BOTANICAL GAZETTE

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FLORAL SUCCESSION IN THE PRAIRIE-GRASS FORMATION OF SOUTHEASTERN SOUTH DAKOTA

THE PREVERNAL, VERNAL, AND ESTIVAL ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 113

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(WITH THREE FIGURES)

The western part of Iowa, the eastern and northeastern counties of Nebraska, and southeastern South Dakota lie in the drainage basin of the Missouri. This tri-state area is well within the prairie region of that vast and far-reaching prairie province of the middle west. This area is only a part of the Ponca District of POUND and CLEMENTS,[1] being more strictly Dakotan than Nebraskan, and may be considered as representing a transition between the more mesophytic eastern areas of Iowa and those dominantly xerophytic somewhat to the west, with which it shows the closer floristic agreement. Its composition is thus twofold, pointing to the primitive and more xerophytic stages of the past and at the same time prophetic of the mesophytic stages to come. This aberrant character links it strongly to the xerophytic prairie to the west and southwest, from which it is genetically descended, and the prophetic character links it to the more mesophytic prairie of western Iowa, which has encroached ever westward. Under this migration tension from the southeast and east the primitive prairie has retreated, civilization always being a potent factor in this succession.

Study began in this tri-state region in the fall of 1903 at Sioux City, Iowa, and was carried on during that fall and the next summer

[1] POUND, R., and CLEMENTS, F. E., Phytogeography of Nebraska. 1900.

in the contiguous portions of Iowa, Nebraska, and South Dakota. In the fall of 1904, Yankton, South Dakota, became the base station, and for the next three seasons (1904–1907) the work was carried on from that point. During this period the greater part of South Dakota east of the Missouri was visited, and repeated trips were made into contiguous Nebraska and into Iowa, while at the same time detailed study of a restricted area was being prosecuted. This local area upon which study has been focused lies in the township of Yankton and embraces about 49 hectares, being a rectangular strip 1210^{m} north and south by 405^{m} east and west. The topography is uneven and comprises a series of prairie knolls and slopes, separated into two groups by a gentle drainage valley which traverses it in a southwest and northeast direction. The knolls are low and their slopes gentle, scarcely higher than 10 or 15^{m}, with a gradient never exceeding 30 or 40°. The entire area is largely underlaid by glacial gravel and clayey till. The former mainly constitutes the knolls—the humus is here the most shallow, averaging only about 15 to 20^{cm} in depth. Off from the knolls on the level the humus caps the deposit of clayey till. On the lower erosion slopes (25 to 30^{cm}) and in the drainage valley (60^{cm} plus) the humus has accumulated to a greater depth, sufficient in the latter to bury the till beyond the zone of root activity. The humus is in all cases till or gravel modified by atmospheric, organic, and biotic agencies.

To insure uniformity the nomenclature of BRITTON and BROWN'S *Illustrated flora* has been followed, except where it has conflicted with the verification of grasses made for me through the United States Department of Agriculture by Mr. PERCY L. RICKER and Mr. D. A. BRODIE, to whom I am greatly indebted for this courtesy.

This problem has been carried on under the direction of Dr. HENRY C. COWLES, to whom I wish to acknowledge my indebtedness for many valuable suggestions and criticisms during the progress of the investigation.

Geology and topography

To appreciate fully existing conditions, an epitome of the post-Cretaceous geological development of the region is necessary. The Cretaceous was terminated by that great uplift and crustal movement which formed the Rocky Mountains and gave birth to the major

features of the Missouri valley drainage. This movement particularly affected this region by elevating it from an estuary condition to a point considerably above sea-level, and even probably many feet above its present level. This uplift inaugurated a period of vast erosion, and before the advent of the ice the Missouri had cut its present great valley at least 20 to 25^{m} below its present level.

With the Pleistocene came the glaciers. While doubtless there were five periods of glacial advance and recession in the region, we need concern ourselves now only with the second, the Kansan, which spread from the Keewatin center and deposited over this entire region the Kansan drift sheet, obliterating the questionable pre-Kansan. The Illinois, Iowan, and Wisconsin epochs followed successively, only the latter reaching into southern South Dakota, where a lobe of the Altamont moraine pushed down between the Big Sioux and Missouri Rivers, reaching approximately to Vermillion, South Dakota.

The Kansan must have seriously interfered with the established preglacial drainage, greatly rejuvenating it, at least along minor lines. It seems probable also that subsequent erosion mainly sought out previous lines, largely reestablishing the post-Pliocene drainage system. The Wisconsin likewise disturbed and caused a readjustment of this drainage system, which could have differed but little from that previously worked out in the Kansan. Upon this readjustment of the post-glacial Wisconsin drainage topography, there followed the deposition of that much mooted deposit, the loess.

The region divides itself naturally into two great topographic types, the rolling upland prairie and the flood plain, which cuts the prairie in a general northwest and southeast direction. On either side the flood plain is limited by the escarpments of the Missouri. From this flood plain extend the minor flood plains of its tributaries, further dissecting the upland. The vast valley is cut out from 25 to 50^{m} deep in the upland and presents a flood plain varying from a narrow terrace to frequently 10^{km} in width.

The upland now presents an almost perfectly developed erosion topography, predetermined in the Kansas drift sheet and subsequently veneered by the Wisconsin drift and loess deposit. The latter, which frequently has a depth of 50^{m} to the south of the Wisconsin drift area, thins out northward. The escarpment bluffs are

steep and high, but pass back into a complex of gently rounded, semi-detached hills, which present a sinuate or undulating sky line of jumbled peaks; it is a vast mountain system in miniature. Back a few miles from the bluffs these hills pass imperceptibly into the low, rolling prairie hills, which extend with scarcely a variation in either direction. So perfectly is this tributary drainage system established that upon the prairie swamps and "sloughs" rarely occur. The small streams which have threaded the upland are characterized by ravines of depth and precipitousness, especially in the loess, where they usually end abruptly in a bluff, again dividing the upland into a series of ridges, intricately related, which pass back into the low, rolling hills of gentle profile.

Origin of the prairie

The uplift of the Rocky Mountains, which terminated the Cretaceous, introduced a modifying element which exercised an ever-increasing influence upon the climate of the Great Plains region. Intercepting the eastward-moving moisture-laden winds from the Pacific, a decrease in the annual precipitation to the east of the range must of necessity have followed. The greatest reduction would have been nearest the mountains, decreasing to the eastward. When this interior continental land was finally left by the interior sea and opened to migration, invasion must have been in large degree controlled by this graduated distribution of rainfall. The subsequent origin of the Cascades could have served only to accentuate this distributional difference and reduction in precipitation. Under such conditions the Tertiary phytogeographical distribution of this central region must have been adjusted. Whatever the source, it would seem highly probable that while the entire Mississippi valley was occupied by the rich Tertiary forest, the region lying to the west and bounded by the Rocky Mountains and extending northward into Assinaboia was, on account of the low precipitation, denied to tree invasion and came to be occupied by a prairie formation, increasing in its xerophytism westward just as it does today.

