

St. Croix Savanna Scientific and Natural Area, Washington County, MN

General Description

The Eastern Broadleaf Forest (EBF) Province historically was characterized by extensive forests of mesic hardwood tree species common to much of the eastern United States. In Minnesota, the western border of the province was bounded by expansive prairies. Numerous and sometimes large areas of prairie were also present within the province. Between the prairies, which burned regularly, and the mesic hardwood forests, which rarely burned, are lands that burned occasionally during droughts or exceptionally dry falls and springs. These lands burned often enough to prevent large expanses of forests from forming but not enough to favor development of prairies. The vegetation of these lands was predominantly brush, consisting of shrubs and of trees stunted by fire or resprouting after fire. The pattern of trees, brush, and arassland in these areas was described in the 1800s by land surveyors as barrens, savanna, openings, thickets, groves, or parkland. Natural remnants of this vegetation have developed into woodlands or forests following the decline in fire frequency that came with Euro-American settlement in the region. The descriptions of Fire-Dependent Forest/Woodland (FD) communities in this guide are based largely on current examples of these previously more fire-prone communities. The majority of these examples are on sandy, gravelly, or otherwise droughty sites where succession to closed-canopy Mesic Hardwood Forest (MH) communities has been slowed by harsh growing conditions.

As the name implies, FD communities are or have been strongly influenced by wildfires. In the past, fires in the deciduous woodlands of the EBF Province were capable of killing stands of trees and other aboveground vegetation under the right climate, fuel, and topographic settings. However, even intense fires in these deciduous woodlands did not generate the kinds of conflagrations possible in closed-canopy coniferous forests of the Laurentian Mixed Forest (LMF) Province, where crown fires generate enough heat to totally consume branches of live trees, coarse woody debris, litter, and even some soil organic matter. By comparison, fires in the deciduous woodlands of the EBF Province were more regenerative than destructive. The typical cycle involved topkilling of plants and vegetative recovery by resprouting. Plant mortality was primarily due to attrition rather than consumption in a single fire. These fires did enhance plant reproduction by exposing mineral soil, triggering seed dispersal, breaking seed





dormancy, and increasing light and heat conditions on the ground. The fires prevented accumulation of litter and humus, thus affecting nutrient cycling, nutrient availability, and soil-forming processes linked to humus.

In the EBF Province, the native plant community classes in the FD System occur on distinctive sites and soils. In the past, when fires were more frequent, landscape context was more important than inherent site characteristics in determining where FD communities occurred. Local relief, the distribution of water bodies, slope, aspect, soil texture, and the vegetation itself were all contributing factors. In general, hummocky topography, steep slopes, numerous lakes and wetlands, north and east aspects, and fine soil textures favored MH communities. Flat, lakeless, and sandy landscapes favored Upland Prairie (UP) communities, as did very steep, south- to west-facing slopes with shallow soils over bedrock in southeastern Minnesota. FD communities developed in areas intermediate or transitional between these two extremes. At present, the EBF Province is highly developed for agriculture and urban uses. The context that created the mosaic of FD, MH, and UP communities is gone. Prairies no longer serve as an ignition source for the wildfires that maintained FD communities and that limited MH communities to the most protected sites. Gone also are herds of bison and elk, which probably supplemented fire in shaping the composition and structure of FD communities.

The EBF Province is an ecotone between subhumid prairie and humid forest climates and experiences modest fluctuations between these climate regimes over cycles of tens to hundreds of years. The pattern, structure, and composition of vegetation in the province in the past were sensitive to these fluctuations in climate. Although fire was the most immediate cause of vegetation patterns in the province, fuel conditions and the probability of fire were influenced by climate cycles. As a result of fluctuation in climate and its effect on fire probability, any given site in the province could cycle among vegetation types over time, causing temporal variation in soil development on the site. For this reason, soils in the province often have mixed grassland, woodland, and forest characters, and differences in the soils associated with FD, MH, and UP communities are not strong. In general, in the current climate and the absence of wildfire, any terrestrial site in the province will succeed toward communities of the MH System. (This is in strong contrast to the LMF Province, where FD communities are strongly correlated with droughty, often sandy, poor soils that tend to become even poorer over time under the regime of catastrophic fires characteristic of conifer-dominated FD communities).

