorado north of the city of Colorado Springs (Fig. 1). He profiled this vegetation in

his graduate theses (1947; 1949) and related publication (1952) as unique remnant vegetation with strong floristic similarities to the Midwest prairies. His work provides a detailed portrait of regionally anomalous vegetation, even then known to be limited in extent, as it existed nearly seventy years ago.

In this study, we reanalyzed the structure of grassland vegetation in the Black Squirrel Creek drainage near the Arkansas River-Platte River Divide north of Colorado Springs (Fig. 2) that was focus of the Livingston work. We compared its current state to its description in the Livingston work, and added additional documentation of associated wetland communities and their vascular flora. Although these components were not a specific focus of the original studies, contemporary conservation interest in these elements suggested their importance as part of the regional ecological profile. The objectives of our study were to:

- Document the vascular flora of the mesic and hydric communities and
 to assess the extent to which this flora contains elements from the
 Midwest prairie or other regional components such as montane
 species typically occurring in the foothills, and to highlight species of
 concern
- Document the types of wetland habitats occurring in the grassland matrix and their signature flora, plant associations and hydrogeomorphic profiles
- Compare the current dominant plant species and composition of the vegetation to the 1940's profile considered representative of
 Midwestern tallgrass prairie. In particular, we examined whether the

relative rank of the dominant grass species had changed with respect to contribution to cover and their frequency.

REGIONAL VEGETATION CONTEXTS: SHORTGRASS, MIDGRASS AND TALLGRASS PRAIRIE

The eastern Colorado plains encompass a wide range of plant communities across diverse topography and edaphic substrates (Ramaley 1919; Shantz 1923; Weaver and Fitzpatrick 1934). The grasslands here represent the western edge of the Great Plains where collective vegetation types and many individual biotic components have been highly diminished from their historic presence (Rondeau et al. 2011). Shortgrass prairie (also known as shortgrass steppe senus Lauenroth et al. 2008) with its signature species blue grama, Bouteloua gracilis (Willd. ex Kunth)Lag. ex Griffiths (nomenclature herein follows the U.S. Dept. of Agriculture National Resources Conservation Service Plants Database 2013 (www.plants.usda.gov); see Appendix 1 for full citations and exceptions) is the dominant regional vegetation (Weaver 1954: Neeley et al. 2006; Lauenroth et al. 2008). However, in the piedmont zone along the foothills east of the Colorado Front Range, a mixed grass prairie prevails. In mixed prairie, grama grass is present in conjunction with a high representation of species in Elymus (ryegrass), Hesperostipa (needlegrass), Muhlenbergia (muhly) and Poa (bluegrass) along with Schizachyrium scoparium (Michx.) Nash (little bluestem), Sporobolus cryptandrus (Torrey) A. Gray (sand dropseed) and Koeleria macrantha (Ledeb.) Schult (Junegrass). This vegetation is extensive north and east of Colorado Springs, where the topographic watershed

known as the Palmer Divide separates the drainages of the South Platte River to the north and the Arkansas River to the south.

Limited occurrences of tallgrass prairie vegetation (Vestal 1914, 1917, 1919; Moir 1972; Bock and Bock 1998) exist east of the Front Range in areas where edaphic conditions enhance soil moisture (Branson et al. 1965). The Colorado Natural Heritage Program (2012) tracks four tallgrass communities of conservation concern: xeric tallgrass prairie dominated by big bluestem and prairie dropseed (Andropogon gerardii Vitma and Sporobolus heterolepis (A.Gray)A.Gray), or big bluestem and little bluestem (A. gerardii- Schizachyrium scoparium (Michx.)Nash), and mesic tallgrass prairie dominated by blue bluestem and prairie sandreed (A. gerardii-Calamovilfa longifolia (Hooker)Scribner), or big bluestem with Indiangrass (A. gerardii-Sorghastrum nutans (L.)Nash). These associations are part of the mixed vegetation that comprise the Western Great Plains Foothill and Piedmont Grasslands (Colorado Natural Heritage Program 2005).

At the species level, Colorado tallgrass prairies parallel those found in the Midwest where signature taxa include Andropogon gerardii, Sporobolus heterolepis, Panicum virgatum L., Hesperostipa spartea (Trinius) Barkworth), Sorghastrum nutans, and Calamovilfa longifolia (e.g. Weaver 1954; Freeman 1998). The relative amounts of these species typically differ among central and western states (Weaver 1954; Weaver and Albertson 1956) according to precipitation and temperature regimes and soil types; in Colorado, it has long been recognized that these communities similarly vary along a north-south gradient (Robbins 1910; Vestal 1914, 1917, 1919).

South and southeast of the Palmer Divide, isolated examples of tallgrass prairie occur within a ponderosa pine forest- grassland matrix known as the Black Forest savannah (Shaddle 1939; Fig. 1). Studies by Vestal (1917), Shaddle (1939), and Williams and Holch (1946) noted the unusual vegetation and flora here; this region and surrounding grasslands became the focus of the Livingston studies (1941, 1947, 1949, 1952) in which he highlighted the similarity of the grassland vegetation and flora to Midwestern "true prairie", and suggested it represented fragmented relict communities from the Pleistocene (Livingston 1952; Weaver and Albertson 1956). Although relatively recent studies of tallgrass vegetation in eastern Colorado have been conducted in the Boulder area ca. 150 km north of the Black Forest (e.g. Moir 1972; Baker and Galatowitch 1985; Bock and Bock 1998; Neid et al. 2009), no assessment of the Black Squirrel Creek vegetation has been done since Livingston, although surveys by the Colorado College Herbarium and the Colorado Natural Heritage Program (Doyle et al. 2001; 2001b) have shown the area to be rich in unusual species and ecological communities.

STUDY SITE. The Black Squirrel Creek system, a complex, anastomosed network of drainages into the main creek channel, begins near the summit of the Palmer Divide (Fig. 2; Fig. 3) in the Black Forest and extends southeast, ultimately draining into the Arkansas River east of the city of Pueblo. In the upper quarter of the drainage, the creek typically has perennial flow, but this becomes intermittent aboveground to the south. Our primary study area was located on the upper Black Squirrel drainage between the municipalities of Falcon and Peyton, with an elevation range of ca. 2000 to 2200 m (6500 to 7100 feet). Quantitative data were taken on the core area

covering ca. 770 ha. (1900 acres) on ca. 3100 ha. (7700 acre) ranch that encompasses the main stem of Black Squirrel Creek with perennial flowing water as well as with many subsidiary drainages with intermittent flow and standing water. We took additional floristic and qualitative information south of the core area for a distance of ca. 10 km in order to encompass the area utilized in the 1940's studies. The topography consists of gently rolling uplands of mixed grass prairie on Quaternary deposits of eolian sand (Morgan and Barkmann 2012) separated by lowland drainages and swales with small discontinuous wetlands, seeps, springs, and seasonal ponds supported by groundwater. Our study focused on the mesic and hydric flora and vegetation occurring in these drainages, associated wetlands, and streambeds of Black Squirrel Creek and its tributaries rather than the xeric and mixed grass vegetation of the uplands that is widely represented on the eastern plains.

CLIMATE. Longterm annual precipitation since 1956 for this region averages ca. 38 cm (17 in.; Western Regional Climate Center, data for Eastonville, CO) with ca. 75% of this occurring from spring rains in April to May, and a July-August pulse from thunderstorms. Interannual variation in precipitation can be extreme in Colorado, with severe droughts occurring in the 1950's, 1970's, early 1980's, and early 2000's (Henz et al. 2004). Local rainfall tracks the topographic gradient, where higher elevations near the top of the drainage receive more rainfall in the summer and more winter storm events; these are often highly localized and precipitation events can vary over short distances. Longterm temperature records (Western Regional Climate Center; data for Colorado Springs 1948-2005) indicate an average daily high

of 26.6° C (79.9° F) – to an average low of 12.7° C (54.8° F) in the growing season months of June to August, while January temperatures range from an average high of 5.9°C (42.6° F) to a low of 16.6° F (-8.5 C). These climatic parameters do not differ significantly than those reported by Livingston (1947) for the years of his study. GEOLOGY. Livingston (1952) and Branson et al. (1965) noted the relationship between soils of perennial high moisture and the persistence of tallgrass prairie vegetation in Colorado, azonal conditions promoted by soil composition and water table dynamics. In our study area, two aquifers play a significant role in local hydrology that impact soil moisture: the alluvial Black Squirrel Creek aquifer and the underlying Dawson Formation bedrock aquifer composed of andesitic sandstone (Bittenger 1976; Robson 1988; Topper 2008; Morgan and Barkmann 2012). Subsurface topography slopes steeply south, shaped by the ancestral Black Squirrel Creek now covered with glacial alluvium that forms the Black Squirrel Creek aquifer of Pleistocene gravels and coarse sand. This ranges in depth from 0-215 m; close to the headwaters of Black Squirrel Creek it is relatively shallow but becomes deeper to the southeast. The alluvial aquifer is a significant source of well water for domestic, agricultural and municipal uses (Topper 2008) and provides localized high water table occurrences. However, in our study area the alluvial layer is relatively thin or absent, and much of the subsurface water here that supplies the seeps and springs is likely to be primarily a result of the Dawson Formation bedrock aquifer (R. Topper, pers. comm.), a Late Cretaceous-Tertiary sandstone widely exposed in the Palmer Divide and close to the surface in the upper Black Squirrel Creek drainage. Since the aeolian and alluvial surface deposits of the area are highly

1 1 1

permeable, runoff is low, and both aquifers receive recharge from precipitation (Topper 2008). The interface of the alluvial and bedrock aquifers is regionally complex with no detailed mapping of localized hydrological regimes yet available, and it is likely that both the alluvial and bedrock aquifers supply groundwater across the entirety of the drainage.