Toward the close of the Tertiary (late Pliocene) fossil evidence points conclusively to climatic change. A retrogressive succession of floral waves swept southward under the influence of the gradually

falling temperature of the Pleistocene. In this glacial movement, the plains region, unable to support tree growth, acted as an entering wedge, causing an east and west divergence. One wing of the migration, dominantly coniferous, followed the Rocky Mountains southward; the other, typically deciduous, sought the Mississippi and its tributary valleys as a migration track; while the prairie moved directly toward the Gulf. At the time of maximum ice advance the descendants of the Tertiary forest were mobilized in the southern Appalachians about the Chattanooga region as a center (ADAMS :02), while the prairie formation concentrated in the southwestern United States, with a possible center in the region of northeastern Texas and eastern Oklahoma and southern Kansas.

With final glacial retreat from this region and subsidence of the glacial sea, migration tension was removed and distribution tension became active. The life waves now in succession rolled northward. The content of our flora demands a consideration of the third wave only. A study of the floristics shows indisputably the commingling of forms of diverse geographical affinity. An unmistakable floristic relation, in many cases specific, exists with a southwestern and southeastern center of post-glacial dispersal.[2] To the east and southeast the deciduous forest type becomes increasingly characteristic, while to the west and southwest the plain or prairie type gradually predominates; the region thus lies in the western border of the tension zone in which migration from these two competing centers of distribution meet. From the southeast the dispersal route has been up the Missouri valley; while the northwestern migration has spread diagonally across natural drainage lines, following the upland plains.

Forest invasion of the prairie

When the arborescent elements of the southeastern biota, migrating up the valleys of the Mississippi and of the Missouri and its tribu-

[2] BESSEY ('99, p. 82) says: "There are 66 or 67 species of native trees in Nebraska, and 56 or 57 have advanced to the state from the southeast." MACMILLAN ('92, pp. 653, 721) has shown that 66 per cent. of genera indigenous to the Minnesota Valley are eastern and 62 per cent. southern, while 32.5 per cent. of the total species are of southeastern origin. Of the native trees of South Dakota at least 75 per cent. show indubitable southeastern affinities. The presence of such genera as Opuntia, Cactus, Yucca, Mentzelia, Croton, Bouteloua, Bulbilis, Lygodesmia, and Aplopappus strongly bespeaks the southwestern alliance.

taries, reached the prairie region they were unable to occupy the high lands, but occupied the flood plains and adjacent slopes. There is no evidence to indicate that the then existing topographical and climatic conditions differed radically from those of today. Again these elements have today their most widespread distribution, a condition at once intelligible when related to physiographic development in the working-back of streams and the increase of flood plain. Two salient points may now be noted: the initial and the continuous subsequent preemption of the upland by the prairie formation, and secondly the continuation of initial climatic conditions. The initial causes which operated to restrict tree invasion and ecesis upon these prairie-covered uplands would thus seem to have their duplication in those natural factors which operate to that end at the present time.

Under the discussion of ecological factors of the region it will be shown that there is a coincidence of factors operating most antagonistically against tree growth upon the upland. The almost entire absence of fungi upon the prairie cannot but be significant. The roots of most of these deciduous trees are obligatively provided with symbiotic mycorhiza and the absence of their specific fungus would preclude advance. Hence fungal infection of the prairie soil must precede or at least accompany forest encroachment. Again, the difficulty of seed germination, almost impossible either because of a dense sod or a lack of soil moisture, successfully checks invasion. In consideration of these precarious climatic factors, peculiar edaphic conditions, and the fact that if planted upon the prairie trees thrive, I am led to the view that the question of non-invasion upon the prairie proper is primarily and initially one of pre-occupation and the inability of seedlings successfully to withstand the extremely severe conditions of the first winter's exposure. In the positive and coincident interaction of unfavorable biological and climatic conditions may be found a cause sufficient to account for tree absence upon the prairie and the slow migration of tree species into this region.

While these causes are all sufficient, yet we must not disregard a secondary and artificial though highly cooperative factor, which in recent times must have served in many places to prevent tree establishment. I refer to prairie fires; yet even in the absence of prairie fires for half a century the prairie stands uninvaded except in cases

of physiographic development (BESSEY '99). And again, as the prairie existed as a climatic formation long before these fires, either of Indian or Caucasian origin, swept the prairies, it would appear that this fire factor has been overestimated by many and is in no sense to be regarded as the fundamental factor. That there is, nevertheless, an extremely slow advance of the forest usually through the medium of its forerunner, the shrub association, whose pioneer *Symphoricarpus occidentalis* is followed by *Rhus glabra*, is very evident.

While the above factors are seemingly adequate to account for tree absence upon the western upland prairie, yet in light of the prairie as a natural climatic formation it would seem more proper to make the problem one accounting for the occasional presence rather than the general absence of trees. A future paper is planned to discuss the factors controlling this encroachment.

The period of growth resumption

Not until about the first week in March are climatological conditions at all favorable to an awakening of vegetation, and then only on infrequent days; but the month as a whole is marked by the opening of flower and leaf buds of trees and the beginning of the germination of prevernal annuals and the formation of the basal rosettes of the perennials, though some tide over from the previous season. The prevernal bloomers naturally make most rapid progress, aided by their geophytic habit. Not infrequently the temperature falls below freezing and killing frosts ordinarily result. Light snow storms, which rarely occur, may temporarily retard growth. The conditions become progressively more favorable and pass insensibly into the period of the prevernal flowers.

The usual snows and rains of the early part of the month assure abundant moisture. The chresard, which is about 18 to 20 per cent. in the early days of the month, decreases to about 14 per cent. at the middle, and to about 12 per cent. toward the last of the month, thus giving an average chresard of some 15 per cent. The different exposures of the prairie hills, knolls, and ravines progressively recover from the effects of winter in the following order: southeast to southwest, southwest to northwest, northeast to southeast, and northwest to northeast. The frost clings to the northern exposure in ravines,

only leaving toward the latter part of the month, particularly when this exposure is forested. On March 16 on a northwest exposure of a prairie knoll the frost was recorded at the following depths: at base of slope 13.97^{cm}, at middle of slope 30.48^{cm}, at crest considerably below 35^{cm}. Thus the base of the exposure recovers much more slowly than the crest, a condition holding equally true for all exposures; hence vegetation starts earlier upon the upper slopes. However, the chresard increases toward the base of the slope. On March 16 the slope in question showed a chresard at the crest of 7.1 per cent., at the middle of 14.1 per cent., and at the base of 18.2 per cent., the differences being more pronounced and the chresard greater than in any subsequent aspect.

The physical conditions of the period are shown in the adjacent table.

Temperature*			Wind*			Rain*			Light*			Soil§			Mean relative humidity†	Relative evaporation‡
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Relative¶ intensity	Mean cloudiness	Sunshine per cent.	Mean holard	Mean echard**	Mean chresard		
22° C.	−17 C.	2° C.	N. W.	7666	10.3	8	$.11^{cm}$	3.35^{cm}	.459	5.2	51	21.3%	7.2%	14.7%	75.2	.510

* Data from Yankton, United States Weather Bureau, being the means of ten years (1894–1904). The nearness of the station to the field makes the data very representative.

