photo by Tim Whitfeld, MN DNR

Glacial Lakes State Park, Pope 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 midheight 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)*, both midheight grasses, are the most important associated graminoids. Sedges *(Carex* spp.) are sometimes common in UP communities but are typically a minor graminoid component. The most common and widespread woody species are the low semi-shrubs leadplant *(Amorpha canescens)* and prairie rose *(Rosa arkansana)*, and the tall shrub wolfberry *(Symphoricarpos occidentalis)*. Purple prairie clover *(Dalea purpurea)*, heath aster *(Aster ericoides)*, and stiff goldenrod (*Solidago rigida*) are common forbs. The main vegetation layer in UP communities is usually less than 40in (1m) high, although some forbs and the flowering stalks of the tall grasses exceed this height as the growing season progresses.

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, shrubs and fire-tolerant trees can persist, forming brush-prairie and savanna communities. 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. Taller shrubs typical in brush-prairies include Bebb's willow *(Salix bebbiana)*, American hazelnut *(Corylus americana)*, and Saskatoon juneberry *(Amelanchier alnifolia)*, which contribute to a patchy shrub layer that is usually less than 5ft (1.5m) tall. Savannas typically have scattered trees, sometimes clumps of trees, growing in a prairie matrix. There is typically a patchy shrub layer up to 6ft (2m) tall, while trees are seldom more than 33ft (10m) tall. Bur oak is the most common and widespread tree, but northern pin oak is sometimes present in savannas close to the edge of the Eastern Broadleaf Forest (EBF) Province. Small, open-grown, often gnarled bur oaks are most distinctive. Savanna and brush-prairie communities intergrade. In the

absence of fire, they rapidly succeed to woodlands. Today, most brush-prairies occur in the Tallgrass Aspen Parklands (TAP) Province of northwestern Minnesota.

Historically, UP communities dominated the landscape of both the Prairie Parkland (PPA) and TAP provinces. Based on records from the Public Land Surveys that preceded intensive settlement, UP communities occupied about 80% of the PPA Province and 60% of the TAP Province. Most of the balance was occupied by Wetland Prairie, Wet Meadow, Open Rich Peatland, and Marsh communities that formed in low positions in the landscape. 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% of the presettlement upland prairie and savanna communities in the PPA Province, and more than 95% in the TAP 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 create a more favorable environment for 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 average fire-return interval in that landscape. Rivers, lakes, and rough topography inhibit the spread of fires. 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 dominance of the PPA and TAP provinces by UP communities before Euro-American settlement reflected these climatic and landscape influences. Both provinces are predominantly low-relief landscapes with relatively few, widely scattered, mostly small lakes. Natural lakes occupy less than 2% of the PPA Province and less than 1% of the TAP Province, compared with almost 5% of the EBF Province and more than 9% of the Laurentian Mixed Forest (LMF) Province. Limited areas of sharper relief, typically with a greater density of lakes as well, do occur in the PPA Province, but because they are surrounded by more level, fire-promoting topography, fires historically occurred within them frequently enough to prevent extensive forest formation. The greater importance of brush-prairie and woodland in the TAP Province probably reflects a cooler climate and greater duration of snow cover in the spring than in the PPA Province: the cooler, moister soil conditions at the time of spring fires afford some protection to the root crowns of woody plants

Grazing and browsing by large mammals, primarily bison and elk, were major processes in presettlement prairies, but it is unlikely that these played as significant a role as fire in the formation and maintenance of prairies. Bison and elk are primarily grazers, with a preference for grasses, which would have limited their role in suppressing woody vegetation. White-tailed deer are browsers and occurred in woodlands on the margins of prairies and along rivers, but their numbers were unlikely to have been sufficient to significantly influence the distribution of woody vegetation. Grazers probably influenced the relative abundances of plant species through their effects on regeneration and interspecific competition. These animals are major dispersers of seeds and are

especially important for dispersals of more than a few meters. Mechanical disturbance of the soil by their hooves is critical for the regeneration of many of the short-lived plant species that are part of UP communities. Grazing also stimulates recruitment of new individuals of longer-lived plant species and affects competitive interactions among them. Reduction in the height and density of the grass canopy by grazing allows shorter plant species to persist in UP communities.

Grazing and fire apparently interacted in a way that helped distribute their effects evenly throughout the prairie and provided periods of respite from both disturbances. New plant growth following fire is more palatable and nutritious than older growth, so grazers tended to follow fires. Areas neglected by grazers accumulate greater fuel loads and thus burn more readily than grazed areas. Thus, in the past, a cycle of burning, followed by grazing, abandonment by grazers, and, after fuel buildup, burning again, characterized the UP system. UP communities are readily degraded by repeated season-long grazing; conversely, prolonged absence of grazing, even with periodic fire, probably results in greater dominance by taller species, as described above. Therefore, the movement of herds to new areas seeking the superior forage of recently burned prairie was likely important in maintaining the full component of species in upland prairie communities. It is not known whether the long-term absence of large grazers will result in the disappearance of species from UP communities.

