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Sixty-one years of secondary succession on rangelands of the Wyoming High Plains

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Abstract

The slow and uncertain rate of recovery of plant communities after severe disturbance is a major problem on rangelands. Earlier studies sketched the outline of secondary succession on mixed-grass prairie, but were based on 1 or 2 years of observation on different areas disturbed at different times in the past, or several years of observation of a single area. To provide a more complete picture of succession over decades, we began observations in 1977 on 4 areas disturbed from 1 to 51 years previously, and on undisturbed areas of the same 2 soil types with and without grazing. Observations continued for 11 years. Secondary succession proceeded through the usual stages: annual forbs, perennial forbs and annual grasses, short-lived perennial grasses, and long-lived grasses. Western wheatgrass [*Pascopyrum smithii* (Rydb.) A Love] was an exception because it appeared much earlier and in much greater abundance than other long-lived perennial grasses. Blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex. Steud.] may be another exception; total recovery of this grass may require centuries. Time of appearance in succession seemed to be related to availability of propagules and ease of establishment; persistence of species was related to competitive ability. Abundance of many species fluctuated widely from year to year, but fluctuations did not appear to be related to precipitation. After 61 years, secondary succession had not returned plant communities to the climax state.

Key Words: competition, disturbed land, mixed-grass prairie, plant communities, revegetation, vegetation structure

Haug and VanDyne (1968) and Laycock (1991) reviewed studies of secondary succession on disturbed rangelands in the western US, but found few detailed studies of secondary succession on mixed-grass prairie similar to that on the Wyoming High Plains.

Judd and Jackson (1939) and Judd (1940) identified 4 stages of secondary succession on abandoned fields in Nebraska and Montana: an annual weed stage, from 1 to 3 or more years after abandonment; a mixed annual-perennial stage on fields abandoned 2 to 4 years; and a perennial grass and forb stage after 3 to 8 years preceded the fourth or climax stage, occurring as early as 8 years but usually requiring 10 to 15 years. As length of cultivation increased, the time to reach each stage also increased. Small and narrow fields recovered more rapidly than large fields and fields adjacent to undisturbed prairie recovered more rapidly than those at some distance. Moderate grazing seemed to hasten recovery, while close grazing had the opposite effect.

Tolstead (1941) identified similar stages in secondary succession on old fields in South Dakota[1]. In southern Alberta, on range where undisturbed vegetation was similar to that on Wyoming mixed grass prairie, cover of blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex. Steud.] was less on abandoned and naturally revegetated sites than on comparable undisturbed sites, even after 56 years of secondary succession (Dormaar and Smoliak 1985).

On the shortgrass prairies of northeastern Colorado, Costello (1944) and Shantz (1917) identified 5 and 6 stages, respectively, in recovery of abandoned land. They concluded that the climax mixed prairie association may appear 20–25 years after abandonment but may require 40–50 years. Shantz (1917) studied narrow roads; sources of propagules were never more than a few meters away, and some propagules may have been present in the road when it was abandoned. Costello (1944) studied large fields, where propagules likely were destroyed by years of cultivation and sources of new propagules were some distance away, depending on the size of the fields. Coffin and Lauenroth (1988), Glenn and Collins (1992), and Samuel and Hart (1992) noted the importance of gap size and distance to seed sources in revegetation of disturbances on rangeland.

Reichhardt (1982) found that blue grama was the dominant species by 20 years after disturbance of shortgrass, and buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] was co-dominant by 40 years after disturbance. Reichhardt considers that these grasses survived all through the years in which the fields were cultivated, and agrees with Costello (1944) and Hyder et al. (1971, 1975) that establishment of blue grama from seed under the present climatic conditions on shortgrass prairie is highly unlikely, for reasons presented by Briske and Wilson (1978) and Wilson and Briske (1979).

Most of the previous studies on mixed-grass and shortgrass prairie involved single observations of different fields disturbed at different times in the past, or repeated observations of a single field or of several fields all disturbed at approximately the same time. In 1976, Current (1978) identified 4 areas on the High Plains Grasslands Research Station, northwest of Cheyenne, Wyo., from which vegetation had been removed at different dates in the past. These areas provided a unique opportunity to study secondary succession on land denuded from 0 to 50 years in the past. We followed secondary succession on these areas for 11 years, and linked the data from the 4 areas to compile a 61-year history of revegetation with gaps of only a few years. The technique is similar to that used in dendrochronology, in which many series of tree rings, each providing a record of growth response to climate for a few years or decades, are linked to provide a centuries-long climatic record (Bannister 1970). We also compared the vegetation under secondary succession to undisturbed and ungrazed vegetation on the same 2 soil types, and to undisturbed and grazed vegetation on one soil.