† Data from Sioux City, United States Weather Bureau, being the mean of 8 A. M. and 8 P. M. observations from July 1, 1889, to December 31, 1903. The station is about 30 miles south of Yankton.

‡ Relative evaporation is determined by the formula: R.E. = saturation deficit × average hourly wind velocity × mean temperature centigrade ÷ 1000. It is recognized that such a result is by no means quantitative, yet it may well serve relatively as an index, invaluable in contrasting the floral aspects.

§ Soil data all from station B, Solidago slope, N. W. exposure. For technique see CLEMENTS, Research methods in Ecology. 1905.

¶ Relative light intensity equals sunshine per cent. of theoretical maximum light intensity as determined for Yankton by method of sun's altitude.

** Determined from an experiment on the Windsor bean. It will be used as an index of the non-available water. The chresard is then directly computed from the holard.

Prevernal floral aspect

Floral activity begins only in the first week of April, and is characterized by the

slow and progressive flowering of six forms, extending up to the last week in April, when an apparent break in floral continuity occurs, no forms flowering for a week or ten days. This break very naturally segregates the prevernal floral aspect.

In addition to the floral forms this aspect is conspicuous as the time of appearance of the rosettes of the vernal, serotinal, and autumnal perennials, and seedling annuals of these same aspects. No facies is established, and the tone of the formation is that of winter and early spring, mainly produced by the standing brown stalks of *Solidago rigida*, *Helianthus scaberrimus*, and *Verbena stricta* of the autumnal aspect, which gives everything a brownish cast, enlivened here and there by the mats of *Antennaria campestris* and *A. neodioica*, and at the base of slopes and in depressions by the green of *Poa pratensis* sod. At the base of slopes now and then are to be seen clumps of green produced by the unfolding leaves of colonies of *Symphoricarpus occidentalis*. To complete the aspect, dotted here and there are the floral forms which characterize it. Ruderal species are noticeably absent.

The pertinent climatological conditions of the prevernal floral aspect may be obtained directly from the adjacent table. On only 63 per cent. of the days does the mean average temperature rise above 6° C., with a range between −6° and 29° C. Coupling this with an average soil temperature of 13° C., growth conditions are seen to be far from favorable. The prevailing wind direction is northwest and with a mean

PREVERNAL CLIMATOLOGY

Temperature	Maximum	29 C.
	Minimum	−6° C.
	Mean	11° C.
Wind	Prevailing direction	N. W.
	Total movement	7919
	Hourly velocity	11
Rain	Days	10
	Mean daily	.26cm
	Total	7.87cm
Light	Relative intensity	.547
	Mean cloudiness	4.7
	Sunshine per cent.	63
Soil	Mean holard	20%
	Mean echard	7.2%
	Mean chresard	12.8%
Mean relative humidity		63.7
Relative evaporation		4.392

hourly velocity of 11 miles, which is not exceeded during the other aspects. Precipitation is slight (7.87^{cm}) and falls on only about 33 per cent. of the days. The average cloudiness of the sky (4.7) is low, and the sunshine (63 per cent.) is correspondingly higher, resulting in a low light intensity (0.547). The saturation deficit is here not at its maximum (36.3), but, augmented by the high wind velocity, evaporation, which must necessarily serve as a rough comparative index of transpiration, is rising in amount. While far more favorable for vegetation, it becomes progressively more so, the last half of the aspect presenting conditions in soil and air noticeably more congenial to growth. The chresard decreases steadily during the aspect from 14.8 per cent. on April 17 to 12.2 per cent. on April 25, and a marked difference in holard was evident at crest (15.8 per cent.), slope (18.4 per cent.), and base (22.6 per cent.) on April 18. The average chresard is 12.8 per cent.

SPECIES OF THE PREVERNAL ASPECT

FACIES.—None.

PRINCIPAL SPECIES.—Antennaria campestris,† Carex pennsylvanica,† Peucedanum nudicaule,† Pulsatilla hirsutissima.*†

SECONDARY SPECIES.—Astragalus crassicarpus,† Peucedanum foeniculaceum,* Draba micrantha, Ranunculus ovalis.

* Not occurring in area proper but in vicinity. † Forming associations.

The earliest flowering form is Pulsatilla and occurs copiously to subcopiously and characteristically upon the upper slopes of the prairie hills. It appears several days earlier upon the south to southwest exposure, which holds equally true for the other prevernal bloomers. The early warming-up of this exposure accounts for the above phenological precocity. But the greatest abundance of these prevernal forms occurs on the north to northeast exposure. Maturation follows close upon anthesis, which likewise holds for all prevernal flowering species.

Pulsatilla is followed by the blooming, during the first week of April, of *Peucedanum foeniculaceum* and *P. nudicaule*. The former with its umbel of yellow flowers is of rare occurrence; but the latter with its umbel of white flowers appears even copiously in restricted plats, and in its distribution occurs mainly upon the upper xerophytic

slopes of prairie knolls where the grasses are bunched and the association more or less open, though rarely seen at the crests; it thus not infrequently exerts a subtone effect at short range. It is perennial by means of its geophytic root. With the elongation of its peduncle and spreading of its umbel in maturation during the last week of the aspect, it becomes more conspicuous and persists thus far into the vernal aspect.

The beginning of the second week of the prevernal aspect sees *Carex pennsylvanica* in full bloom. It occurs copiously, extending well up to the crests of knolls, but more abundantly on lower slopes, yet never influences the tone of the aspect. In places Carex may assume almost facial rank, but always maintains a bunchy or isolated distribution, which, however, is quite general. The peculiar yellowish-green shade of its leaves and its yellow staminate spikes which appear after the stigmas make it conspicuous. It is a perennial of xerophytic tendencies, propagating itself by rootstocks and stolons.

Carex is shortly followed by the flowering of *Antennaria campestris*, and with its white tomentose leaves, scapes, and papillate heads, it gives a characteristic local tone to this floral aspect, even from a distance. It occurs usually gregariously, being one of the two mat-forming species of the formation, and is very generally distributed throughout, facilitated by its perfect adaptation to wind dispersal. The mats themselves may be isolated or gregarious, as many as twenty having been noted in a plat of $64^{sq\ m}$, yet single mats frequently cover $16^{sq\ m}$, averaging about 1000 plants to the square meter. Propagation is by stolons and migration is centrifugal, with a slow but positive occupation. Mats unite and take complete possession of extensive plats, yet it yields before *Poa pratensis*, in no way being able to hold its own against this sod-forming mesophyte.

The prevernal floral aspect of the formation is terminated by the appearance of *Ranunculus ovalis*, *Astragalus crassicarpus*, and *Draba micrantha* toward the end of the third week of April. They appear in bloom almost simultaneously, but in no way contribute equally to the aspect. Draba occurs only where the soil is exposed and the grass is bunched, hence on upper xerophytic slopes, and appears to be forced out whenever a close association is formed. It is an annual of marked xerophytic tendencies, its leaves being basal and heavily

pubescent with stellate hairs. It is scarce and its small white flower inconspicuous, so in no respect does it influence the floral tone. Ranunculus is even more restricted, occurring sparsely on lowest slopes and in depressions on the higher slopes, and is apparently related to a high water content of the soil. Its yellow petals soon fall, and its presence might easily be overlooked in a casual survey of the formation. It is a perennial and is an index of mesophytic conditions. Astragalus, with its racemes of violet-purple flowers, is easily marked in the formation. While generally distributed, its abundance is sparse to subcopious, yet frequently it assumes a gregarious habit. It is a perennial of thickened tap roots which branch above and eventually fragment behind, establishing new individuals. Its migration is slow; dispersal is effected mainly by gophers, which store the fruits for winter consumption. However, ecesis is very certain.