Plant Adaptations

Plants that occur in FD communities have seeds or vegetative structures that can survive fire and are good at colonizing burned sites. Many FD plants are opportunists that can take advantage of the short periods following fire when nutrients are relatively abundant and light levels are high. Such plants must also survive frequent drought and potentially long periods between fires when light levels decrease beneath increasingly dense shrub and tree canopies. The most evident characteristic of FD plants in this region of Minnesota is their ability to sprout prolifically. The trees, shrubs, and many of the herbs are capable of storing considerable amounts of carbohydrates belowground in roots, rhizomes, or other specialized organs and then sprouting vigorously after aerial stems are destroyed by fire. These plants seem to be particularly plastic in allocating resources to underground or aboveground tissues, depending on the impact of fire on their overall vigor.

At present, FD communities in the EBF Province have a mixture of species with life history traits and morphological features that are generally associated with either UP communities or MH communities. This is because the composition of FD communities includes plants adapted to the historic, fire-prone conditions of the sites on which they





occur as well as plants adapted to the current shadier conditions. As an example, FD communities tend to have graminoid cover dominated by sedges, as is true for MH communities, but also have grass species that are equally at home in prairies. In addition, the flora of FD communities includes ferns, which are common in MH communities and rare in UP communities, but the ferns in FD communities are limited to the most widespread species such as lady fern, rattlesnake fern, and bracken. Many additional fern species common in MH communities that are shared with UP communities are summer- and fall-blooming herbs, shrubs with spines and prickles, shrubs with fleshy fruits, half-shrubs, annual plants, and plants with sticky, animal-dispersed seeds.

The dominant trees of FD communities are oaks and aspen. Bur oak is by far the most common tree species, but northern pin oak, white oak, and northern red oak (as well as black oak in southeastern Minnesota) are dominant in some stands. The oaks and aspen are well adapted to repeated burning because of their ability to store resources in their root systems and resprout after fire. The oaks develop peculiar growth forms (often referred to as "grubs") when subjected to fire. When the tree trunk or stem is killed, a callus develops over the top of an enlarged root mass near the ground surface. These trees continue to send up sprouts from the root collar at the margin of the mass, forming a ring of stems. Such rings commonly achieve 3-foot diameters, and individual stems up to 5 feet apart may be connected to the same rootstock. These sprouts grow quickly at first, but growth eventually slows, especially when the stems are overtopped by aspens or by adjacent trees that survived the fire.

Quaking aspen survives repeated burning by forming suckers that sprout from an extensive network of roots. This produces a dispersed, thicketlike growth of new sprouts. These sprouts, like those of the oaks, often seem stunted, with growth of individual stems slowing after a rapid initial burst. It is significant that in the EBF Province land surveyors in the 1800s commonly listed aspen and oak as "underbrush" rather than "timber." Aboveground, the FD communities of the province were incredibly dynamic, with the density and height of woody plants ever changing in response to fires. Belowground, however, were massive rootstocks of oaks, aspens, and many of the common shrub species. These rootstocks can attain great age, and there is every reason to believe that oak grubs, aspen clones, and colonies of shrubs could continuously occupy a site for centuries.

Floristic Regions

FD communities in Minnesota are grouped into four floristic regions, based on general differences in species composition (Fig. FD-1). Two of these floristic regions are represented in the EBF Province: the Southern Floristic (FDs) Region and the Central Floristic (FDc) Region. FDs communities are common throughout the province, whereas FDc communities are rare, being limited to a few areas along the boundary of the EBF Province with the Laurentian Mixed Forest (LMF) Province. Communities of the Northwestern Floristic (FDw) Region and Northern Floristic (FDn) Region are not known to occur in the EBF Province.