Long-term patterns of variation in soil moisture are the strongest determinant of variation in species composition among plant communities in the UP System. The soil-moisture regimes in UP communities form a continuous gradient from wet-mesic to dry, but species composition responds less continuously. The wet-mesic to dry-mesic segment of the gradient is characterized by changes in the relative abundances of species, while a spike in species replacement marks the transition to the truly dry moisture regime. UP community classes in the mesic segment are dominated by tall grasses and have dense vegetation cover. Classes in the dry part of the moisture gradient are characterized by much greater abundance of midheight grasses and short grasses relative to tall grass species, and have sparser vegetation cover. The soil-moisture regime for a given climate is determined primarily by soil texture and composition, and topographic factors. Soils of the mesic prairie classes are generally finer-textured loams, although coarser-textured soils may support mesic prairies if the water table is shallow enough for plant roots to easily reach at least the capillary fringe during much of the growing season. In the dry prairie classes, soils are coarse textured and highly permeable, or if fine textured, are on steep slopes. The coarse-textured substrates include wind-reworked sands (dunes) and soils formed in glacial lakeshore, outwash, or ice-contact deposits. These soils are typically loamy sands with a substantial gravel fraction. The soils that support communities in the UP System are classified as mollisols (base-rich mineral soils with a deep, humus-rich surface horizon), except the sand substrates of dry communities, in which very high permeability and wind disturbance limit soil profile development.

Plant Adaptations

Adaptations to frequent fire are prominent in the flora of the UP System. Plants with herbaceous life-forms, unlike woody plants, do not lose much investment when fire destroys their aboveground parts, and therefore strongly dominate UP communities. The only generally common woody plants are semi-shrub species that do not form substantial aboveground woody structures. Stems of these plants deteriorate within 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. 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 these communities 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 these communities—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 and can replace lost leaf tissue simply by adding new cells to the leaf base to reelongate the blade.

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 is 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, high-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). UP communities in the southern part of the PPA Province (from Traverse County south) are recognized as being in the UPs Region; all UP communities north of this in the PPA Province and in the TAP Province are in the UPn Region. 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. Table UP-1 lists the most geographically widespread species with high fidelity for either the northern or southern

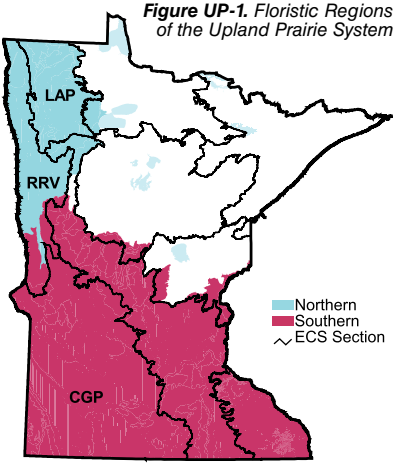

Figure UP-1. *Floristic Regions of the Upland Prairie System*

Table UP-1. *Plants useful for differentiating the Northern and Southern Floristic Regions of the Upland Prairie System. (Species frequencies in this table are based on all samples across the range of each floristic region in Minnesota.)*

	Common name	*Scientific Name*	frequency (%) UPn	UPs
Northern Floristic Region	Glaucous false dandelion	*Agoseris glauca*	24	1
	Tufted hair grass	*Deschampsia cespitosa*	24	-
	Veiny meadow-rue	*Thalictrum venulosum*	14	-
	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
	Aromatic aster	*Aster oblongifolius*	1	21
	Scribner's panic grass	*Panicum oligosanthes*	2	21
	Clammy ground cherry	*Physalis heterophylla*	-	16
	Hoary vervain	*Verbena stricta*	-	16
	Whorled milkweed	*Asclepias verticillata*	-	16
	False boneset	*Kuhnia eupatorioides*	-	13
	Round-headed bush clover	*Lespedeza capitata*	-	12
	Butterflyweed	*Asclepias tuberosa*	-	10

floristic region. None of these species has very high frequency within its respective floristic region. In part this is because the species occur preferentially in either dry or mesic prairie classes rather than in all of the UP classes in the region. In addition, many of the species listed for the UPs Region are not widespread geographically, being restricted to just a part of the region.

Additional data and analysis may support moving the boundary between these two regions 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, geographic variation in the 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 floristic region are greater than the floristic region differences within the dry and mesic classes.