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[1]Nomenclature on older studies is sometimes outdated; our nomenclature follows Britton and Brown (1913), Hallsten et al. (1987) and Lackschewitz (1991).

Table 1. Descriptions of study areas.

Years disturbed First	Last	Type of disturbance	Soil series[1]	Area	Grazed during study?	Section[2]
				ha		
1926	1926	Plowed, seeded	Ascalon	15.4	Yes	8
1932 (app.)	1941	Plowed, cultivated yearly	Altvan	1.0	Yes	9
1965	1965	Scraped	Altvan	0.3	No	3
1966	1976	Scraped yearly	Altvan	1.5	No	3
		Not disturbed	Altvan	—	Yes	8
		Not disturbed	Altvan	—	No	3
		Not disturbed	Ascalon	—	No	3

[1]Stevenson et al. 1984; both Ascalon and Altvan are Aridic Argiustolls.
[2]All in Township 14 North of Base Line, Range 67 West of 6th Principal Meridian.

Materials and Methods

Study Areas

Four disturbed and 3 undisturbed areas were studied; peak standing crop, contribution of major species and species groups to peak standing crop, and frequency of occurrence of major species on each area are presented in Figures 1–3.

Current (1978) determined the history of these areas (Table 1). The areas last disturbed in 1926 and 1941 and the undisturbed but grazed Altvan sandy clay loam (Aridic Argiustoll) were in the public domain until 1914. Under private ownership 1914–1925, they were grazed at 20 to 30 head of cattle per section (259 ha) in most years, but up to 100 head per section in a few years. The area last disturbed in 1926 was plowed that year and seeded to hay (species unknown), which soon died. In 1928 the 2 sections became part of the Cheyenne Horticultural Field Station, now the High Plains Grasslands Research Station. In the early 1930's, about 1 ha in Section 9 was plowed and windbreak trees were planted; the area was cultivated annually through 1941. Most of the trees died within a few years after planting; none were visible in a 1956 aerial photograph. These areas were grazed by 4 to 8 head of draft horses per section 1930–1954; 100 ewes with lambs per section in the summers of 1954–1957; and 40 steers per section in the summers of 1957–1973. From 1973 to 1987 these areas were included in grazing studies with stocking rates of 0.4 to 1.3 AUM/ha (Hart et al. 1983, 1988, and 1993).

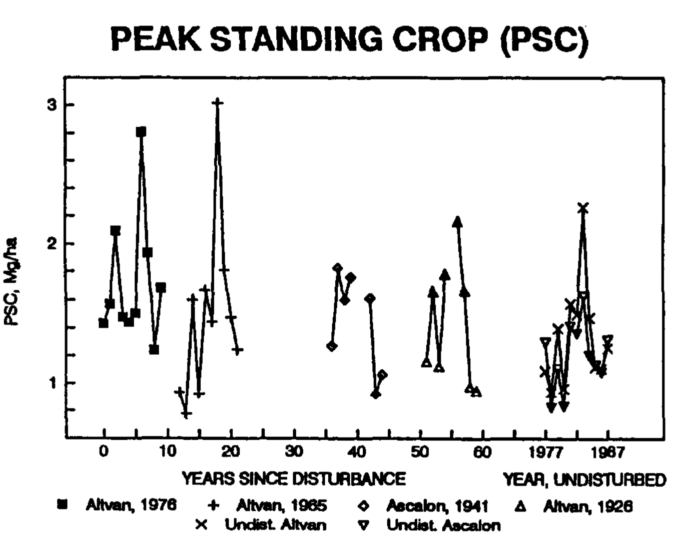

Fig. 1. Peak standing crop of aboveground biomass on disturbed rangeland, 1–61 years after disturbance, and on undisturbed rangeland on 2 soil types. Symbols not connected by lines indicate intervening year(s) in which no data was taken. See Table 2 for standard errors of means; errors were sometimes too small to be distinguished clearly on figure.