Materials and Methods

The study area was surveyed intensively from May to August 2011 throughout the growing season, although prior floristic collections had occurred regularly since 2000 and sporadically since the 1970's. We conducted qualitative surveys of topography and floristic composition of significant plant communities on each section of the main and subsidiary drainages every two weeks during 2011. We documented the vascular flora as completely as possible, combining new collection with existing recent ones at the Carter Herbarium of Colorado College (COCO); primary voucher specimens are at COCO, with duplicates at COLO and CSU. Vegetation communities and significant species and wetland features along the main drainage and its key tributaries were mapped using geospatial coordinates and entered into ArcGIS.

Initial surveys along the drainage of Upper Black Squirrel Creek provided qualitative assessments of the current extent and condition of grassland communities in sites as close as possible to those in the original studies by Livingston. Due to landscape modification in housing developments and roads or inability to obtain permission for access, the most intact extant communities in which we were able to take quantitative data were located ca. 10 km north of the

original Livingston plains sites, and a similar distance south of his forest-grassland interface plots (Livingston 1947; 1952) within the same hydrologic system in comparable topography. We were able to access some of his original sites for floristic information, although we did not take quantitative data there due to obvious disturbance from intensive grazing and anthropogenic surface alterations.

Livingston utilized nine 100 m line transects in seven locations: four sites, each with a single transect, were in the Black Forest within a ponderosa pine-savannah community at 2200-2300 m (7200 to 7500 ft.), and three locations (one with 3 transects) were along the Black Squirrel Creek drainage in grasslands at ca. 2000 m (6500 ft.). The original transects each encompassed ten quadrats of 1 x 0.5 m.; in comparison, we used four 105 m transects, each with 20 similarly sized quadrats spaced 5 m apart. This modification allowed us to assess more effectively the small-scale heterogeneity characteristic of the region. All transects were located at approximately 2100 m (7000 ft.) in elevation.

Transects 1 and 2 were located along the north-facing bank of the main stem of Black Squirrel Creek (Fig. 3) in vegetation that met our criteria for sufficient length with the presence of indicator species *Sorobolus heterolepis, Andropogon gerardii, Hesperostipa spartea,* or *Sorgastrum nutans*. These transects were parallel, ca. 10 m apart, and offset so that they overlapped by one half their length. We located two additional transects along subsidiary drainages in vegetation with similar criteria: Transect 3 was in a side drainage ca. 1 km north of transects 1 and 2, and Transect 4 was located in a tributary drainage, ca. 2 km northwest of transects 1 and 2. To match the protocol, timing, and data format of Livingston, we

surveyed the vegetation in late August following his methodology for assessing basal and relative cover and frequency of dominant taxa.

Basal Cover and Relative Cover. In each quadrat, we estimated the total basal cover as a percentage of the total area, as well as the percent cover of bare ground and litter combined, then averaged these over each transect of 20 quadrats. For each quadrat we estimated the total cover of all plants, the relative cover of combined graminoids (Poaceae, Cyperaceae, Juncaceae and Juncaginaceae) as a percentage of the total vegetative cover, and the contribution of each identifiable species to the total graminoid cover.

Frequency. For each quadrat we recorded each graminoid species. To calculate a frequency metric and rank of the dominant taxa, we summed the quadrat data for each transect individually, and calculated the mean across all four transects.

Results

VASCULAR FLORA

The flora reported here (Appendix 1) represents only the hydric and mesic habitats and does not encompass species restricted to the more xeric uplands. However, some components of this upland vegetation extend into the drainages, particularly in the open gravels of stream banks and terraces, and are included on the species list, though noted as a xeric component.

In the flora we defined notable elements (Table 1) as being either 1. Rare (tracked as being of conservation concern by the Colorado Natural Heritage Program) 2. Regionally uncommon (based on herbarium records from COCO and prior studies by Kelso and regional information provided in Culver and Lemly

(2013) or Weber and Wittmann (2012) 3. Foothills/Montane elements, topographic disjuncts that typically occur in higher elevation locations of the Front Range as noted by Weber and Wittmann (2012) and herbarium records at COCO or 4. Midwestern elements, associated with the characteristic Midwest Prairie flora as explicitly noted by Shantz (1928), Weaver and Fitzpatrick (1934), Weaver (1954), or Livingston (1952).

In the current study, we documented almost 300 taxa representing 62 families as currently recognized in the U.S.D.A. Plants Database (www.plants.usda.gov). The highest species diversity is in the Asteraceae (50 species), Cyperaceae (18 species), Juncaceae (12 species) and Poaceace (43 species). The flora includes relatively few noxious weeds, only one of which, purple loosestrife (*Lythrum salicaria*), which exists sporadically in a side drainage of Black Squirrel Creek, is an A list species. Although a detailed floristic list was not an objective of the Livingston studies, we found almost everything he noted as present, with only a few exceptions (Appendix 1).

Over one fifth of the flora is regionally associated with foothills/montane rather, and notably, at least a similar proportion is characteristic of the Midwest prairies. By contemporary phytogeographic perspectives and greater documentation of the Great Plains flora, this is almost certainly an underestimate, but to simplify the comparison, we used for reference only those species explicitly listed in early studies as characteristic of the Midwest. Eight of the "Midwest" species are locally also characteristic of the foothills/montane zone. Eighteen plant species occurring in the Black Squirrel Creek drainage are locally uncommon, and

nine are tracked by the Colorado Natural Heritage Program as being of conservation concern in the State of Colorado.

WETLAND HABITAT CLASSIFICATIONS

We identified eight general wetland habitat types characterized by distinct hydrogeomorphic characteristics and floristic profiles (Table 2). Our classification follows the Colorado Natural Heritage Program (Carsey et al. 2003) and includes general categories of Riverine Wetlands sourced by ongoing streamflow,

Depressional Wetlands supported by ground water filling a depression on a permanent or intermittent basis, and Slope Wetlands that are supported by groundwater on gentle to moderate slopes. Each habitat type occurs in multiple instances throughout the Black Squirrel drainage. Vegetation associations listed for each hydrogeomorphic class follow those used by Colorado Natural Heritage (2003; 2013) classifications as closely as possible.

RIVERINE WETLANDS

Stream Channel Tall Willow Shrubland. In our study site, this community occurs in a limited extent on the northwestern edge of the main Black Squirrel Creek drainage, covering about a kilometer in length; shrub cover diminishes further downstream, but reoccurs in patches along the drainage in wide stream meanders with shallow subsurface water. The primary vegetation community is sandbar willow-mesic graminoid shrubland dominated by Salix exigua (narrowleaf willow) with occasional occurrences of other tree and shrub species of willow (e.g. S. irrorata, S. ligulifolia, and S. amygdaloides); the forb component is limited but includes patchy occurrences Rudbeckia hirta (black-eyed Susan), Helianthus nuttallii (Nuttall's sunflower),

Glycyrrhiza lepidota (wild licorice), Agrimonia striata (agrimony), Monarda fistulosa (beebalm), and patches of Cirsium canadensis (Canada thistle).

Stream Channel Herbaceous Vegetation. The open gravels of the main stream channel and occasional side drainages support a linear strip of diverse obligate wetland forbs, sedges, and rushes where stream flow forms riffles around gravel banks and sandbars. The gravel stream channels are notable for their abundance and diversity of rushes, including the rare Juncus brachycephalus (smallhead rush), as well as Gentianopsis virgata (lesser fringed gentian). Both of these species are Midwest prairie elements known in Colorado only from this region. Although dominated by non-woody vegetation, the stream channels also support occasional occurrences of young saplings of Populus deltoides (plains cottonwood) or species of Salix.