Given the paucity and localized occurrence of FDc communities, the EBF Province is essentially a single floristic region of fire-dependent vegetation (FDs) that is functionally quite different from the conifer-dominated forests and woodlands of the LMF Province, where FDn and FDc communities are prevalent. Most noticeable is that the plants growing in the FD communities of the EBF Province are generally not dependent on fire at any stage of their life cycles but are clearly tolerant of fire. Fire may alter the growth form of these plants and influence the allocation of resources among roots, stems, bark, leaves, or fruits, but most of these species can be found in habitats that lack any direct evidence of fire. In fact, there are many herbaceous plants that are widespread in FD communities in the EBF Province that never occur on sites in the LMF Province that burn



with any regularity. These plants have life history strategies—such as shade tolerance, seedling banks, and storage organs—that are most often associated with plants common in communities of the MH and Floodplain Forest (FF) systems.

FDs communities are predominantly deciduous, with very dense shrub layers and low abundance of grasses. They are not inherently flammable and tend to develop structures and fuels that make them less likely to burn as they age. In the past, however, they were subject to creeping surface fires because they occurred next to prairies. In some instances, these fires killed shrubs and small trees, thereby creating dry woody fuels for subsequent, more intense fires.



Statewide, FDs communities occur in habitats that are much richer and slightly moister than those of FDc communities. Several geologic and soil properties are consistent with FDs sites being richer than FDc sites. Most impressive is that 83% of the FDs vegetation samples used in developing this classification occur on calcareous drift, sediment, or loess from the Red River, Des Moines, and Grantsburg glacial lobes. Eighty-four percent of FDc samples occur on noncalcareous or slightly calcareous drift or outwash from the Superior. Rainey, and Wadena glacial lobes, Surprisingly, with the exception of nutrient status, the soil characteristics commonly associated with calcareous and noncalcareous landscapes are not so divergent between FDs and FDc sites. There is broad overlap in soil texture in the coarse soil-texture classes. Only those FDs communities present on loess occur on consistently fine-textured soils. Free carbonates tend to occur deep within the soil for both FDs communities and FDc communities. In FDs communities, free carbonates are usually present about 42in (105cm) below the soil surface. In FDc communities, free carbonates are often absent or about 49in (125cm) deep when present. The upper soil horizons in FDs communities have 1.3-3.3% organic matter content while FDc communities have 1.0-2.5% organic matter. Rooting zone pH tends to be slightly acid or near neutral for both FDs communities (5.9-7.2) and FDc communities (5.0-6.7).

The four native plant community classes in the FDs Region are distinctive and geographically separated from one another—arguably, the classes could be separated by geography and substrate alone. Southern Dry-Mesic Oak-Aspen Forests (FDs36) occur on till plains and moraines in the Hardwood Hills Subsection in Polk and Mahnomen counties. Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) occur on sandy and gravelly soils throughout the Hardwood Hills Subsection south of Mahnomen County and across the Anoka Sand Plain and St. Paul Baldwin Plains and Moraines Subsections. Southern Dry-Mesic Oak (Maple) Woodlands occur also on steep slopes along the Minnesota River with excessively drained gravelly till. Southern Dry-Mesic Pine-Oak Woodlands (FDs27) and Southern Dry-Mesic Oak-Hickory Woodlands (FDs38) are restricted to the Paleozoic Plateau Subsection, with the former occurring on sandy alluvial bottoms and the latter on loess-covered bedrock in association with bedrock bluff prairies.

The four FDs community classes arrived at similar vegetative conditions by different pathways. In the Paleozoic Plateau, mesic forests of oak, elm, maple, basswood, and ironwood developed in the early Holocene Epoch, about 9,000 years ago, and





persisted until about 5,500 years ago. Except at the most protected sites, these forests were replaced by prairie at that time, and prairie persisted until about 3,000 years ago. At about 3,000 years ago, woodland vegetation began to develop, possibly with communities analogous to Southern Dry-Mesic Pine-Oak Woodlands (FDs27) forming on sites occupied by sand prairies and barrens, and Southern Dry-Mesic Oak-Hickory Woodlands (FDs38) encroaching on sites occupied by bluff prairies. This pattern appears to have remained fairly stable until recent times, when some areas of fire-dependent woodland began to succeed to mesic forest.