Vernal floral aspect

Toward the last of the first or the beginning of the second week in May there is a floral outburst inaugurated by the blooming of *Nothocalais cuspidata* and *Lithospermum angustifolium*, closely followed by *Castilleja sessiliflora*, *Lithospermum canescens*, *Viola pedatifida*, and *Oxalis violacea*, which marks the inception of the vernal floral aspect. Forms are now progressively added up to about the first week of June, when the aspect is distinctly terminated by the general blooming of certain sod-formers. *Astragalus crassicarpus* and *Ranunculus ovalis* have extended over into this aspect, the former reaching its maximum flowering about the second week in May, thus entering conspicuously into the vernal period. The fruiting scapes of *Peucedanum nudicaule* enter into the tone, while *Antennaria campestris* with its white fruiting heads is now more noticeable than earlier. The deadened brown tone of the prevernal aspect is at last relieved and replaced by the green of the grassy sod, which is rendered somewhat bizarre by the very general distribution of some twenty-eight flowering forms, the largest number occurring in any aspect. No floral facies is developed except in the case of *Poa pratensis* at the base of slopes, and then only in the later part of the aspect. Most of the prairie annuals have by the later part of the aspect ap-

peared and those of the following aspect are now all ready to bloom. Much growth has taken place in the summer perennials and they have apparently outstripped the autumnal forms. Together they overtop the majority of the vernal group, and toward the end of the aspect the large cauline leaves of Solidago and Helianthus of the autumnal aspect render many of the low-statured bloomers quite hidden, except in the very open associations on the highest slopes and crests. Four ruderals bloom in this aspect but have little influence on the formation.

The summary clearly indicates the significant climatological facts. Physiological activity ensues practically throughout the aspect; the temperature range of 31° C. to 2° C., with a mean of 16° C., rarely inhibiting growth. The wind is dominantly from the south and east quarters. It reaches during this aspect a less total movement and so a less mean hourly velocity than in the prevernal, but the atmosphere has a much lower relative humidity; the relative evaporation is thus nearly twice as great. Couple this with the highest light intensity (.704) and the beneficial results of 8.19^{cm} of precipitation on twelve days are much reduced. The chresard shows a marked decrease from 14.1 per cent. on May 10 to 7.4 per cent. on May 22, though the average chresard for the aspect is 10.7 per cent. The base (12.7 per cent.), slope (14.6 per cent.), and crest (8.8 per cent.) on May 22 still showed a gradation in holard, though the distinction of position is less marked than in the prevernal aspect.

VERNAL CLIMATOLOGY

Temperature	Maximum	31 C.	
	Minimum	2 C.	
	Mean	16 C.	
Wind	Prevailing direction	E.	
	Total movement	6877	
	Hourly velocity	9.2	
Rain	Days	12	
	Mean daily	.26^{cm}	
	Total	8.19^{cm}	
Light	Mean cloudiness	5.2	
	Sunshine per cent.	73	
	Relative intensity	.704	
Soil	Mean holard	17.9%	
	Mean echard	7.2%	
	Mean chresard	10.7%	
Mean relative humidity		51.7	
Relative evaporation		7.109	

SPECIES OF THE VERNAL FLORAL ASPECT

FACIES.—Poa pratensis† (base of slopes and in depressions).

PRINCIPAL SPECIES.—Spiesia Lamberti sericea, Sisyrinchium angustifolium†, Antennaria campestris,*† Spiesia Lamberti, Castilleja sessiliflora.†

SECONDARY SPECIES.—Viola pedatifida,† Oxalis violacea,† Lithospermum canescens, Carex Meadii,† Meriolix serrulata, Hedeoma hispida, Plantago Purshii,† Antennaria neodioica,† Lithospermum angustifolium, Oxalis stricta, Carex festucacea,† Polygala alba, Poa compressa,† Astragalus crassicarpus.*†

TERTIARY SPECIES.—Pentstemon gracilis, Nothocalais cuspidata, Linum rigidum, Lappula texana, Astragalus plattensis, Gaura coccinea, Senecio plattensis, Psoralea esculenta, Vicia linearis, Osmodium molle, Astragalus hypoglottis, Viola cucullata.

RUDERAL SPECIES.—Lepidium virginicum, Melilotus officinalis,† Melilotus alba,† Lappula Lappula.

* From earlier aspect. † Forming associations.

The first week in May is marked by the flowering of *Nothocalais cuspidata* and *Lithospermum angustifolium*. The solitary yellow head of the false calais, frequently 5^{cm} in width terminating a long (20 to 30^{cm}) naked scape, makes it very conspicuous, though it is never more than sparse to subcopious. It is largely confined to loosely sodded ridges and high slopes, and is pronouncedly of xerophytic tendencies. It is perennial by an excessively thickened root. The achenes are heavily provided with pappus, assuring a wide dissemination.

Nothocalais has scarcely bloomed before the puccoons are in flower, *L. angustifolium* appearing several days before the hoary puccoon (*L. canescens*). The former with its terminal leafy racemes of light-yellow flowers and its sparse occurrence remains an inconspicuous element. The hoary puccoon occurs throughout with the other, but more abundantly. Its orange-yellow flowers in a compact leafless umbel make it perhaps the most conspicuous though it is not the most abundant element in the vernal aspect. Both of the puccoons are abundantly pubescent and in their structure and distribution show marked xerophytic tendencies. They are perennials by deep thick roots. The smooth nutlets preclude all but a very limited migration.

Castilleja sessiliflora, Viola pedatifida, Oxalis violacea, Sisyrinchium angustifolium, and *Spiesia Lamberti sericea* bloom pro-

gressively during the second week of the aspect, and together produce a very noticeable change in the floral tone, a change which is further accentuated by the forms that occur later. The yellow tone given by the puccoon becomes dotted here and there by yellow, blue, violet, white, and purple, and a bizarre tone is the result. Castilleja occurs rarely and of a very restricted distribution, being confined to associations upon upper slopes, where its pale-yellow flowers render it always inconspicuous. The thickened perennial roots are parasitic upon the roots of other plants. Many flowering stalks may arise from one root, thus assuming a bunch habit. The high immobility of the seeds, resulting in a very restricted distribution, accounts for its gregarious habit and local occurrence upon the prairie.

Viola pedatifida with its bright-blue flowers and unrestricted distribution and sparse to subcopious abundance exerts a characteristic effect on the vernal tone. The prairie violet is a perennial from a fleshy short rootstock.