SLOPE WETLANDS

Moist Shelves. These heterogeneous surfaces are located primarily along the main drainage channel above the creek channel depression and along some subsidiary drainages. Surfaces are flat to gently sloping, with moisture accumulating as a result of springs and runoff above. Moister areas hold a greater abundance of facultative or obligate wetland species, interspersed with xeric elements. Vegetative cover is primarily composed of graminoids and mixed forbs with occasional shrub patches. Sporobolus heterolepis is particularly widespread here, and the shelves support extensive occurrences of a Sporobolus heterolepis dominated community with occasional instances of Andropogon gerardii, along with patches of Andropogon gerardii-Sorghastrum nutans associations (big-bluestem-Indiangrass). The

Sporobolus-dominated communities range in width from 5 m to almost 40 m; depending on the topography, lengths can be short patches of 10 m to longer extents over 50 m. Drier areas include heterogeneous mixed grass vegetation with Muhlenbergia montana, Calamovilfa longifolia, Schizachyrium scoparium, Poa pratensis, and Koeleria macrantha.

Moist Banks. These encompass a significant portion of the drainage system and hold some of the highest diversity of forbs. One of the most significant species occurring here is the state-rare Liatris ligulistylis (Rocky Mountain blazing star) locally abundant here. The moist banks typically occur on side drainages with a U-shape profile and receive consistent subsurface moisture from seeps and springs; their surfaces are steeper than moist shelf habitats, and they usually include seeps that ooze perennial moisture. Plant associations include mixed mesic tallgrass communities with components of Sporobolus heterolepis, Calamovilfa longifolia, Sorghastrum nutans, Stipa spartea, and Schizachyrium scoparium. Andropogon gerardii clumps are common, but this species does not form a dominant component of the vegetative cover. Like moist shelf communities, bank communities can sometimes occurring as lengthy strips to 50 or more meters, or as shorter patches interspersed with depressional wetlands.

DEPRESSIONAL WETLANDS

Nebraska Sedge Bogs and Meadows. These associated habitats are both dominated by Carex nebrascensis, and typically occur adjacent to streams and marshy areas with a high water table overlain by a layer of sediment and organic material. In the bogs, Glyceria (manna grass) may be present here, along with a limited number of

forbs such as members of the Polygonaceae and *Helenium autumnale* (common sneezeweed). Tributary channels above the water flow of drainage bottoms support the more abundant sedge meadow community, which can also occur along shallow channels where no visible surface water is apparent. Sedge meadows are drier, and more floristically diverse in hydrophytic graminoids, with Nebraska sedge occurring along with *Juncus arcticus* (mountain rush), other sedge species such as *Carex disperma* (softleaf sedge), and bulrushes (*Scirpus* and *Schoenoplectus*). The forbs include hydrophytes such as *Lobelia siphilitica* (great blue lobelia) and *Scutellaria galericulata* (marsh skullcap), both regionally uncommon but locally abundant here, as well as the widespread *Mentha arvensis* (wild mint) and representatives of the Polygonaceae.

Open Seeps. Open seeps underlain by clay lenses occur frequently throughout the drainage system. Groundwater emerges through the soil to create a shallow layer of standing water 1-2 cm deep over saturated clay-rich mud with little to no vegetative cover. Seeps range from ca. 1 m² to 100 m² in area, and are located above stream level along shallow bank margins. The surfaces are dotted with low hummocks, vegetation-covered mounds from 10 to 50 cm in height and width. These habitats encompass an unusual flora composed of species more typical of higher elevations (e.g Eleocharis quinqueflora, Dodecatheon pulchellum and Parnassia palustris; fewflower spikerush, shooting star, and grass of Parnassus, respectively) along with a number of state-rare species, all Midwestern prairie elements, such as Carex crawei (Crawe's sedge) Hypoxis hirsuta (golden star), and Gentianopsis virgata.

Fens. One of the most significant wetland plant communities found in the Black Squirrel drainage is a fen, characterized by a deep peat layer below holding substantial subsurface water (Culver and Lemly 2013). This habitat type is very rare east of the Front Range in Colorado, although diverse types occur commonly in the higher elevations. The Black Squirrel Creek fen, in a subsidiary drainage north of the main channel below a large open seep, is characterized by the abundance of Carex simulata (analogue sedge), with occasional components of Eleocharis acicularis (needle spikerush), Schoenoplectus pungens (threesquare), and Carex nebrascensis. A widespread matrix of C. simulata is characteristic of higher elevation fens and indicative of peatland development (Culver and Lemly 2013). The few forbs present include Helenium autumnale and Parnassia palustris.

Ponds. Throughout the main and subsidiary drainages, a number of small ponds occur. These are generally less than 9.3 m² (ca. 100 ft. ²) in area, with a depth of 0.3 m (1 ft) to over 1.5 m (4 ft), depending on precipitation. The ponds hold abundant amphibians, aquatic insects, crustaceans, and other larger vertebrates such as minnows, along with diverse floating and emergent plant species. Pond associations include an emergent cattail marsh (*Typha*) community, and a floating aquatic community with the carnivorous species *Utricularia minor* (bladderwort) occurring in the standing water of shallow ponds, along with more common aquatics such as *Sagittaria* (arrowhead), *Alisma* (water plantain), *Sparganium* (burreed), and *Potamogeton* (pondweed).

VEGETATION TRANSECTS

Vegetative and Graminoid Cover. Our transects were primarily situated on moist banks and moist shelves, although they also encompassed Nebraska sedge meadows and bogs as well as open seeps. They varied in their amounts of vegetative cover (Table 3; Fig. 4) and the relative percent cover of graminoids, forbs, or litter/bare ground (Table 3; Fig. 4). On average, total basal vegetative cover was slightly over 50%, and graminoids constituted almost 80% relative cover. The dominant grass contributors to cover, Sporobolus heterolepis, Muhlenbergia montana, Schizachyrium scoparium, Sorghastrum nutans, and Calamovilfa longifolia (Table 4), parallel key components documented by Livingston (1952). Common but lesser contributors in both studies included Andropogon gerardii, Hesperostipa spartea, and Panicum virgatum.

The variation among and within the transect quadrats reflects the characteristic local heterogeneity of small-scale vegetation patterns (Tables 3,4). Transect 1 was the most hydric, with abundant subsurface water and a small seep dominated by Juncus arcticus. This transect had the highest overall cover of our 4 transects, composed primarily of Sorghastrum nutans, Sporobolus heterolepis, and Schizachyrium scoparium, together composing ca. 29% of the total, and the rest lesser components of Muhlenbergia, Bouteloua, Calamovilfa, Panicum, and Koeleria. Although adjacent to transect 1, transect 2 showed somewhat different community structure where the microtopography of the terraces contributed to variable soil moisture and textures. This transect was also dominated by Sorghastrum nutans, contributing one quarter of the vegetative cover, with Schizachyrium scoparium contributing an additional 20%. Sporobolus heterolepis contributed considerably

lesser cover here (7%). In general, this transect on a lower terrace showed a greater presence of more xeric elements such as *Muhlenbergia montana* and *Calamovilfa longifolia* than transect 1 above it, and somewhat less overall vegetative cover.

Transect 3, located on a side drainage, had comparatively lower cover than transects 1 and 2, with less than 50% overall; 90% of the cover was contributed by graminoids dominated by *Sporobolus heterolepis, Calamovilfa longifolia* and *Andropogon gerardii*, together accounting for ca. 59% relative cover. Of our four transects, this was the only one in which *A. gerardii* appeared to a notable extent, contributing 12% relative cover.

In transect 4, located in a large subsidiary drainage with a perennial secondary stream, vegetative cover was also less than 50%. This was composed primarily of *Muhlenbergia montana*, *Sporobolus heterolepis*, and *Schizachryrium scoparium* that together comprised 73% of the graminoid cover. Notably, *Hesperostipa spartea* and *Sorghastrum nutans* were more frequent here than in the other transects, although they contributed relatively little to cover. Both species are regionally uncommon to rare (but not considered rare statewide), and when they do occur, typically do so in disparate clumps. This characteristic pattern was apparent in transect 4, and underscores the decoupled metrics of a species contribution to cover, from overall frequency of occurrence of individual species in these communities.

Grass Species Frequency Rankings

Across all the transects, the most common species to encounter were Muhlenbergia montana (frequency of ca. 42% of all quadrats; Table 4), Schizachyrium scoparium (37% frequency), Sorghastrum nutans (36% frequency), Calamovilfa longifolia (35% frequency), Sporobolus heterolepis (34% frequency), and Juncus arcticus (32% frequency). Grass taxa of second tier frequency included Hesperostipa spartea (16% frequency), Bouteloua gracilis (15% frequency), Andropogon gerardii (9% frequency), and Poa pratensis (9% frequency). The highest frequency non-graminoid taxa (data not shown) include a high representation of Midwest prairie elements, notably Glycyrrhiza lepidota, Oligoneuron rigidum, Artemisia ludoviciana, Symphotrichum ericoides, Rosa arkansana, Helenium autumnale, Equisetum arvense, Dalea purpurea, and Symphotrichum laeve. These species are all relatively common components of the regional mixed grass prairie vegetation; only Helenium autumnale is an elevational disjunct more common in the Foothills/Montane zone than on the plains.