At sites where Southern Dry-Mesic Oak-Aspen Forests (FDs36) are now present, boreal species such as spruce, birch, and some (jack) pine persisted into the very early Holocene Epoch, until about 8,500 years ago. These woodlands were then replaced by prairie, with oak also appearing in the landscape. This condition persisted until about 4,000 years ago, when forests of mesic and fire-dependent hardwood trees developed that are similar to those present today. Southern Dry-Mesic Oak-Aspen Forests (FDs36) most likely began replacing the patches of prairie or brush prairie and continue to occupy drier sites in the landscape.

Curiously, the sites on which Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) occur have topography and soil parent material similar to sites on which FDc communities occur in the LMF Province across the border from the EBF Province. The differences between Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) and FDc communities seem to be related to their paleohistory, which is virtually identical until the late Holocene Epoch, from 3,000 to 300 years ago. Forests or woodlands of jack pine and perhaps red pine formed on these sites in the early Holocene Epoch, about 10,000 years ago. Dry upland prairies replaced these pine forests about 8,000 years ago. Beginning about 4,000 years ago, pines started to reclaim these lands and have been doing so until modern times. Pine forests formed on sites now occupied by Central Poor Dry Pine Woodlands (FDc12) about 3.500 years ago, on sites now occupied by Central Dry Pine Woodlands (FDc23) and Central Dry-Mesic Pine-Hardwood Forests (FDc34) about 2,000 years ago, on sites occupied by Central Rich Dry Pine Woodlands (FDc24) about 300 to 600 years ago, and not at all on sites occupied by Southern Drv-Mesic Oak (Maple) Woodlands (FDs37). Thus, Southern Dry-Mesic Oak (Maple) Woodlands (FDs37) differ from FDc communities only in that they occur on sites that were not reinvaded by jack pine (and associated ground-layer plants).

Plant Indicators of FDc vs. FDs Communities

Plant species with high fidelity for FDc communities relative to FDs communities are listed in Table FD-1. Many of these plants are strongly associated with the coniferous forests abundant throughout the adjacent LMF Province. Most occur in upland pine forests, but others occur in both upland and wetland settings where conifers are present. These plants tend to be evergreen or have overwintering leaves, such as wintergreen (Gaultheria procumbens), pipsissewa (Chimaphila umbellata), bearberry (Arctostaphylos uva-ursi), and round-leaved pyrola (Pyrola rotundifolia). Another guild of plants common in FDc communities but not in FDs communities are plants of UP communities. Presumably plants like hoary puccoon (Lithospermum canescens), big bluestem (Andropogon gerardii), and smooth blue aster (Aster laevis) occur in FDc communities because these communities were prairies before jack pine invaded these sites in the late-Holocene Epoch. Given the proximity of FDs communities with prairies along the prairie-forest border and in the blufflands, one might have expected prairie plants to be more prevalent in FDs communities than FDc communities. Apparently these sun-loving plants are not successful beneath the canopy of deciduous trees and dense shrub layer that is currently typical of FDs forests and woodlands.

Plants with high fidelity for FDs communities relative to FDc communities appear in Table FD-2. Nearly all of these plants reach their peak presence in floodplain forests





in the FF System and in wet-mesic hardwood forests in the MH System. Shagbark hickory and tall thimbleweed (*Anemone virginiana*) are the only plants in this list with peak presence in FD communities. These two species and golden alexanders (*Zizia aurea*) are the only plants in this list to occur in habitats that burned regularly. The remaining plants are clearly not dependent on fire, because they most commonly occur in habitats that rarely burn. Either they are tolerant of fire and are a natural component of FDs communities, or they have invaded the sites on which FDs communities occur as a result of fire-suppression in modern times. Floodplain forests, wet-mesic hardwood forests, and FDs communities have in common a forest floor with low light levels, soils

 Table FD-1. Plants useful for differentiating the Central from the Southern Floristic Region of the Fire-Dependent Forest/Woodland System.

 frequency (%)

