photo by D.S. Wovcha MN DNR

Weaver Dunes Scientific and Natural Area, Wabasha County, MN

General Description

Upland Prairie (UP) communities are herbaceous plant communities dominated by graminoid species, with a species-rich forb component that can approach codominance with the graminoids. The tall grass big bluestem *(Andropogon gerardii)* and the mid-height grasses prairie dropseed *(Sporobolus heterolepis)* and little bluestem *(Schizachyrium scoparium)* are the most important graminoids. Indian grass *(Sorghastrum nutans)*, a tall grass, and porcupine grass *(Stipa spartea)* and side-oats grama *(Bouteloua curtipendula)*, mid-height grasses, are the most important associated graminoids. Sedges *(Carex* spp.), another graminoid group, are sometimes common in UP communities but are typically a minor component. The most common woody species are low, semi-shrubs; leadplant *(Amorpha canescens)* and prairie rose *(Rosa arkansana)* are the most common and widespread of these. Taller typical shrubs such as American hazelnut (*Corylus americana*) and smooth sumac (*Rhus glabra*) occur primarily in the savanna communities that are part of the UP System. The main vegetation layer in prairie communities is usually less than 40in (1m) high, although some forbs and the flowering stalks of the tall grasses elongate above this height as the season progresses. In savannas there is usually also a patchy shrub layer up to 6ft (2m) tall and a patchy tree canopy up to 33ft (10m) tall.

The herbaceous dominance of prairie communities in Minnesota is closely tied to the frequent occurrence of fire. In circumstances where fire frequency or intensity is reduced, more fire-tolerant shrubs and trees can persist, forming brush-prairie and savanna communities that are considered members of the UP System. Savannas typically have scattered trees, sometimes clumps of trees, growing in a prairie matrix. Bur oak is the most common and widespread tree, but northern pin oak and, in the extreme southeastern part of the state, black oak are also typical. Small, open-grown, often gnarled bur oaks are most distinctive. Jack pine is occasionally important on deep sand substrates. Brush-prairies are characterized by an abundance of taller shrubs, oak “grubs” and sprouts, and quaking aspen suckers that alter the aspect from that of grassland to shrubland or brushland even though the herbaceous prairie plants are still a major component of the vegetation. Savanna and brush-prairie communities intergrade. In the absence of fire, they rapidly succeed to woodland, brush-prairie even more so than

savanna. Today, most brush-prairies occur in the Tallgrass Aspen Parklands Province of northwestern Minnesota.

Historically, UP communities dominated the landscape in the southern end of the Eastern Broadleaf Forest (EBF) Province, in the Oak Savanna Subsection of the MIM and the Rochester Plateau Subsection of the PPL. In the deeply dissected Blufflands Subsection of the PPL, UP communities were confined to steep south- and west-facing slopes and to occasional large deposits of sand in valleys. UP communities also dominated the Anoka Sand Plain Subsection of the MIM. In the Big Woods and Hardwood Hills subsections of the MIM, UP communities were mostly confined to the western edge adjacent to the continuous prairie of the Prairie Parkland (PPA) Province. However, at several places in the north half of the Hardwood Hills Subsection, UP communities extended more deeply into the province. Very little native upland prairie of any kind remains today; conversion to cropland, succession to woodland and forest, and urban and suburban development have destroyed more than 99 percent of the presettlement upland prairie and savanna communities in the EBF Province.

Natural History

Frequent fire (with return intervals of less than 10 years) is critical for the occurrence of upland prairies in Minnesota. Fire frequency is responsive to climate and to landscape properties. The most important factors are the frequency and intensity of drying events that create flammable conditions, and the absence of topographic and water features that impede the spread of fire. Average annual precipitation declines from east to west across the state, with corresponding increases in length of time between rains and frequency of drought events. Even the driest parts of western Minnesota, however, support tree growth. The principal contribution of drier climate in Minnesota to prairie establishment is to increase the likelihood of ignition and spread of fire. Drier conditions also slow the growth of shrubs and trees, increasing the time it takes for them to become large enough to resist being killed by fire or to produce seeds before being killed. Landscape properties that affect the spread of fire also have a large influence on fire return intervals. For a given ignition rate, the larger the proportion of a landscape that burns in an average fire, the shorter the fire return interval in that landscape. Rivers and lakes interfere with the spread of fires, as does steep topography. Conversely, large expanses of gentle relief without water barriers tend to burn in extensive patches. Vegetation itself may facilitate or impede the spread of fire: deciduous forests are much more resistant to fire than grasslands, which burn readily.