Discussion

COMPARISONS OF VEGETATION STRUCTURE: 1940'S AND 2011

Both studies documented considerable variation within and among transects and the overall means cover wide ranges at both time frames. We found greater vegetative cover on our transects (Table 3; on average, around 50%) than what Livingston reported (on average, less than 20%). In 2011, graminoids comprised ca. 80% of this cover, while on the Livingston forest-grassland plots, 85% of this cover was constituted by graminoids, and on the plains plots, 55%. The dominant grass contributors (Table 4) were similar, with *Sporobolus heterolepis* being the top contributor in both time frames. In 2011, *Muhlenbergia montana*, *Schizachyrium*, *Sorghastrum nutans*, and *Calamovilfa longifolia* were also important components;

jointly these species compromised 60% relative cover. In the Livingston study, *Poa pratensis, Bouteloua gracilis,* and *M. montana* contributed most highly on the forest transects in addition to *S. heterolepsis* (55% relative cover) while *S. scoparium, B. gracilis, C. longifolia, and A. gerardii* played key secondary roles on the plains (95% relative cover).

A comparison of the frequency of species occurrence (Table 5) provides a similar picture of a consistent suite of species common to both time frames, albeit with different rankings for individual frequencies. *Muhlenbergia montana*, *Schizachyrium scoparium, Sorghastrum nutans, Calamovilfa longifolia*, and *Sporobolus heterolepis* were the most commonly occurring species in 2011; each occurred in over 30% of the quadrats. On the Livingston plots, *S. heterolepis, Poa pratensis, M. montana* and *Koeleria macrantha* were most frequently encountered in the forest plots, while on the plains, *S. scoparium, B. gracilis, S. heterolepis, C. longifolia*, and *A. gerardii* each occurred in at least 50% of the quadrats.

Allowing for the different locations of the transects and the position of the 2011 study site midway between the Livingston plots, the current community structure of the tallgrass vegetation of Black Squirrel Creek remains comparable to what Livingston described in the early 1940's with respect to the most frequent grass species and those that contributed most strongly to cover. Key species in the 1940's (in particular, Sporobolus heterolepis, Muhlenbergia montana, Schizachyrium scoparium, and Sorghastrum nutans) still remain important in the vegetation now. The greatest differences we found from the earlier studies was in the higher cover apparently now present, and somewhat different frequencies for individual species.

Andropogon gerardii seems to have diminished in both frequency and contribution to cover since the 1940's, although even then it did not appear to be a prevalent vegetation component. Some of these differences may be artifacts of having transects at different locations with different surrounding landscape contexts where precipitation strongly tracks an elevational gradient, or due to limited sampling in a landscape mosaic where topography, edaphic factors, and at least to some extent current and past grazing practices, create small patches of different vegetation or bare ground. Since our plots had a light grazing history and no mowing, in comparison to the Livingston plots that were subjected to grazing and mowing, this may have allowed for greater cover to develop on them.

Although Livingston's characterization of Midwestern grasslands as "true prairie" may be arguable, his analogy of the Black Squirrel Creek vegetation to the Midwestern grasslands was then, and remains now, appropriate with respect to the major grasses present and their relative contributions to cover, as well as to the forb and shrub components, many of which do indeed represent Midwestern elements in the flora as well as the vegetation structure. However, this vegetation is not identical to iconic tallgrass associations of the central prairies and identified elsewhere in Colorado, where *Andropogon gerardii* is the signature species with the highest cover and frequency (Moir 1972; Bock and Bock 1998; Neid et al. 2009). In the Black Squirrel Creek tallgrass associations, *A. gerardii* is not infrequent, but it does not contribute highly to cover. Instead, the most prominent grass here is *Sporobolus heterolepis*, occurring with foothills/montane species such as *Muhlenbergia montana* and xeric or mixed prairie species such as *Calamovilfa longifolia* and

Bouteloua gracilis. Thus, the Black Squirrel Creek tallgrass vegetation may be better described as Sporobolus heterolepis –Muhlenbergia montana grasslands with subsidiary components of Calamovilfa, Schyzachyrium, or Sorghastrum rather than the more classical model of tallgrass communities defined by the dominance of big bluestem. No comparable associations dominated by Sporobolus heterolepis are currently listed by NatureServe (2013), or documented in Colorado.

We concur with the conclusion reached by Livingston (1952) specifically for the Black Squirrel Creek/Black Forest area, and Branson et al. (1965) more broadly for the Colorado mountain front, that adequately high soil moisture is the key factor responsible for the occurrence of any type of mesic tallgrass prairie. Although it must still be speculative these communities are the last relicts of once widespread Pleistocene vegetation, they clearly have endured substantial climatic vicissitudes. In the past century, interannual droughts have occurred regularly, and severe droughts within the context of these comparative studies show little apparent major impact in areas directly supported by ground water resources. Where this type vegetation remains, the Black Squirrel Creek drainage testifies to the capacity of prairie hydrogeomorphic systems to sustain relative stasis in plant communities and their constituent flora through fluctuating temperature and moisture regimes. In conjunction with the communities lining stream banks and drainage swales, the pocket wetlands here are inextricably part of the vegetation mosaic, and, almost certainly, part of its historical longevity. Although small and superficially discontinuous, the imbedded wetlands almost certainly support the metapopulation, corridor, seasonal or annual habitat dynamics for flora and fauna

noted in other prairie systems (Semlitsch and Bodie 1998; Leibowitz 2003) and they provide connectivity of the complex subsurface geology and hydrology that sustain the anomalous vegetation and flora here.

A conclusion of botanical stasis along Black Squirrel Creek is not appropriate, however. Change has occurred since Livingston's studies, perhaps with respect to the change in frequency of certain species, but notably with respect to extent of these grasslands, which now exist as remnants reduced in both number and size since the 1940's. Where widespread mesic grasslands formerly prevailed, housing developments and infrastructure, or altered grasslands with adventive, grazing tolerant, or xeric species sometimes now dominate. In spite of this visible alteration and lessened extent of the tallgrass communities flagged as noteworthy seventy years ago, the upper Black Squirrel Creek drainage system remains a remarkable center of plant diversity where mesic and hydric communities and their biota entwine. This region is still, and increasingly, significant for its numerous rare or uncommon species, its elevational and longitudinal disjuncts, as well as for its unique remaining prairies with clear affiliation to their geographically and temporally distant cousins that are often conspecific even if not with structurally identical.

Literature Cited

- BACHAND, R.R. 2001. The American Prairie: Going Going Gone. A status report on the American Prairie. National Wildlife Federation, Rocky Mountain Natural Resource Center, Boulder, CO.
- BAKER, W. L. AND S. M. GALATOWITCH. 1985. The Boulder Tallgrass Prairies. Boulder County Nature Association Publication No. 3. Boulder, CO.
- BITTINGER, M.W. 1976. The Denver Basin: Its Bedrock Aquifers. Colorado Water Resources Research Institute 31: 1-7
- BOCK, J. H. AND C. E. BOCK. 1998. Tallgrass Prairie: Remnants and Relicts. Great Plains Research: A Journal of Natural and Social Sciences 8: 213-230.
- Branson, F.A., R.F. MILLER, AND I.S. MCQUEEN. 1965. Plant communities and soil moisture relationships near Denver, Colorado. Ecology 46: 311-319.
- CARSEY, K., G. KITTEL, K. DECKER, D.J. COOPER, AND D. CULVER. 2003. Field Guide to the Wetland and Riparian Plant Associations of Colorado. Colorado
- COLORADO NATURAL HERITAGE PROGRAM. 2005. Ecological System Descriptions and Viability Guidelines for Colorado. Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO.
- COLORADO NATURAL HERITAGE PROGRAM. 2012. Tracked Natural Plant Communities.

 Tracked Vascular Plant Species. (Available http://www.cuhp.colostate.edu)

 Accessed June, 2013.
- CULVER, D.R. AND J.M. LEMLY. 2013. Field Guide to Colorado's Wetland Plants. U.S. Environmental Protection Agency Region 8, Denver, CO. Colorado Natural Heritage Program, Warner College of Natural Resources, Colorado State University, Fort Collins, CO.

- DOYLE, G., J. GIONFRIDDO, D. ANDERSON, AND D. CULVER. 2001a. Survey of critical Wetlands and riparian areas in El Paso and Pueblo Counties, Colorado. Colorado Natural Heritage Program, College of Natural Resources, Colorado State University, Fort Collins, CO.
- Doyle, G., Armstrong, J., Gionfriddo, J., Anderson, D., Stevens, J., and R. Schorr. 2001b.