				 , (/0)	
		Common Name	Scientific Name	FDc	FDs
	ĝ	Wintergreen	Gaultheria procumbens	41	-
	feri	One-sided pyrola	Pyrola secunda		5
	į	Pipsissewa	Chimaphila umbellata	26	5
	5	Bearberry	Arctostaphylos uva-ursi	24	-
	vergreen or ove leaves	Jack pine (U)	Pinus banksiana	22	1
		Round-leaved pyrola	Pyrola rotundifolia	16	-
		Balsam fir (U)	Abies balsamea	16	-
		Red pine (U)	Pinus resinosa	15	-
		Twinflower	Linnaea borealis	15	-
	ш	Bunchberry	Cornus canadensis	14	-
		Hoary puccoon	Lithospermum canescens	27	3
		Big bluestem	Andropogon gerardii	23	2
	ΪŢ	Smooth blue aster	Aster laevis	21	2
egion	fin	Slender wheatgrass	Elvmus trachvcaulus	17	-
	Prairie af	Grav goldenrod	Solidago nemoralis	15	1
		Oval-leaved milkweed	Asclepias ovalifolia	11	-
		Kalm's brome	Bromus kalmii	11	-
		Virginia ground cherry	Physalis virginiana		-
Ř		Wood betony	Pedicularis canadensis	10	2
ic		Lowbush blueberry	Vaccinium angustifolium	81	8
ist		Prickly or smooth wild rose	Rosa acicularis or B blanda	71	17
<u>S</u>		Pale vetchling		51	10
Ш		Prairie willow	Salix humilis	49	-
a		Veiny pea	Lathyrus venosus	46	7
tr		False melic grass	Schizachne purpurascens	41	3
en		American vetch	Vicia americana	35	1
Ũ		Pussytoes	Antennaria spn	31	7
		Yarrow	Achillea millefolium	28	5
		Harebell	Campanula rotundifolia	28	5
	her	Poverty grass	Danthonia spicata	26	2
		Hairy goldenrod	Solidago hispida	24	2
	ð	Sharp-pointed rice grass	Orvzonsis pungens	23	-
		Pin cherry	Prunus pensylvanica	22	3
		Balsam ragwort	Senecio pauperculus	20	-
		Cow wheat	Melamovrum lineare	19	-
		Kalm's hawkweed	Hieracium kalmii	18	1
		Bluebead lilv	Clintonia borealis	17	1
		Fringed brome	Bromus ciliatus	16	2
		Blue giant hyssop	Agastache foeniculum	16	-
		Sand cherry	Prunus pumila	16	-
		Sand or dog violet	Viola adunca or V conspersa	15	-
		Clustered multiv grass	Muhlenbergia glomerata	13	-
		Gradiorida mariny grado	manionoorgia giomorata		

(U) = understory tree





with comparatively high amounts of incorporated organic matter, and little or no humus on the surface. These conditions are characteristic in floodplain forests because floodwaters tend to remove organic matter on the soil surface and bury organic surfaces under fresh alluvium. In modern wet-mesic hardwood forests, earthworms exotic to Minnesota have accomplished much the same thing by totally mixing the humus into the mineral soil. Frequent surface fires in FDs communities (see below) prevent accumula-

Table FD-2. Plants useful for differentiating the Southern from the Central Floristic Region of the Fire-Dependent Forest/Woodland System.