The distribution of upland prairies in the EBF Province before Euro-American settlement reflected these climatic and landscape influences. UP communities predominated in large, continuous areas of subdued relief; in most of the province, hilly topography and abundant lakes and rivers—combined with a slightly cooler and wetter climate than that in the PPA Province—impeded the spread of fire enough to allow woodlands and forests to dominate. The most extensive areas of open prairie communities in the EBF Province were on the level to gently rolling and well-drained landscape of the Oak Savanna Subsection of the MIM. Oak savanna communities dominated the west side of the subsection on a band of end moraines of the Des Moines Lobe that created sufficient relief to favor savannas over open prairies. Similarly, oak savanna was the predominant UP community in the Rochester Plateau Subsection of the PPL east of the prairies of the Oak Savanna Subsection. The Rochester Plateau Subsection is somewhat dissected by deep valleys of streams draining to the Mississippi River, and expanses of open prairie communities were confined to the largest remnants of the plateau between valleys. Smaller prairies occurred on very steep, south- and west-facing slopes on the sides of the valleys; these occurred also in the more deeply dissected Blufflands Subsection of the PPL where none of the original plateau surface remains. The Anoka Sand Plain Subsection of the MIM was the other large non-forested region in the EBF Province. Droughty soils formed in outwash and lacustrine sands, together with very low-relief

topography, make this subsection an environment favorable for fire. However, the predominant UP communities here are savannas, probably reflecting this subsection's isolation by surrounding forests from more extensive prairie regions and consequently from fires originating in the prairies. All fires in this subsection had to originate within its relatively small area. In contrast, there was no significant barrier to the spread of fires into the Oak Savanna Subsection of the MIM from the prairie-dominated region to the west and south in the PPA Province, increasing the frequency of fires in this part of the EBF Province sufficiently that open prairies rather than savannas predominated.

The interplay of landscape properties and soils with fire in shaping vegetation is sensitive to climate. During the drier, warmer conditions of the middle Holocene Epoch, beginning about 8,000 years ago, the landscape features in the EBF Province were not enough of an impediment to fire to protect forest vegetation, and prairies and savannas occupied most of the province during that time. Return of cooler, moister conditions beginning about 4,000 years ago tipped the balance and allowed woodlands and forests to expand out of stream bottoms and other refugia to reclaim all but the most fire-prone parts of the province.

Grazing and browsing by large mammals including bison, elk, and deer were major processes in presettlement prairies, but it is not clear that these played as significant a role as fire in the formation and maintenance of prairie. The activities of these animals clearly were important for the movement of seeds and other plant propagules and for the persistence in prairies of many short-lived species associated with mechanical disturbance. It is probable that grazing activity also stimulated recruitment in longer-lived species and probably affected competitive interactions among them. Reduction in the height and density of the canopy of tall grasses effected by grazing prevented competitive exclusion of smaller-stature plant species. These influences affect relative abundances of species, but it is not known whether the long-term absence of large grazers will result in the disappearance of species from upland prairie communities.

Soil moisture is the strongest determinant of variation among plant communities in the UP System. Although the soil-moisture gradient in upland prairies is more or less continuous from dry to wet-mesic, plant community classes in the UP System are grouped into two segments, dry and mesic, with the mesic segment spanning dry-mesic to wet-mesic conditions. Classes in the dry segment are characterized by much greater abundance of midheight and short grasses relative to tall grass species, as well as sparser vegetation cover. Classes in the mesic segment are dominated by tall grass species and have dense vegetation cover. Substrate properties are a second determinant of community variation in the system, with community classes in the dry segment of the gradient divided into plant community types based on substrate properties. The categories of substrate are sand (often aeolian deposits but also lacustrine, fluvial, and colluvial deposits), sand-gravel (outwash and ice contact deposits), thin soils (loess and residuum) on steeply sloping bedrock formations, and steeply sloping unsorted glacial till. The moisture-retaining capacity of these substrates varies from least in the sand category to intermediate in the sand-gravel to most in the thin soil over bedrock and unsorted till; in the last there can be considerable variation depending on relative amounts of fine- and coarse-textured material in the till. Although the thin soils on steep bedrock slopes in the PPL Section have a high moisture-retaining capacity, their thinness severely limits their storage capacity. Nutrient availability also varies among these categories in the same order as moisture-retention capacity. There is no substrate-based division of the mesic segment of UP communities at this time, but additional data collection and analysis may support recognition of a mesic sand soil community type. Soils that support communities in the UP System are classified as mollisols (very dark, base-rich mineral soils), except the sand substrates of dry communities, in which very high permeability and susceptibility to wind disturbance limit soil formation.

Plant Adaptations

Adaptations to frequent fire are prominent in the flora of the UP System. First, of course, is the overwhelming predominance of herbaceous life-forms. The only generally common woody plants are semi-shrub species that do not form substantial aboveground woody structures. Stems of these plants deteriorate in a few years and the plants rely on new stems from the base—such as those produced following fire—to maintain vigor. These shrubs also share the adaptation of producing flowers and fruit in the first year on new stems arising from the base of the plant after fire. Taller shrubs are common only where fire frequency or intensity is reduced, as in savanna and brush-prairie communities. The oaks that occur in savanna and brush-prairie communities all resprout from stumps when top-killed and can flower and fruit even when reduced to shrub size by repeated fires. One of these species, bur oak, has thickened, corky bark that affords some protection from fire damage to the underlying cambial tissue. Quaking aspen, a tree species typical in brush-prairie communities, suckers copiously from an extensive network of horizontal roots when the aboveground stems are killed, and it can persist indefinitely if fire intervals are long enough to allow the suckers to replenish the root system.