The areas last disturbed in 1965 and in 1976 and the ungrazed undisturbed Ascalon sandy loam (Aridic Argiustoll) and Altvan were part of Fort Francis E. Warren (now F.E. Warren Air Force Base) until 1979. These areas were grazed very lightly or not at all from 1900 to the early 1960's; a few mules may have grazed there during World War I (Beetle 1952). Some time between 1962 and 1965 a fence was built around about 57 ha including these areas (Current 1978; personal communication Capt. A.B. Williams, USAF) and they have not been grazed by livestock since then. Two areas inside this fence were set aside for dispoal of outdated munitions. To reduce the danger of fire, these areas were scraped with a road grader to move all vegetation. After scraping to a depth of 5–10 cm, the soil was redistributed over the area. The area described as last disturbed in 1965 was scraped only in that year. The area last disturbed in 1976 was scraped each year beginning in 1966. Undisturbed areas, 2 on Ascalon and 3 on Altvan, were identified within the same 57 ha containing the areas last disturbed in 1965 and 1976.

Measuring Production and Vegetative Composition

From 1977 through 1987, study sites of 1.0 to 1.4 m^2 were located on each study area; those on the areas last disturbed in 1926 and 1941 were protected by exclosures. We located 3 to 6, 2 to 3, 3 to 9, and 3 to 9 study sites on areas disturbed in 1926, 1941, 1965, and 1976, respectively, and 3 to 6 on undisturbed Altvan and Ascalon. The number of sites per area varied with size of area and, among years, with the amount of labor available for clipping. In late July or early August of each year, two 0.18-m^2 quadrats were clipped within each site. In some years labor was so short that sites were not clipped on all areas. Clipped herbage was separated into blue grama, western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Love], needleleaf sedge (*Carex eleocharis* Bailey), other graminoids, annual forbs, and perennial forbs, dried at 60° C for 48 hours, and weighed.

In each disturbed area and in each undisturbed area on the 2 soil types, 2 or three 30.5 m × 22.9-m (100 ft × 75 ft) plots were established. Each year 10 transects, each 7.6 m (25 ft) long, were located. One transect was located randomly within each 3.05-m (10 ft) interval along the 30.5 m long side of the plot, and perpendicular to that side. A 40 × 40-cm frame with a 5 × 5-cm frame nested inside was placed at each 30.5-cm (1 ft) mark along each transect. Occurrence of blue grama, western wheatgrass, needleandthread (*Stipa comata* Trin. & Rupr.), needleleaf sedge, and scarlet globemallow [*Sphaeralcea coccinea* (Pursh.) Rydb.] in both the 5 and 40-cm frames, and all other species in the 40-cm frame, was recorded (Hyder et al. 1965, 1966).

Data Analysis

Total herbage production was analyzed within years across areas, using analysis of variance with quadrats as samples. Frac-