Oxalis violacea seems somewhat restricted to middle and lower slopes, where it may occur densely in open, matlike patches, resulting from a slow centrifugal migration through bulb formation coupled with a positive ecesis. Though acaulescent and of low stature, its gregarious habit and rose-purple flowers, with their green background of palmately trifoliate leaves, make it in restricted plots of primary floral importance in the aspect. It likewise occurs sparsely but generally distributed over all parts of the formation, with the exception of crests and Poa sod, where it exerts only a minor effect. The shallow scaly brown bulbs indicate its perennial nature. Dissemination is by propulsion, the few seeds formed being not distantly ejected from the pentalocular ovary by the recurving of the loculicidally dehiscing carpels. In this we have a still further explanation of its gregarious tendency.

Characterized by a general distribution, a subcopious abundance, and the "bunch-habit" of growth which aggregates its many blue and white flowers, *Sisyrinchium angustifolium* becomes of first prominence in the vernal floral aspct. It is perennial by short fibrous rootstocks. It is abundantly fertile, and the smooth ovoid seeds are discharged but weakly by the loculicidally dehiscing tricarpellate capsule.

The stemless loco-weeds, *S. Lamberti* and its somewhat earlier flowering and more abundant silky variety, *S. Lamberti sericea*, are acaulescent perennial herbs from thick deep roots. Their dense spikes of dark-purplish flowers borne on long peduncles, a restricted though subcopious distribution upon the higher slopes, and silky pubescence make them very conspicuous, easily dominating in the aspect. The middle of the aspect is controlled by the variety, but the type, which flowers some ten days later, holds the floral dominance for the remainder of the vernal aspect. The type is decidedly more mesophytic in its structure and distribution, and it seems evident that the variety is very possibly a xerophytic mutant of *S. Lamberti*. Propagation occurs through fragmentation of the perennial root, producing as in Astragalus a gregarious habit. A limited seed dispersal furthers this patchy distribution.

Noteworthy on account of their rarity in the aspect are *Astragalus plattensis*, *A. hypoglottis*, and *Viola cucullata*, all flowering toward the end of the second week in May. The Astragali occur only in open association toward the crest and are strikingly inconspicuous. They are both decumbent and perennial. The two-valved pod of *A. plattensis* is fleshy and dehiscent and its seed dispersal is accomplished through limited propulsion. *Viola cucullata* is noteworthy, as only a single individual has been recorded in the area and that on the middle slope of a northwest exposure, doubtless the result of fortuitous distribution.

The third week is characterized by the blooming of *Antennaria neodioica*, *Carex Meadii*, *C. festucacea*, *Vicia linearis*, *Senecio plattensis*, and *Pentstemon gracilis*. Early in the third week *Antennaria neodioica* flowers; it appears to be more mesophytic than *A. campestris*, occupying the lower slopes, and it occurs less abundantly, but with the fruiting scapes of the earlier species the antennarias are scarcely second to any forms in conspicuousness. *A. neodioica* is a stoloniferous perennial and forms mats, its rosettes living over winter. It is easily distinguished even at a distance by its large and lighter-colored mats, and by the fact that it flowers while the other species is undergoing maturation and distribution.

The carices appear at about the same time toward the last of the week. *C. Meadii*, however, is earlier and occurs sparsely on lower

slopes and is found inclusive in Poa sods. *C. festucacea* occurs likewise on lower slopes, but more abundantly and assumes the "bunch-habit" of growth. Both the carices perennate and propagate vegetatively by rhizomes. They contribute little if any to the floral tone of the aspect.

Florally associated with the carices, as just noted, are *Vicia linearis*, *Senecio plattensis*, and *Pentstemon gracilis*, to which are soon added *Lappula texana* and *Plantago Purshii*. Vicia occurs rarely, is confined to lower slopes, and exerts no tone effect; it is a perennial form and is pollinated by bees. Senecio, also of rare occurrence, seems to be confined to mesophytic portions of the formation. It is conspicuous on account of its numerous yellow heads and ray flowers. But for its limited occurrence it might easily dominate the tone, and in the vicinity of Sioux City it was recorded as controlling the aspect. The achenes are provided with a copious pappus and a wide distribution is assured. It is a perennial, and its scarcity seems to indicate that it is of decidedly mesophytic tendencies; it may be considered prophetic in our area. *Pentstemon gracilis*, though rarely a component in any plot, is an interesting form. It is confined to the mesophytic portions of the prairie and has been noted as abundant in western Iowa. Its rarity in our area is explained as in the case of Senecio; it is a perennial, and its smooth though numerous seeds are limited in their distribution. *Lappula texana*, the hairy stick-seed, is also a minor element, occurring mainly on lower slopes in sparse abundance. It is much branched and its numerous small blue flowers exert but a restricted effect. It is an annual and very fertile, producing numerous nutlets whose margins are each bordered by a single row of bristles with recurved tips; distribution is entirely by aid of animals. It continues to bloom well into the estival aspect. The prairie plantain, *P. Purshii*, is a woolly annual whose indeterminate spikes rise some 20^{cm}. Of copious abundance and of gregarious habit, it frequently becomes conspicuous at short distances. Its flowers bloom progressively up the spike, reaching the maximum in the early estival aspect and continuing well into July. Its highly immobile seeds prevent other than a limited distribution, thus readily accounting for its gregarious habit.

The fourth week of the aspect, about the last week in May, is

remarkable for the general flowering of *Poa pratensis*. *P. compressa* is associated, but occurs sparsely and principally upon the upper slopes. The relative place of these two forms has been hard to determine, but it seems that *P. compressa* occurs as a forerunner of the bluegrass. In its distribution *P. pratensis* is confined to depressions and lower slopes, and is always indicative of the highest soil-water content, the most favorable exposure, and richest humus. In these situations it forms a dense sod, frequently exclusive, which is constantly pushing up the slopes replacing the bunch-grasses, outlying individuals frequently reaching the higher slopes. It is perhaps one of the most mesophytic of prairie forms, and is almost invariably the forerunner of the prairie shrubs, *Symphoricarpus occidentalis* and *Rhus glabra*. It reaches its highest development on the northwest exposure, and it is up this exposure that the flood-plain and ravine forest of this region has made its greatest advance upon the prairie. Poa is the first facies to bloom, but as noted above is of restricted distribution. It is a perennial and propagation is rapid by the abundant rootstocks, which leads to dense sod.

With the bluegrass are successively added *Oxalis stricta*, *Linum rigidum*, and *Polygala alba*. Never very abundant and of low stature, they add but little to the tone of the aspect, as they are overtopped by the oncoming facies of later aspects. Oxalis appears on lower slopes, possessing frequently a gregarious distribution. It may be either annual or perennial. The few seeds are restrictedly dispersed by the dehiscing capsules. Linum is a decidedly xerophytic annual, being a relict of earlier stages. It appears in the open association on the upper slopes and along prairie crests. It is never common and its fugacious petals prevent all but entire inconspicuousness. Its seeds are few and their mobility little. Polygala is sparingly distributed over the lower slopes of prairie knolls, always working up to higher positions with the increase of mesophytic conditions, but it never remains in the Poa sod. It is perhaps one of the best indices of progressive mesophytism among the prairie species. It is a perennial from woody rootstocks. Seeds are borne two in a capsule and migration is very slow.