		Common Name	Scientific Name	FDc	FDs
		Clayton's sweet cicely	Osmorhiza clavtonii	19	82
		Pointed-leaved tick trefoil	Desmodium alutinosum	6	70
		Lopseed	Phrvma leptostachva	2	66
	od Forest Affinity	Common enchanter's nightshade	Circaea lutetiana	2	51
		Wild geranium	Geranium maculatum	4	43
		Prickly gooseberry	Ribes cynosbati	8	43
		Rattlesnake fern	Botrychium virginianum	2	31
		White snakeroot	Eupatorium rugosum	-	26
		Red elm (U)	Ulmus rubra	3	21
		White oak (U)	Quercus alba	1	19
		Bitternut hickory (U)	Carya cordiformis	1	18
		Black raspberry	Rubus occidentalis	2	18
		Rugulose or yellow violet	Viola canadensis or V. pubescens	4	18
	S.	Bottlebrush grass	Elymus hystrix	3	17
	D I	Elliptic pyrola	Pyrola elliptica	2	16
	sic Ha	Agrimony	Agrimonia spp.	-	15
		Zigzag goldenrod	Solidago flexicaulis	2	15
5	Ne:	Elm-leaved goldenrod	Solidago ulmifolia	-	14
G	-	Bloodroot	Sanguinaria canadensis	1	14
R B		Climbing bittersweet	Celastrus scandens	2	13
U		Blue conosn	Caulophyllum thalictroides	-	12
÷		Shining bedstraw		-	12
Ξ		American spikenard	Aralla racemosa		12
.		Tail loaved aster	Astor urophyllus		10
	_			2	
eri	t Affinity	Prickly ash	Zanthoxylum americanum	1	64
극		American elm (LI)	Vitis riparia	3	63
2		American eim (0)	Olinus americana	0	40
Š		Box elder (U)	Acer negundo Ribos missourianos	2	43
		Honowort	Cryptotaopia canadopsis	-	29
	5e	Nanyberry	Viburnum lentado	-	20
	ピ	White avens	Geum canadense	-	21
	<u> </u>	Stickseed	Hackelia spp	2	19
	ble	Hackberry (U)	Celtis occidentalis	-	17
	8	Gregarious black snakeroot	Sanicula gregaria	-	17
	운	Greenbriar	Smilax hispida	3	15
		Aniseroot	Osmorhiza longistylis	1	12
		Kidney-leaved buttercup	Ranunculus abortivus	-	11
		Lady fern	Athyrium filix-femina	5	33
	ther	Shagbark hickory (U)	Carva ovata	-	18
		Eastern red cedar (U)	Juniperus virginiana	-	15
		Side-flowering aster	Aster lateriflorus	3	14
	윤				
	f	Golden alexanders	Zizia aurea	-	13
	gh	Golden alexanders Jack-in-the-pulpit	Zizia aurea Arisaema triphyllum	-	13 11

(U) = understory tree





tion of thick humus layers, and these forests, like wet-mesic hardwood forests, have a long history of earthworm activity.

Natural History and Fire Regimes of FDc vs. FDs Communities

The natural rotation periods of fires in FDc and FDs communities are similar (Table FD-3). In the past, communities in both floristic regions were far more likely to experience surface fires than catastrophic fires that killed existing trees and caused regeneration of forest stands. In general, FDc communities have rotations of 30 years for surface fires, and rotations of 110–130 years for catastrophic fires. Central Dry Oak-Aspen (Pine) Woodlands (FDc25) are somewhat exceptional among FDc communities, with rotations of just 10 years for surface fires. FDs communities have rotations of 10–20 years for surface fires, and 100–150 years for catastrophic fires. The chances of any fire resulting in significant mortality of canopy trees ranges from about one in four for FDc communities, where catastrophic fires were roughly as frequent as surface fires.

Both FDc and FDs communities are remnants of what the land surveyors described in the late 1800s as "upland brush with scattered timber." At present, their structure

Table FD-3. Historic tree species composition and disturbance regimes in FDc and FDs communities

	Historic Tree Species Frequency by Class and Stand Age				His Ro (Historic Disturbance Rotation Periods by Class (in years)				
	young forest age	young forest species	mature forest age	mature forest species	old forest age	old forest species	Stand- Regenerating Fire	Moderate Surface Fire	All Fires	Catastrophic Windthrow
Cer	Central Floristic Region ranges —					80- 130	10-30	10-25	>1000	
FDc24	0 - 55 yrs	jack pine	75 - 155 yrs	jack pine red pine	> 155 yrs	jack pine (white pine)	130	30	23	>1000
FDc25	0 - 55 yrs	bur oak quaking aspen (jack pine) (northern pin oak)	55-135 yrs	bur oak (northern pin oak)	> 135 yrs	jack pine bur oak	80	10	9	
FDc34	0 - 55 yrs	quaking aspen* red pine (white pine) (jack pine)	95-135 yrs	red pine (white pine)	>195 yrs	white pine (red pine)	110	30	23	>1000
Southern Floristic Region ranges					110- 150	10-20	10-20	>1000		
FDs27	0+ yrs	bur oak (black oak) (northern pin oak)			1		135	15	14	
FDs36	0-35 yrs	quaking aspen (bur oak)	75-135 yrs	bur oak (quaking aspen)	>175 yrs	bur oak (American elm) (white pine)	100	20	18	>1000
FDs37	0-75 yrs	bur oak (northern red oak)	>75 yrs	bur oak white oak (northern red oak)	ı		110	10	9	>1000
FDs38	0-55 yrs	bur oak (northern red oak)	55-135 yrs	bur oak	>135 yrs	bur oak (white oak)	150	15	11	>1000