 Survey of critical biological resources, El Paso County, Colorado. Natural

 Heritage Program, College of Natural Resources, Colorado State University, Fort

 Collins, CO.
- HENZ, J., S. TURNER, W. BADINI, AND J. KENNY. 2004. Historical perspectives on

 Colorado drought. Pp. 1-22 *In:* Colorado Drought and Water Supply Assessment.

 Colorado Water Conservation Board. (Available

 http://www.cwcb.state.co.us/technical-resources)
- FREEMAN, C. C. 1998. A flora of Konza Prairie: historical review and contemporary patterns. Pp. 69-80 in Knapp, A.K., Briggs, J.M. Hartnett, D.C. and S.L. Collins. Grassland Dynamics: Longterm ecological research in tallgrass prairie. Oxford University Press, N.Y.
- KELSO, S. 2012. Flora of the Pikes Peak Region. Dept of Biology, Colorado College. Available http://www.coloradocollege.edu/academics/dept/biology/herbarium.
- LAUENROTH, W.K., I.C. BURKE, AND J.A. MORGAN. 2008. The Shortgrass Steppe. Pp. 3-13 in W.K. Lauenroth and I.C. Burke (eds.). Ecology of the Shortgrass Steppe.

 Oxford Univ. Press, N.Y.
- LEIBOWITZ,S.G. 2003. Isolated wetlands and their functions: an ecological perspective. Wetlands 23: 517-531.
- LIVINGSTON, R. B. 1941. The Effect of Altitude on the Composition of Grasslands on the Plains of Central Colorado. Thesis submitted to master's program, Duke University, 1-70.

- LIVINGSTON, R. B. 1947. An Ecological Study of the Black Forest Region and Adjacent Plains. Thesis submitted to doctoral program, Duke University, 1-133.
- LIVINGSTON, R. B. 1949. An Ecological Study of the Black Forest, Colorado. Ecological Monographs 19: 123-144.
- LIVINGSTON, R. B. 1952. Relict true prairie communities in central Colorado. Ecology 33: 72-86.
- MOIR, W. H. 1972. Tall grass prairie in Colorado and its aesthetic value. The Second Midwest Prairie Conference, University of Wisconsin. Ed. J.H. Zimmerman. 40-46.
- MORGAN, M.L. AND P. E. BARKMANN. 2012. Eastonville Quadrangle Geologic Map, El Paso Co. Colorado. Colorado Geological Survey, Dept. of Natural Resources, Denver, CO.
- NATURESERVE. 2013. (Available www.natureserve.org/explorer) Accessed August 2013.
- NEELY, B. (and 16 others). 2006. Central Shortgrass Prairie Ecoregional Assessment and Partnership Initiative. The Nature Conservancy of Colorado and the Shortgrass Prairie Partnership. 124 p.
- NEID, S., J. LEMLY, J. SIEMERS, K. DECKER, AND D. CULVER. 2009. Survey of Critical

 Biological Resources in Boulder County, Colorado (2007-2008). Colorado

 Natural Heritage Program, College of Natural Resources, Colorado State Univ.,

 Fort Collins, CO.
- NICHOLSON, R. A. AND G. K. HULETT. 1969. Remnant grassland vegetation in the Central Great Plains of North America. J. of Ecology 57: 599-612.
- RAMALEY, F. 1919. Xerophytic grasslands at different altitudes in Colorado. Bull. Torrey Bot. Club 46: 37-52.
- ROBBINS, W.W. 1910. Climatology and vegetation in Colorado. Botanical Gazette 49:256-280.

- ROBSON, S. G. 1988. Alluvial and Bedrock Aquifers of the Denver Basin—Eastern

 Colorado's Dual Ground-Water Resource. U.S. Geological Survey Water-Supply

 Paper 2302.
- RONDEAU, R., K. DECKER, J. HANDWERK, J. SIEMERS, L. GRUNAU, AND C. PAGUE. 2011.

 The State of Colorado's Biodiversity. Prepared for The Nature Conservancy by the Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO.
- SAMSON, F. AND F. KNOPF. 1994. Prairie conservation in North America. Bioscience 44: 418-421.
- SEMLITSCH, R.D. AND J.R. BODIE. 1998. Are small isolated wetlands expendable?

 Conservation Biology 12: 1129-1133.
- SHADDLE, P. H. 1939. An Ecological Study of the Vegetation of the Black Forest of Colorado. Thesis submitted to master's program at University of Colorado, 1-29.
- SHANTZ, H.L. 1923. The natural vegetation of the Great Plains Region. Annals of the Association of American Geographers 13: 81-107.
- TOPPER, R. 2008. Upper Black Squirrel Creek Basin Aquifer Recharge and Storage Evaluation. Colorado Geological Survey, Denver, CO.
- UNITED STATES CENSUS BUREAU. 2010. Demographic Statistics on Black Forest-Peyton,

 CO. American FactFinder, U.S. Census.
- UNITED STATES DEPT. OF AGRICULTURE, NATURAL RESOURCE CONSERVATION SERVICE.

 PLANTS Database (Available http://plants.usda.gov). Accessed June 2013.
- VESTAL, A.G. 1914. Prairie vegetation of a mountain front area in Colorado. Botanical Gazette 58: 377-400.
- VESTAL, A. G. 1917. Foothills vegetation in the Colorado Front Range. Botanical Gazette 64: 353-385.
- VESTAL, A.G. 1919. Phytogeography of the eastern mountain front in Colorado I.

 Physical geography and distribution of vegetation. Botanical Gazette 68: 153-193.

72-86.

- WEAVER, J. E. 1954. North American Prairie. Johnsen Publishing Company. Lincoln, NE.
- WEAVER, J.E. AND F.W. ALBERTSON. 1956. Grasslands of the Great Plains. Johnsen Publishing Company. Lincoln, NE.
- WEAVER, J. E. AND T. J. FITZPATRICK. 1934. The Prairie. Ecological Monographs 4: 109-295.
- WEBER, W. AND R.C. WITTMANN. 2012. Colorado Flora: Eastern Slope. Univ. Press of Colorado. Boulder, CO.
- WESTERN REGIONAL CLIMATE CENTER. Division of Atmospheric Science, Desert Research
 Institute and National Oceanic and Atmospheric Administration. Regional
 Climate Center. Historical Data for Eastonville, CO. (Available:
 http://www.wrcc.dri.edu). Accessed June 2013.
- WILLIAMS, T.E. AND A.E. HOLCH. 1946. Ecology of the Black Forest of Colorado. Ecology 27:139-149.

Appendix 1. Annotated Checklist of the Vascular Flora Upper Black Squirrel Creek

Drainage, El Paso Co., Colorado

Species list for vascular flora occurring in mesic and hydric communities of the upper Black Squirrel Creek drainage from 7000 6500 feet in elevation. The list includes some upland species occurring sporadically in the drainage system and gravel stream channels, but which are more typically found in the surrounding xeric mixed grass and shortgrass matrix in the surrounding uplands. Nomenclature (including family designations) and common names follow the National Resource Conservation Service database (www. Plants.USDA.gov: accessed 8/2013) except as noted. Nomenclature commonly used in Colorado (e.g. Weber and Wittmann, 2012) is given in parentheses. Voucher specimens are at COCO. Noteworthy species are coded as follows: FM Species generally occurring in Foothills/Montane zone 2000-3200 m (ca. 7000-10,500 ft.) Distributions follow Weber and Wittman 2012; Culver and Lemly 2013; Kelso, 2012); occurrence on the prairie is restricted.

MWP Species prominent in Midwest prairie as explicitly noted by Shantz (1923), Weaver and Fitzpatrick (1934: Tables 15; 16), Weaver (1954), and Livingston (1952). Earlier nomenclature used in these publications cross-referenced with NRCS Plants Database synonyms.

R Rare species listed as of conservation concern and tracked by the Colorado Natural Heritage Program (2012): State Conservation rankings are as follows: S1: Critically Imperiled, S2: Imperiled, S3: Vulnerable

U Locally or regionally uncommon or local endemic (Kelso 2012; Weber and Wittmann 2012)

X Xeric element of uplands extending into mesic vegetation

L indicates a species noted in the Livingston studies; name in brackets indicates a species not recollected but observed in our study site. Species not observed are so noted. Unless otherwise noted, these are locally common components of the plains flora, typically in xeric areas.

Species with no specific coding are locally widespread components of regional vegetation.