As the vernal floral aspect is drawing to a close, several minor elements bloom, extending vernal floral activity over into the first

few days of June. *Gaura coccinea, Meriolix serrulata, Psoralea esculenta, Hedeoma hispida,* and *Osmodium molle* now progressively appear. Though flowering during the transition from vernal to estival aspect, these forms reach their maximum display during the early estival; particularly is this true of Meriolix, Hedeoma, and Osmodium. They should be considered transitional species, which appear during the unsettled climatological conditions between the vernal and estival periods, and are not specially indicative of either. Of subcopious occurrence and largely overtopped by leafy stalks of autumnal forms they must be ranked as almost neutral in the floral aspect. *Gaura coccinea* is a relict of more xerophytic stages and occurs primarily though sparsely in the open association of upper slopes and crests. It is an annual and a low and obscure element. It bears a few-seeded indehiscent nut of little mobility. Meriolix may also be considered as a relict of the xerophytic stages of the prairie, having its present distribution limited to the open association along crests and upper slopes, where it frequently occurs subcopiously. Its large yellow flowers make it conspicuous, but only at short range, as low stature relegates it to a sublayer. It is a slightly shrubby perennial from a woody root, producing numerous seeds which are strikingly immobile. It continues blooming up into the autumnal floral aspect, but reaches its maximum in the early estival. Psoralea is rare and of solitary occurrence on middle slopes; add to this its inconspicuous fading-blue flowers and it is scarcely seen upon the prairie by the casual observer. It is a perennial from a large edible farinaceous tuberous root. In the autumnal aspect, breaking off close to the ground, it becomes a tumble-weed. Its rarity is problematical. Hedeoma, a low annual, scarcely ever more than 20^{cm} high, occurs subcopiously and not infrequently copiously upon middle slopes. Its low stature and leafy branches completely hide its abundant small blue flowers, rendering it ever inconspicuous. Osmodium occurs sparsely though quite generally over the whole formation, with the exception of the very crests. It is a perennial with several stalks, terminated by leafy, pendent, scorpioid racemes of greenish flowers, arising from a thick root. It is also quite unnoticeable. The smooth nutlets possess limited mobility.

The estival floral aspect

Marked by a conspicuous decrease of the vernal floral display, a decided climatological change, the flowering of certain sod-formers initiated by *Panicum Scribnerianum* and followed by *Koeleria cristata* and *Stipa spartea*, and the rapid addition of several prominent estival flowers, which all results in a complete shift of the floral tone, the estival floral aspect begins toward the last of the second week in June and extends well up into middle July, when it is terminated by a climatological and floral change even more pronounced.

Toward the end of the vernal aspect the leafy stalks of oncoming facies render the floral tone weak and in places drown it in a sea of dark green; however, the estival forms like Erigeron, Delphinium, Brauneria, Ratibida, Kuhnistera, and others seem to push rapidly above these, forming a higher floral stratum than the vernal, but to be overtopped later on by the still higher stratum of autumnal forms.

With the shifting of climatological conditions, which is very generally appreciated, comes the blooming of *Rosa arkansana*, *Erigeron ramosus*, *Delphinium carolinianum*, and *Brauneria pallida*, which with the sod-formers noted above are always indicative of the inception of the estival aspect. The physical factors of the soil have become less contrasting on the various slopes and between different positions on the same slope; still the south exposure seems slightly earlier. The middle and base of slopes closely approach in absolute water content and are less separated from the crests in this respect than in earlier aspects. Correspondingly there appears a more uniform plant-covering at this time. It is to be noted that the holard is markedly much lower than in the vernal aspect.

During this time Solidago, Helianthus, and Aster have become vegetatively of primary importance and give the general tone of dark green to the aspect. Extending over from the vernal aspect and largely occurring on the upper slopes are *Polygala alba*, which on account of its indeterminate inflorescence blossoms through the the entire estival aspect, Meriolix, and *Gaura coccinea*. Hedeoma and *Oxalis stricta* continue blooming on the middle slopes. The dominating species added in this aspect are *Koeleria cristata*, *Ratibida columnaris*, *Symphoricarpus occidentalis*, and *Verbena stricta*. The floral forms added in this aspect are twenty-one in number, nine

less than appeared in the vernal aspect. It should also be noted that six new ruderals are added. *Panicum capillare* and *Hordeum jubatum* not infrequently attain no small significance. The latter frequently establishes in waste situations exclusive associations. Its permobile awned spikelets being readily carried by wind or animal, its migration is rapid. In the autumnal aspect *P. capillare* becomes detached at the surface, and the large and profusely branched panicles go tumbling over the prairie until lodgment stops the distribution.

In addition to the floral delineation of the estival from the vernal aspect, it is strongly set off by a change in the climatological conditions. With the introduction of hot dry days and prevailing southern winds the estival aspect begins. The precipitation is slightly higher than in the vernal aspect, but its effect is strongly offset by an average mean temperature some 5° higher than in the vernal. The average hourly wind velocity is 0.9 less and the relative humidity 3.4 lower, the lowest of any aspect. Coupled with these conditions is the fact that the relative evaporation is 1.6 higher, the greatest evaporation of any aspect occurring in the estival.

The holard has a slight rise in the aspect due to the heaviest mean daily rainfall of the season. The chresard thus rises to 11 per cent. on June 6 to fall to 8.9 per cent. on June 22 and 6.5 per cent. on July 7. On June 22 distinction of position seemed nearly eliminated, the base, slope, and crest registering a holard of 15.9, 16.1, and 16.6 per cent.

ESTIVAL CLIMATOLOGY

Temperature	Maximum	35° C.
	Minimum	6° C.
	Mean	21° C.
Wind	Prevailing direction	S. to E.
	Total movement	5839
	Hourly velocity	8.1
Rain	Days	13
	Mean daily	.31 cm
	Total	9.29 cm
Light	Mean cloudiness	4.7
	Sunshine per cent.	56
	Relative intensity	.551
Soil	Mean holard	16%
	Mean echard	7.2%
	Mean chresard	8.8%
Mean relative humidity		48.3
Relative evaporation		8.794

respectively. Yet the average chresard for the aspect (8.8 per cent.) shows a steady decrease from that of the vernal (10.7 per cent.).

SPECIES OF THE ESTIVAL FLORAL ASPECT

FACIES.—Koeleria cristata,† Poa pratensis.*†

PRINCIPAL SPECIES.—Ratibida columnaris,† Amorpha canescens,† Erigeron ramosus,† Symphoricarpus occidentalis,† Verbena stricta,† Festuca octoflora.†

SECONDARY SPECIES.—Brauneria pallida, Delphinium carolinianum, Rosa arkansana, Linum sulcatum, Panicum Scribnerianum, Meriolix serrulata,* Euphorbia marginata, Potentilla hippiana, Plantago Purshii,* Hedeoma hispida,* Polygala alba,* Hedeoma hispida.*

TERTIARY SPECIES.—Stipa spartea, Aristida purpurea, Allionia linearis, Acerates viridiflora linearis, Osmodium molle,* Anemone cylindrica, Physalis heterophylla, Gaura parviflora, Gaura coccinea.*

RUDERAL SPECIES.—Hordeum jubatum, Ixophorus viridis, Panicum capillare, Melilotus alba,* Lappula Lappula,* Verbena bracteosa, Allionia nyctaginea, Potentilla monspeliensis, Melilotus officinalis,* Lepidium virginicum.*

* From earlier aspect. † Forming associations.