bold = >50% normal = 25-50% (italics) = 10-25% *includes big-toothed aspen





is better described as woodland or even forest. Before Euro-American settlement, the number of trees per acre in FDc communities was about one-third that of MH communities in the same general region (i.e., MHc communities). For FDs communities, historic density was about a third or a fourth that of MHs communities. Today, there is no difference in tree density between FDc or FDs communities and MHc or MHs communities, respectively. A clear consequence of fire suppression has been for tree canopies to develop in FDc and FDs communities, filling the gaps created in the past by frequent surface fires. The effect of tripling the density of pines in FDc communities is to make them more flammable and capable of carrying crown fires. The effect of tripling or quadrupling the density of bur oak, aspen, and birch in FDs communities is to create a less flammable community composed mostly of deciduous trees and shrubs. The mean cover of woody trees and shrubs in FDs communities is 163%, meaning that these communities have nearly double canopies of woody vegetation, which maintain humid subcanopy conditions and provide enough shade to stifle the production of herbaceous fine fuels.

There is no reason to assume that colonies of hazelnuts, dogwoods, or other native deciduous woodland shrub species in Minnesota are much more likely to burn as they age. It is also unlikely that they would burn much hotter because of accumulated fuel or because of intrinsic properties such as the accumulation of flammable chemicals in living tissue that occurs in some species of western shrubs. Rather, in the past Minnesota's native shrubs likely formed the dominant vegetation layer in uplands where the fire regime was imposed on the landscape by context more than site properties or the developmental stage of these brushlands. FDc and FDs communities probably burned frequently because they were next to or surrounded areas of prairie. Where there were extensive areas of FDs communities in the historic landscape, it almost always appears they were in areas between prairies and true forests. Where there were extensive areas of FDc communities, they almost always contained areas of prairies. sandy river terraces, or perennial Indian settlements. Grasslands and wet hay meadows within short distances of forests were of great value to Indians and European settlers alike. These openings attracted game and provided food for the settlers' horses and livestock. These grasslands consistently produced dried fine fuel, people commonly set them ablaze, and they commonly brought fire to the edge of FDc and FDs communities. Under dry conditions the fires burned through FDc and FDs communities, while under wetter conditions they did not.

The spatial configuration of trees and brush in historic FDc and FDs communities is difficult to reconstruct from Public Land Survey (PLS) records. Raw estimates based on distances of bearing trees to survey corners suggest there were about 14 trees per acre in FDc communities and about 9 trees per acre in FDs communities. However, the same calculations for communities where densities of trees should have been unaffected by fire (e.g., MH communities) suggest that PLS reconstructions underestimate tree density by five to as much as ten times. Such calculations are misleading because they suggest there were trees on almost every acre of land. Direct descriptions are more useful. For both FDc and FDs communities, the surveyors described about half of the land survey corners as some kind of forest or woodland. The remaining corners were variously described as scattered timber, savanna, thickets, barrens, openings, groves, brush, or prairie. It is interesting that vast areas of Minnesota were surveyed with rather casual mention of the upland vegetation; it was simply described as either forest or prairie. In the EBF Province, where the forest and prairie biomes meet, the surveyors' vocabulary flourished. They were clearly attempting to describe something of great spatial complexity. Detailed maps of the trees referenced in the PLS notes indicate that trees grew on sites where they escaped fire or where the fires were of low intensity. Topography and surface water determined the pattern of such sites. Fluctuations in climate, especially as it affected lake levels and water tables, determined just how protected from fire these sites were from year to year.