Amaranthaceae

Froehlichia gracilis (Hook.)Moq. (slender snakecotton) X

Alismataceae

Sagittaria cuneata Sheldon (arumleaf arrowhead) Sagittaria latifolia Willd. (broadleaf arrowhead) Alisma triviale Pursh (northern water plaintain)

Anacardiaceae

Toxicodendron rydbergii (Small)Greene (poison ivy) FM, MWP

Apiaceae

Cicuta douglasii (D.C.) J.M. Coulter & Rose (western water hemlock) MWP Berula erecta (Hudson) Coville (cutleaf water parsnip)

Apocynaceae

Apocynum cannabinum L. (Indianhemp)

Asclepiadaceae

Asclepias hallii A. Gray (Hall's milkweed) R (S3), FM Asclepias speciosa Torr. (showy milkweed)

Asteraceae

Achillea millefolium L. (common yarrow) L

Agoseris glauca (Pursh) Raf. (pale agoseris)

[Ambrosia artemisiifolia L. (annual ragweed) L]

Antennaria microphylla Rydb. (littleleaf pussytoes) X; L as A. parviflora

[Artemisia campestris L. ssp. caudata (Michx.) Hall & Clements (field sagewort) L]

Artemisia frigida Willd. (prairie sagewort) X.L

Artemisia ludoviciana Nutt. (white sagebrush) MWP, L (as A.gnaphalodes)

Bahia dissecta (A.Gray)Britton (ragleaf bahia) X

Bidens tenuisecta A.Gray (slimlobe beggarticks)

Carduus nutans L. (nodding plumeless thistle)

Noxious weed of limited occurrence on the study site; few individuals.

Cirsium arvense(L.)Scop. [Breea arvense] (Canada thistle)

Noxious weed of limited occurrence on the study site

Cirsium flodmanii (Rydb.)Arthur: (Flodman's thistle)

Conyza canadensis (L.) Cronquist (Canadian horseweed) L (as Leptilon canadensis)

Cosmos parviflorus ((Jacq.) (southwestern cosmos) U

Southwestern species known primarily as regional endemic to the Black Forest region; locally common along Black Squirrel Creek on gravelly stream channels.

Erigeron bellidiastrum Nutt. (western daisy fleabane)

Erigeron compositus Pursh (cutleaf daisy) FM

Erigeron divergens Torr. & A. Gray (spreading fleabane)

Erigeron flagellaris A. Gray (trailing fleabane)

Erigeron glabellus Nutt. (streamside fleabane)

Erigeron lonchophyllus Hook. [Trimorpha lonchophylla] FM

Erigeron subtrinervis Rydb. ex Porter & Britton (threenerve fleabane)

Erigeron vetensis Rydb. (early bluetop fleabane) FM

Grindelia squarrosa Dunal (curlycup gumweed)

Helenium autumnale L. (common sneezeweed) FM, MWP, L

Helianthus annuus L. (common sunflower)

Helianthus nuttallii Torr. & A. Gray (Nuttall's sunflower)

Helianthus petiolaris Nutt. (prairie sunflower) L

Helianthus pumilus Nutt. (little sunflower)

Helianthus pauciflorus Nutt. ssp. (Rydb.)O. Spring. & E. Schilling [Helianthus rigidus] (stiff sunflower) MWP, L

Heterotheca canescens (D.C.) Shinners (hoary false goldenaster) L (as Chrysopsis villosa)

Lactuca tatarica (L.)Meyer (blue lettuce)

Liatris ligulistylis (A. Nelson) K. Schum. (Rocky Mountain blazingstar) R (S1/S2), MWP, L Common in seeps and tallgrass communities on the study site.

Liatris punctata Hook. (dotted blazingstar) MWP, L

Lygodesmia juncea (Pursh)D. Don ex Hook. (rush skeletonplant)

Oligoneuron album (Nutt.)G.L. Nesom [Unamia alba] (prairie goldenrod) R (S2/S3), MWP, L

Oligoneuron rigidum (L.)Small (stiff goldenrod) MWP, L(as Solidago rigidum)

[Packera neomexicana (A. Gray) W.A. Weber & Á. Löve var. mutabilis (Greene) W.A. Weber & Á. Löve (New Mexico groundsel) L (as Senecio mutabilis)]

Packera pseudaurea (Rydb.) W.A. Weber & A. Löve (falsegold groundsel) FM

Packera tridenticulata (Rydb.) W.A. Weber & A. Löve (threetooth ragwort)

Pseudognaphalium canescens (D.C.) W.A. Weber (Wright's cudweed)

Ratibida columnifera (Nutt.) Woot. & Standl. (upright prairie coneflower)

Rudbeckia hirta L. (black eyed Susan) FM, MWP, L

[Salsola tragus L. (prickly Russian thistle) L (as Salsola pestifer)]

Senecio spartioides Torr. & A. Gray (broomleaf ragwort)

Solidago gigantea Aiton (giant goldenrod)

Solidago missouriensis Nutt. (Missouri goldenrod) MWP, L

Solidago nana Nutt. (baby goldenrod) FM

Solidago nemoralis Aiton (gray goldenrod) L

Solidago velutina D.C. (three-nerve goldenrod)

Symphotrichum ericoides (L.)A. Löve and D. Löve (white heath aster) MWP, L (as Aster multiflorus)

Symphotrichum laeve (L.) A. Löve and D. Löve (smooth aster) FM, MWP, L (as Aster geyeri)

Symphotrichum lanceolatum (Willd.) G.L. Nesom (white panicle aster)

[T. megapotamicum (Spreng.)Kuntze (Hopi tea greenthread) L as Thelesperma gracile]

Tragopogon dubius Scop. (yellow salsify)

Tripleurospermum perforatum (Merat)M. Lainz (scentless false marigold) FM

Tetraneuris acaulis (Pursh)Greene (stemless four-nerve daisy)

Boraginaceae

 $Cryptantha\ cinerea\ (Greene)$ Cronquist ($Oreocarya\ suffruticosa$)(James' cryptantha) ${f X}$

[Lappula occidentalis (S. Watson)Greene (flatspine stickweed) L]

Mertensia lanceolata (Pursh)D.C. (prairie bluebells)

Onosmodium bejariense DC var. occidentale (Mack.)B.L. Turner (Onosmodium molle ssp. occidentale) (softhair marbleseed)

Plagiobothrys scouleri (Hook. & Arnott)I. M. Johnst. (Scouler's popcorn flower)

Brassicaceae

Arabis holboelii Hornem. var. retrofracta Rydb. (Boechera retrofracta])second rockcress) FM

Barbarea orthoceras Ledeb. (American yellowrocket)

Draba nemorosa L. (woodland draba) FM

Sisymbrium loeselii L. (small tumbleweed mustard)

Cactaceae

Pediocactus simpsonii (Engelmann) Britton & Rose (mountain ball cactus) FM

Opuntia polyacantha Haworth (plains prickly pear) L

Campanulaceae

Campanula rotundifolia L. (bluebell bellflower) FM

Lobelia siphilitica L. (great blue lobelia) U, MWP, L

Common on the study site; regionally uncommon species

Caprifoliaceae

Symphoricarpos occidentalis Hook. (western snowberry)

Caryophyllaceae

Arenaria hookeri Nutt. [Eremogone hookeri] (Hooker's sandwort)

Stellaria longifolia Muhl. ex. Willd. (longleaf starwort) FM

Paronychia jamesii Torr. & A. Gray (James' nailwort) X

[Silene scouleri Hook. (simple campion) L]

Species common in the foothills/montane zone but not currently known from this area

Chenopodiaceae

Chenopodium graveololens Willd. [Teloxis graveolens] (fetid goosefoot)

Chenopodium leptophyllum (Moq.)Nuttall (narrowleaf goosefoot), L

Cycloloma atriplicifolium (Spreng.) J.M. Coulter (winged pigweed)

Suaeda calceoliformis (Hook.) Moq. [Suaeda depressa] (Pursh seepweed)

Clusiaceae

Hypericum scouleri Hook. (Scouler's St. Johnswort) [Hypericaceae: Hypericum formosum] FM

Commelinaceae

Tradescantia occidentalis (Britton) Smythe (prairie spiderwort)

Crassulaceae

Sedum lanceolatum Torr. (spearleaf stonecrop)

Cyperaceae

Carex aurea Nutt. (golden sedge) FM, U, L

Carex brevior (Dewey)Mack. (shortbeak sedge) L

Carex crawei (Dewey) (Crawe's sedge) R (S1), FM

Carex disperma Dewey (softleaf sedge) FM

Carex douglasii Boot (Douglas' sedge)

Carex echinata Murray (star sedge) [Carex angustior] FM, U

[Carex filifolia Nutt. (threadleaf sedge) L]

[Carex heliophila Mack. = C. inops L.H. Bailey ssp. heliophila (Mack.)Crins (sunsedge) L]

[*Carex oreocharis T. Holm (grassyslope sedge) L- not observed this study]

Carex pellita Muhl.: wooly sedge [Carex lanuginosa]

Carex nebrascensis Dewey (Nebraska sedge) L

[*Carex hallii Olney [C. parryana Dewey ssp. hallii [specimen coll. R.B. Livingston 1430:

@COCO;] (deer sedge)]