Koeleria cristata is a perennial bunch-grass and a very important sod-former, and may be considered one of the forerunners of the blue-grass. It occurs generally distributed higher up the slopes, where not infrequently it may reach facial rank. Above it seems to be encroaching upon the grama and buffalo grasses and so is quite lacking at the crests. *Panicum Scribnerianum* is likewise a perennial of the bunch habit and is closely associated with Koeleria in distribution, but never appears so abundantly as to become a facies. It is evidently more of a mesophyte than the latter and follows it up the slopes. In the formation studied it is mostly confined to the lower part of the middle slopes. It blossoms slightly before Koeleria. *Stipa spartea* is likewise a bunch-grass and the most xerophytic of these three grasses. It is sparsely distributed upon the uppermost slopes and crests and never forms a facies. It must be rated as an unimportant element in sod-establishment in the formation.

Almost coincident with the sod-formers listed above, blooms the prairie rose, *Rosa arkansana*. It is the first woody perennial to bloom and is distributed over upper slopes and crests where in the latter habitat it commonly becomes copiogregarious. Its abundance, large pink flowers, general anthesis, and height make it always one

of the most conspicuous elements of the early estival aspect. Its prominence, however, is of passing duration, as the petals fall after several days and it passes into obscurity. Mobility is limited, resulting largely in the gregarious distribution. With Rosa, blooms *Delphinium carolinianum*. It is a perennial with a thick heavy rootstock, and occurs sparsely as a xerophyte in the open association upon upper slopes and crests. It is closely associated ecologically with the bunch-grasses and invariably seems to follow them. Its single erect stalk, some 6 to 8^{dm} high, bears a large terminal raceme of conspicuous white flowers. Rising thus so conspicuously, these plants seem like sentinels of the prairie and a few individuals are noticeable at some distance. Many seeds are produced, but mobility is slight.

The anthesis of *Erigeron ramosus* usually precedes that of Delphinium but follows that of Rosa, only a day or two separating them. Erigeron is a perennial or annual occurring along upper slopes, where it assumes a copiogregarious habit of growth. It seems quite restricted, few scattering individuals being noted. It is some 7 or 8^{dm} high, with several stalks rising from a single root, which are terminated by spreading corymbs bearing numerous flowers with yellow disks and abundant white rays; thus it is very conspicuous. The achenes are provided with a double pappus, but mobility would seem limited, judging from the gregarious tendency of distribution. Brauneria, though occurring sparsely upon the highest slopes and crests, is one of the most conspicuous early estival bloomers. It is a xerophytic perennial with a large thick root. A single stalk, some 7 or 8^{dm} high, is terminated by a single large head of flowers frequently 5^{cm} across. The numerous long pinkish ligulate ray-flowers surround a large reddish-brown hemispheric head bristling with abundant roughish chaff; in all a very prominent structure. The achenes are crowned with a short-toothed pappus, thus insuring mobility, though of a low degree. It is to be noted that Brauneria has a blooming period of nearly two months, so it remains a conspicuous element even into the following aspect.

Scarcely have these forms flowered, when two species of secondary importance begin to make their contribution to the floral aspect, blooming progressively during the earlier part of the third week of June. They are *Anemone cylindrica* and *Physalis heterophylla*.

These two perennials add little or nothing to the tone of the aspect, as they are of sparse occurrence and decidedly inconspicuous. Anemone occurs rarely though widely on upper and middle slopes. Physalis is of rare occurrence on lower slopes, but would be noticeable except for the pendent inflorescence which hides the yellow flowers beneath the leaves. The former rises some 50 to 60^{cm}, with its exposed cylindrical head of numerous woolly achenes, which are subject to wide dispersal. The immobile fruit of the latter and its ventral position cooperate to insure a very restricted dissemination.

The last days of the third week and early part of the fourth are marked by the general flowering of three forms, *Ratibida columnaris*, *Symphoricarpus occidentalis*, and *Verbena stricta*, all of primary importance. *Gaura parviflora*, *Linum sulcatum*, and *Allionia linearis*, three flowering forms of minor significance, are added at about the same time. Linum is an annual some 40^{cm} high, occurring sparsely upon the lower slopes. Its humble place in the floral tone is largely due to its limited occurrence, for its yellow flowers (1.5^{cm} in diameter) would otherwise make it a notable element. Gaura is noteworthy mainly as a matter of record, a few specimens only being noted on the middle slope of a northwest exposure. It is an annual and frequently reaches a height of 1^{m} or more. Allionia is a perennial occurring rarely upon middle slopes. The straw-colored involucre incloses one to three small purplish flowers and it is always of minor prominence. The anthocarpous fruit has little mobility. About this time are also added two sod-forming species, *Festuca octoflora* and *Aristida purpurea*. Aristida is of rare occurrence and contributes little to the floral aspect or plant covering. Festuca, on the other hand, is a sod-former of some significance upon lower and middle slopes, being easily replaced however by Poa, which seems to follow it. It is apparently a pioneer form, taking rapid possession of available ground in the open association by means of its heavy, thick, matlike sod.

In Ratibida the long yellow ligulate ray-flowers first spread about June 20, but it is not until several days later that there is a general display and the tube flowers of the columnar disk begin to open. They flower first in a band at the base of the indeterminate head, progressing up at the rate of about 3 to 5^{mm} a day. The plants are

some 7.5^{dm} high, and each of the branches is terminated by a very striking head; yellow drooping rays, 6 to 9 in number and frequently 3^{cm} long, surround a deep-brownish columnar head some 4^{cm} high. The prairie cone-flower occurs copiously upon lower and middle slopes, extending crestward (*fig. 1*). In the former locations it frequently assumes almost facial rank and gives a bright-yellow tone to the entire floral aspect. It is a prolific and continuous bloomer, dominating the aspect through the month of July and the greater part