Another obvious adaptation of plants to the fire environment of the UP System is that the perennating organs—buds, tubers, root collars, and other tissue from which new growth originates—are generally deep enough below the soil surface to escape damage in prairie fires. In general, plants of the UP System invest heavily in belowground growth, with biomass below ground in tallgrass prairies estimated to be two to four times that above ground. There are several selective forces that produce this result, but sequestering nitrogen—a limiting nutrient in tallgrass prairies—from loss in fire is probably one. Related to this is sequestration of nutrient and energy reserves to support rapid regrowth following grazing. The graminoid life-form is itself an adaptation to grazing, as the meristematic tissue from which new growth arises is at the base of the plant where it is inaccessible to grazers, which consume only easily replaceable leaf tissue.

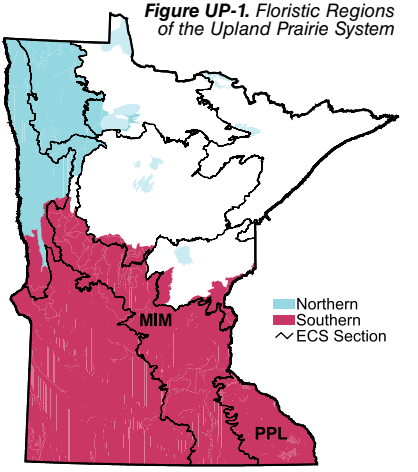
The other major selective pressure to which plants of the UP System are adapted is water limitation. The large amount of root biomass characteristic of prairie plants enables them to capture whatever soil moisture is available. In addition to a dense web of roots in the upper soil layer, most species have some roots that extend into the subsoil to tap deep moisture reserves. There are also a variety of morphological adaptations to reduce water loss from leaves. Leaf and stem pubescence and finely divided or dissected leaves are examples and are most common in species characteristic of the dry communities in the UP System. The ability of grasses to fold or roll leaf blades is another example. The dominant grasses of the UP System also utilize the C_4 metabolic pathway in photosynthetic carbon fixation, a physiological mechanism that makes photosynthesis in the high light and temperature and often water-limited summer prairie environment more efficient with respect to water use (and also nitrogen use).

Floristic Regions

UP communities in Minnesota are grouped into two floristic regions based on differences in species composition, the Southern Floristic (UPs) Region and the Northern Floristic (UPn) Region (Figure UP-1). Only the UPs Region is well represented in the EBF Province. Communities of the UPn Region are present in the northern end of the EBF Province, but they are rare enough that they are not described in this guide. Differences in species composition between UPs and UPn communities are subtle. The composition of the dominant graminoids is remarkably constant throughout the UP System, but there are some differences in the composition of forbs and less important graminoids. These differences mainly involve species that are present in UPs but rarely or never present in UPn communities; there are only a few species in UPn communities that are not also present in UPs communities.

Not all of the species diagnostic for UPs communities occur throughout the UPs Region. Several of these species are restricted to the southeastern part of the state, a few are limited to the southwestern part, and a few occur in the full latitudinal extent of the UPs Region but only along the eastern side. Table UP-1 lists the most geographically widespread species with high fidelity for one or the other of the floristic regions. None of these species has high frequency within either floristic region, because they occur preferentially or exclusively in either dry or mesic classes within the UP System in addition to being geographically restricted as described above.

Figure UP-1. *Floristic Regions of the Upland Prairie System*



These facts raise questions about the legitimacy of recognizing southern versus northern floristic regions. Additional data and analysis may support moving the boundary or creating different floristic regions. Another possibility is the elimination of floristic regions in the UP System. Rather than being an indication of ecologically coherent regions, the geographic variation in species composition of UP communities may be best interpreted as simply the result of independently determined range limits of some of the component species. In fact, the differences between dry and mesic classes within each region are greater than floristic region differences between dry community classes or between mesic community classes.

Table UP-1 *Plants useful for differentiating the Northern and Southern Floristic Regions of the Upland Prairie System.*

	Common Name	Scientific Name	frequency (%) UPn	UPs
Northern Floristic Region	Tufted hair grass	*Deschampsia cespitosa*	24	-
	Glaucous false dandelion	*Agoseris glauca*	20	1
	Blanketflower	*Gaillardia aristata*	8	1
	Spike oat	*Helictotrichon hookeri*	7	-
Southern Floristic Region	Bird's foot coreopsis	*Coreopsis palmata*	-	29
	Gray-headed coneflower	*Ratibida pinnata*	-	25
	Skyblue aster	*Aster oolentangiensis*	-	23
	Scribner's panic grass	*Panicum oligosanthes*	2	22
	Clammy ground cherry	*Physalis heterophylla*	-	16
	Hoary vervain	*Verbena stricta*	-	16
	Whorled milkweed	*Asclepias verticillata*	-	16
	False gromwell	*Onosmodium molle*	1	15
	False boneset	*Kuhnia eupatorioides*	-	13
	Round-headed bush clover	*Lespedeza capitata*	-	12
	Butterflyweed	*Asclepias tuberosa*	-	10