[*Carex praegracilis W.Boott) L-not observed this study]

Carex simulata Mack. (analogue sedge)

Carex xerantica L.H. Bailey (whitescale sedge)

Eleocharis acicularis (L.) Roemer & Schultes (needle spikerush)

Eleocharis obtusata (Willd.)Schult. (blunt spikerush)

[Eleocharis palustris (L.)Roem. & Schult. (common spikerush) L]

Eleocharis quinqueflora (F.X.)HartmannO. Schwartz (fewflower spikerush) FM

Cyperus schweinitzii Torr. (Schweinitz' flatsedge) [Mariscus schweinitzii]

Schoenoplectus acutus (Muhl.) A. Löve & D. Löve (hardstem bulrush)

[Scirpus acutus]

Schoenoplectus pungens (Vahl)Palla (common threesquare)

Schoenoplectus tabernaemontani (C.C.Gmelin)Palla (softstem bulrush) [Scirpus lacustris)

Scirpus microcarpus Presl. & C. Presl (panicled bulrush)

Equisetaceae

Equisetum arvense L.: field horsetail (field horsetail) MWP, L

Equisetum laevigata A.Brown (smooth horsetail) MWP

Euphorbiaceae

[Chamaesyce glyptosperma (Engelm.) Small (ribseed sandmat) L (as Euphorbia glyptosperma)] Euphorbia brachycera Engelm. (horned spurge) X

Fabaceae

Amorpha fruticosa L. var. angustifolia Pursh (false indigo bush)

Astragalus canadensis L. (Canadian milkvetch) U, MWP

Dalea candida Michx. ex Willd. (white prairieclover) MWP

Dalea purpurea Vent. (purple prairieclover) MWP, L (as Petalostemon purpureus)

Gleditsia triacanthos L. (honeylocust)

A single tree occurring on edge of study site near old ranch buildings.

Glycyrrhiza lepidota Pursh (American licorice) MWP, L

Lathyrus polymorphus Nutt. (manystem pea)

Lupinus pusillus Pursh (rusty lupine)

[Melilotus officinalis (L.)Lam. (sweetclover) L (as M. alba)]

Oxytropis multiceps Nutt. (Nuttall's oxytrope)

Robinia neomexicana A. Gray (New Mexico locust)

Occasional trees occurring on edges of study site near old ranch buildings.

[Thermopsis montana Nutt. (mountain goldenbanner) L]

[Trifolium pratense L. (red clover) L]

[Trifolium repens L. (white clover) L]

[Vicia americana Muhl. ex Willd. (American vetch) L]

Gentianaceae

[Gentiana affinis Griseb. (pleated gentian) L]

Gentianella amarella (L.)Borner ssp. acuta (Michx.) Gillette (autumn dwarf gentian) FM, L [Gentianella strictiflora]. As noted by Weber and Wittmann (2012), the densely white flowered form with a stiffly erect inflorescence is very distinctive in this region in the montane zone and in higher elevations on the plains; it is easily recognized as separate from the amarella/acuta form. The form occurring in the Black Squirrel Creek region is the "strictiflora" form, rather than the purple flowered, smaller "acuta" form.

Gentianopsis virgata (Raf.) Holub [lesser fringed gentian] (Gentianopsis procera ssp. crinita; G. crinita) R (CHNP-Not rated), MWP

This species, recently confirmed by Flora of North America experts in the genus, is only known to occur in the upper Black Squirrel Creek drainage. Although not yet listed by Colorado Natural Heritage Program, its state rarity and disjunct connection to the Midwest prairie flora is notable.

Geraniaceae

Geranium atropurpureum A.Heller(western purple crane's bill). [G. caespitosum ssp. atropurpureum] FM

Grossulariaceae

Ribes aureum Pursh (golden currant)

Haloragaceae

Myriophyllum sibiricum Kom. (shortspike watermilfoil)

Hippuridaceae

Hippuris vulgaris L. (common mare's tail) FM

Hypoxidaceae

Hypoxis hirsuta (L.)Coville (common goldenstar) R (S1), MWP

Iridaceae

Iris missouriensis Nutt. (wild iris)

Sisyrinchium montanum Greene (strict blue eyed grass) FM, L (as S. angustifolium)

.Juncaceae

Juncus alpinoarticulatus Chaix (northern green rush)

Juncus arcticus Willd. ssp. littoralis (Willd.) Hultén [J. arcticus ssp. ater] (mountain rush), L (as J. balticus)

Juncus brachycephalus (Engelm.)Buchenar (smallhead rush) R(S1), MWP, L

*Juncus brevicaudatus (Engelm.)Fernald: narrowpanicle rush R (S1); MWP

A specimen of this species under the name J. brachycephalus (Penland 4935; COCO; OSH) was collected by in the Black Squirrel Creek drainage) and later verified by N. Harriman and F. Herrmann (Herrmann, 1975) as the very similar J. brevicaudatus. We have tentatively identified one of our collections as this species. It grows intermixed with J. brachycephalus

Juncus bufonius L (toad rush)

Juncus dudleyi Wieg. (Dudley's rush)

Juncus interior Wieg. (inland rush)

Juncus longistylis Torr. (longstyle rush) L

Juncus marginatus Rostk. (grassleaf rush)

Juncus nodosus L.: (knotted rush)

Juncus saximontanus A. Nelson (Rocky Mountain rush)

Juncus torreyi Coville (Torrey's rush) L

Juncaginaceae

Triglochin maritima L. (seaside arrowgrass) L Triglochin palustris L. (marsh arrowgrass) FM

Lamiaceae

Lycopus americanus Muhl. ex Bartram (American water horehound) MWP

Mentha arvensis L. (wild mint)

Monarda fistulosa L. (wild bergamot) MWP

Prunella vulgaris L. (common selfheal) L

Scutellaria galericulata L. (marsh skullcap) U

Stachys palustris L. (marsh hedgenettle)

Lemnaceae

Lemna minor L. (common duckweed)

Lentibulariaceae

Utricularia minor L. R(S2), FM

Liliaceae

Allium cernuum Roth (nodding onion) [Alliaceae] L Calochortus gunnisonnii S. Watson (Gunnison's sego lily) Lilium philadelphicum L. (wood lily) R(S1), FM, MWP

Lythraceae

Lythrum salicaria L. (purple loosestrife)

This A list noxious weed has invaded one of the subsidiary drainages of Black Squirrel Creek, and is the only significant weed issue in the drainage. It currently is not a monoculture, and many of the rare and unusual species are intermixed with it, making chemical controls problematic.

Malvaceae

Sidalcea neomexicana A. Gray (saltspring checkerbloom) U, FM

Najadaceae

Najas guadalupensis (Spreng.) Magnus (spring water nymph)

Nyctaginaceae

Abronia fragrans Nuttall ex Hook. (snowball sand verbena) X

Mirabilis linearis (Pursh)Heimerl (narrowleaf four o'clock) [Oxybaphus lanceolatus; Oxybaphus linearis]

Oleaceae

Forestiera pubescens Nuttall (stretchberry) [Forestiera neomexicana]

Onagraceae

Calylophus serrulatus (Nuttall) P. H. Raven (yellow sundrops)

Epilobium ciliatum Raf. ssp. glandulosum (Lehm.) Hoch & P. H. Raven (fringed willowherb)

Epilobium leptophyllum Raf. (bog willowherb)

Gaura coccinea Nuttall ex Pursh (scarlet beeblossom)

Gayophytum diffusum Torr. & A. Gray (spreading groundsmoke) FM

Oenothera coronopifolia Torr. & A. Gray (crownleaf evening primrose)

Oenothera flava (A. Nelson)Garrett (yellow evening primrose) U

Oenothera nuttallii Sweet (Nuttall's evening primrose)

Oenothera villosa Thun. (hairy evening primrose) [Oenothera strigosa] L (as Anogra strigosa)

Oxalidaceae

Oxalis dillenii Jacq. (slender yellow wood sorrel)

Orchidaceae

Platanthera aquilonis Sheviak (northern green orchid)

(Limnorchis hyperborea, Platanthera hyperborea) FM

Spiranthes romanzoffiana Cham. (hooded lady's tresses) FM, U

Plantaginaceae (s. str.)

Plantago elongata Pursh (prairie plantain)

Plantago patagonica Jacq. (woolly plantain) L (as P. purshii)

Poaceae

Achnatherum nelsonii (Scribn.)Barkworth (Columbia needlegrass)

Agropyron cristatum (L.)Gaertn. (crested wheatgrass) MWP

Agrostis gigantea Roth. (redtop) L (as A. alba)

Agrostis scabra Willd. (rough bentgrass) FM, L (as A. hiemalis)

Alopecurus aequalis Sobol (shortawn foxtail) FM

Andropogon gerardii Vitman (big bluestem) U, MWP, L (as A. furcatus)

Generally occurring on the study site in dispersed patches; common but sporadic across plands and mesic drainages.