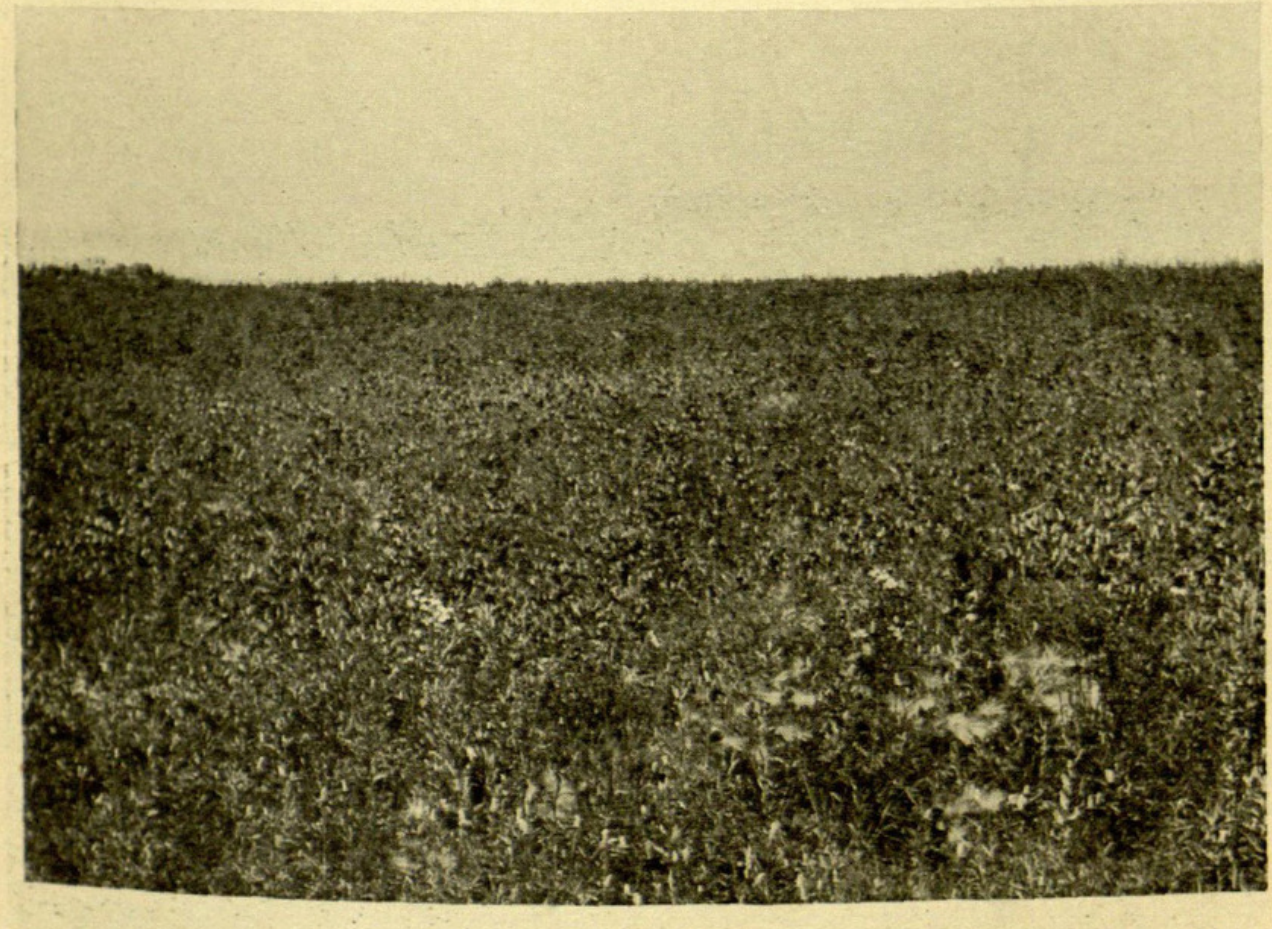

FIG. 1.—Late estival aspect; *Ratibida columnaris* upon a middle slope; the ruderal *Hordeum jubatum* in right foreground.

of August, and extending up to the middle of September. Ratibida is a perennial from a thick root. The achenes are provided with a diminutive pappus of one or two teeth, and so lack of mobility and great fertility result in its copious abundance in restricted localities. It should be recorded that a few specimens with reddish-brown rays having yellow tips and bases have been noted.

At about the time Ratibida is spreading its neutral ray-flowers the earlier flowers of Symphoricarpus appear, reaching their maximum flowering two or three weeks later. The wolfberry is of restricted

distribution, occurring gregariously at the base of slopes and in mesophytic depressions; frequently outlying individuals are found. In the former situations it ranks not infrequently as a facies. It is the largest of the woody perennials of our area, being a profusely branched shrub frequently 1 to 1.25^{m} tall. It is characteristically associated with the Poa sod, which it follows in the latter's advance upon the prairie; the most advanced occupation is upon the north

FIG. 2.—Late estival aspect; Symphoricarpus association in a depression of a northwest exposure; Poa sod in foreground.

to northwest exposures, where it also first appears (*fig. 2*). It is the forerunner of *Rhus glabra*, which in other parts of the prairie follows it closely, together making up the shrub stage, which is succeeded by the *Quercus macrocarpa* and *Ulmus fulva* association as the forest pushes out upon the prairie. While the numerous axillary clusters of pink flowers are not conspicuous from a distance, the masses of dark-green leaves make the Symphoricarpus association very noticeable. Very few seeds are borne in the white globular berries;

immobility and high ecological demands result in its gregarious habit. The berries are persistent and birds may help somewhat in dispersal.

The last of this group to bloom is *Verbena stricta*. About June 25 the purplish-blue flowers make their appearance at the base of the long (15–30^{cm}) indeterminate terminal spikes in a narrow band, which moves upward day by day at the rate of about 1 to 2^{cm}. The maximum flowering, however, seems to be reached about July 10 to 20.

FIG. 3.—Late estival aspect; *Verbena stricta* determining the tone of a lower slope; the white patches are the ruderal *Hordeum jubatum*.

Like Ratibida and for the same reason, it flowers abundantly through July and August and into September. It has a copious and general distribution and not infrequently assumes a dominating influence upon lower (*fig. 3*) and upper slopes as well as crests. It is a perennial from a heavy root and several stalks from the same root give it not infrequently a "bunch" appearance.

During the last days of June and the first days of July, several forms appear to complete the estival floral aspect. In order of flowering they are *Acerates viridiflora linearis*, *Potentilla hippiana*, *Euphorbia marginata*, and *Amorpha canescens*. All assume local

importance except Acerates, reaching their maximum display in the serotinal aspect. Acerates appears rarely and as a solitary xerophyte upon the higher slopes and along crests. It is a perennial with numerous permobile comose seeds, yet its abundance is always low. Its solitary umbel of greenish flowers, which blend with the foliage of the prairie, renders its detection difficult. Potentilla possesses a copiogregarious or a solitary distribution along the middle and lower slopes. It rises 50 to 70^{cm}, with the erect stems terminating in loose cymes of numerous yellow flowers. It thus exercises a local effect in the floral aspect. Through its numerous annual rosettes it also contributes in a limited degree to the plant covering. It is a perennial from a thick root. The numerous achenes are highly immobile, resulting in a limited distribution and the gregarious habit. The white-margined spurge, *Euphorbia marginata*, is an annual which occurs subcopiously on lower slopes and rises erect to a height of 50 to 75^{cm}. The stems bear abundant bright-green leaves and are terminated by three-rayed umbels whose greenish-white flowers are subtended by involucres of numerous white-margined bracts, making the entire umbel a very conspicuous object. *Amorpha canescens* is a prominent perennial shrub (50 to 90^{cm} high) exerting a controlling influence. It is a marked xerophyte and may rise to primary rank upon the crests in a sub-copiogregarious distribution, but rarely occurs upon the lower mesophytic slopes. Its gregarious habit and its abundant and densely white canescent leaflets and densely clustered terminal spikes of dark-blue flowers make it a very striking object, especially when it occurs in such abundance. With sod-establishment it gradually disappears, being a characteristic component of the bunch-grass stage. The indehiscent one-seeded pod is highly immobile.

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