[Andropogon hallii Hack. L]

Occurs sporadically in the area on deep sandy soils, but not present in our site.

Beckmannia syzigachne (Steud.)Fernald (American sloughgrass)

Bouteloua curtipendula (Michx.)Torr.: (sideoats grama) MWP

Bouteloua gracilis (Willd. ex Kunth) Lag. ex. Griffiths (blue grama) [Chondrosum gracile] L

Bouteloua hirsuta Lag. (hairy grama) [Chondrosum hirsutum]

Bromus carinatus Hook. & Arnott (California brome) [Ceratochloa carinata]

Bromus inermis Leyss.: smooth brome [Bromopsis inermis]

Calamagrostis stricta (Timm.)Koeler: slimstem reedgrass FM

Calamovilfa longifolia (Hook.)Scribn.: prairie sandreed MWP, L

Hordeum jubatum L.: foxtail barley [Critesion jubatum] L

Hordeum brachyantherum Nevski (meadow barley) [Critesion brachyantherum]

Distichlis spicata (L.) Greene (saltgrass) L

Occurring with Sporobolus airoides along shallow alkaline drainages, lower portion of study site only and increasingly common to the south.

Elymus canadensis L. (Canada wildrye) MWP

Elymus lanceolatus (Scribner & J.G. Sm.)Gould (thickspike wheatgrass)

Elymus trachycaulus (Link)Gould ex Shinners (slender wheatgrass) L (as Agropyron pauciflorum)

Glyceria striata (Lam.)Hitchc. (fowl mannagrass) FM

Hesperostipa comata (Trin. & Rupr.)Barkworth (needle and threadgrass [Stipa comata] X, L

Hesperostipa spartea (Trin.)Barkworth (porcupinegrass) [Stipa spartea] U, MWP, L

[Hordeum jubatum L. (foxtail barley) L]

Koeleria macrantha (Ledeb.) Schult. (prairie junegrass) MWP, L (as K. cristata)

Muhlenbergia asperifolia (Nees & Meyer) Parodi (scratchgrass) L

Muhlenbergia minutissima (Steud.)Swallen (annual muhly)

Muhlenbergia montana (Nutt.)Hitchc. (mountain muhly) FM

Muhlenbergia richardsonis (Trin.)Rydb. L (as M. squarrosa)

Nassella viridula (Trin.)Barkworth (green needlegrass) (Stipa viridula)

Panicum virgatum L. (switchgrass) MWP, L

Pascopyrum smithii (Rydb.)Barkworth & D.R. Dewey (western wheatgrass) [Agropyron smithii, Elytrigia smithii] L

Phleum pratense L. (timothy) L

Poa annua L. (annual bluegrass)

Poa fendleriana (Steud.) Vasey (muttongrass) FM, L

Poa leptocoma Trinius (marsh bluestem) FM

Poa nemoralis L. ssp. interior (Rydb.) W.A. Weber (inland bluegrass) FM

Poa pratensis L. (Kentucky bluegrass) MWP, L

Schizachyrium scoparium (Michx.)Nash (little bluestem) MWP, L (as Andropogon scoparius)

Sorghastrum nutans (L.) Nash (Indiangrass) U, MWP, L

Spartina pectinata Link: (prairie cordgrass) L]

Sporobolus airoides (Torr.)Torr. (alkali sacaton)

[Sporobolus cryptandrus (Torrey) A. Gray (sand dropseed) L

Sporobolus heterolepis (A.Gray)A. Gray (prairie dropseed) U, MWP, L

Thinopyrum ponticum (Podp.)Z.W. Liu & R.C. Wang (tall wheatgrass) [Elytrigia elongata]

Polemoniaceae

Collomia linearis Nutt. (tiny trumpet)

Polygonaceae

Aliciella pinnatifida (Nutt.)J.M. Porter (sticky gilia) L (as Gilia pinnatifida)

Eriogonum alatum Torr. (winged buckwheat) [Pterogonum alatum] L

Eriogonum annuum Nutt. (annual buckwheat) L

Polygonum amphibium L. (water knotweed) [Persicaria amphibia] MWP

Polygonum convolvulus L. (black bindweed) [Fallopia convolvulus]

Polygonum douglasii Greene (Douglas' knotweed)

Polygonum pensylvanicum L. (Pennsylvania knotweed)

Polygonum lapathifolium L. (curlytop knotweed) [Persicaria lapathifolia]

Polygonum punctatum Elliott (dotted knotweed) (Persicaria punctata)

Rumex crispus L. (curly dock)

Rumex acetocella L. (common sheep sorrel) [Acetocella vulgaris]

Portulacaceae

Phemeranthus calycinus (Engelm.)Kiger (largeflower fameflower)
[Talinum parviflorum] L

Potamogetonaceae

Potamogeton natans L. (floating pondweed)

Potamogeton foliosus Raf. (leafy pondweed)

Primulaceae

Dodecatheon pulchellum (Raf.)Merr. (darkthroat shooting star) FM Lysimachia ciliata L. (fringed loosestrife) U, MWP

Ranunculaceae

Anemone canadensis L. (Canadian anemone) FM, MWP Anemone cylindrica A. Gray (candle anemone) FM, MWP Myosurus minimus L. (tiny mousetail)
Ranunculus cardiophyllus Hook. (heartleaf buttercup) FM Ranunculus trichophyllus Chaix (threadleaf crowfoot)

Rosaceae

Agrimonia striata Michx. (roadside agrimony) U, FM

Fragaria virginiana Miller (Virginia strawberry) MWP

Geum aleppicum Jacq. (yellow avens) FM

Potentilla arguta Pursh (tall cinquefoil) [Drymocallis arguta] FM

Potentilla hippiana Lehm. (woolly cinquefoil)

Potentilla norvegica L. (Norwegian cinquefoil)

Potentilla plattensis Nutt. (Platte River cinquefoil)

Prunus pumila L. var. besseyi (L.H. Bailey) Gleason (western sandcherry)[Prunus bessey;: Cerasus pumila]

Prunus virginiana L. (chokecherry) [Padus virginiana] FM

Rosa arkansana Porter (prairie rose) MWP

Rubiaceae

Galium boreale L. (northern bedstraw) [Galium septentrionale] FM Galium trifidum L. (threepetal bedstraw) MF

Salicaceae

Populus X acuminata Rydb. (lanceleaf cottonwood)
Populus angustifolia James (narrowleaf cottonwood) FM
Populus deltoides Bartram ex Marsh. (plains cottonwood)

Salix amygdaloides Anderss. (peachleaf willow)

Salix exigua Nutt.: (narrowleaf willow)

Salix irrorata Anderss. (deweystem willow) FM

Salix ligulifolia (C.R. Ball) C.R. Ball (strapleaf willow)

Santalaceae

Comandra umbellata (L.) Nutt. (bastard toadflax) X, L (as C. pallida)

Saxifragaceae

Parnassia palustris L. var. parviflora (DC)Boivin (smallflower grass of Parnassus) [Parnassia parviflora] FM

Selaginellaceae

Selaginella densa Rydb. (lesser spikemoss) FM

Scrophulariaceae (s. lat.)

Mimulus glabratus Kunth (roundleaf monkeyflower)

Nuttallanthus canadensis (L.)D.A. Sutton (Canada toadflax) [Linaria canadensis] U

Orthocarpus luteus Nutt. (yellow owiclover) L

Pedicularis canadensis L. (Canadian lousewort) FM

[Penstemon angustifolius Nutt. ex. Pursh (broadbeard beardtongue) L]

Penstemon auriberbis Pennell (Colorado beardtongue)X

This species is extremely common south in the Arkansas River drainage but occurs only in isolated occurrences in the Colorado Springs region.

Penstemon glaber Pursh (sawsepal pentstemon) FM

Penstemon gracilis Nutt. (lilac penstemon)U, FM, MWP

Species uncommon in the foothills and pine savannah regions of the Black Forest area; Found once on our study site.

Penstemon unilateralis A. Gray (one-sided penstemon) [Penstemon virgatus spp. asa-grayi]

Veronica anagallis-aquatica L. (water speedwell) [Veronica catenata]

Veronica peregrina L. (neckweed) L

Veronica serpyllifolia L. ssp. humifusa (Dicks.)Syme (thymeleaf speedwell) FM

Solanaceae

Physalis virginiana Mill.V(irginia groundcherry)

Sparganiaceae

Sparganium angustifolium Michx. (narrowleaf bur-reed) FM

Typhaceae

Typha latifolia L. (broadleaf cattail)

Valerianaceae

Valeriana edulis Nutt. ex Torr. & Gray (tobacco root) FM

Violaceae

Viola sororia Willd. (common blue violet) FM, MWP [V. papilionacea] L (as V. papilionacea)