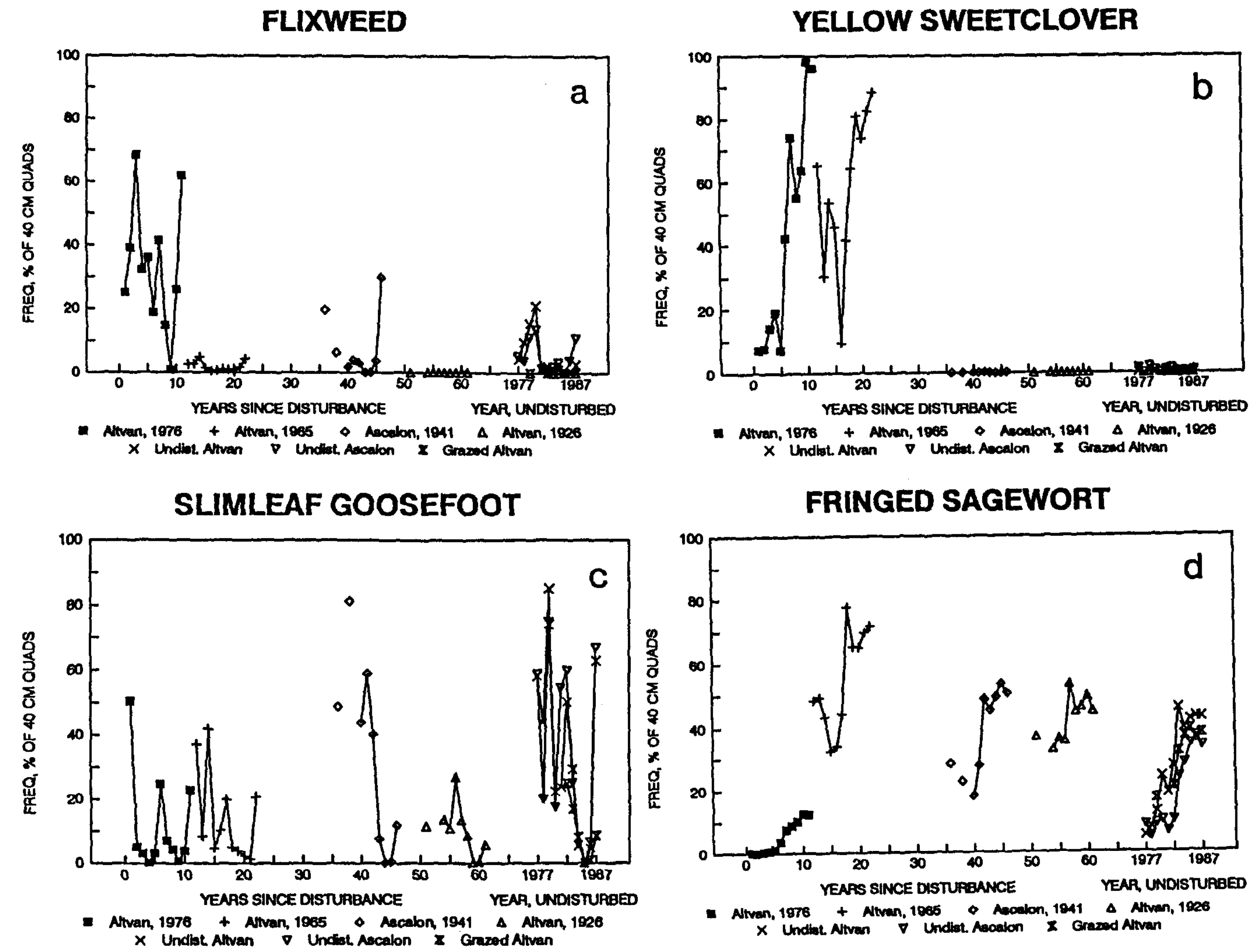

Fig. 2. (continued on facing page). Frequency of occurrence of plant species on disturbed rangeland, 1–61 years after disturbance, and on undisturbed rangeland on 2 soil types: (a) Flixweed (*Descurainia sophia);* (b) Yellow sweetclover *(Melilotus officinalis);* (c) Slimleaf goosefoot *(Chenopodium leptophyllum);* (d) Fringed sagewort *(Artemisia frigida);* (e) Scarlet globemallow *(Sphaeralcea coccinea);* (f) Western wheatgrass *(Pascopyrum smithii);* (g) Blue grama *(Bouteloua gracilis);* (h) Needleandthread *(Stipa comata).* Symbols not connected by lines indicate intervening year(s) in which no data was taken. See Table 3 for standard errors of means; errors were sometimes too small to be distinguished clearly on figures.

Table 2. Precipitation at High Plains Grasslands Research Station, 1977–1987.

Month	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1964-87 Mean
	mm											
Jan	8	17	11	48	7	8	0	24	24	8	6	11
Feb	4	28	6	23	14	6	0	36	6	12	36	15
Mar	43	14	53	45	25	2	108	35	10	17	42	26
Apr	59	23	24	30	24	17	142	114	31	79	46	48
May	73	142	82	72	173	96	87	20	55	34	117	61
Jun	70	52	81	2	20	98	113	65	36	64	50	43
Jul	102	22	47	50	80	97	39	86	99	13	47	50
Aug	39	33	89	20	24	44	37	41	53	40	61	39
Sep	6	5	9	28	30	91	10	27	59	21	20	30
Oct	4	23	19	30	29	26	14	50	29	44	3	23
Nov	14	10	39	14	4	16	52	5	37	26	26	13
Dec	12	33	24	2	16	20	12	10	27	17	38	12
Total	431	401	485	361	445	521	613	514	466	376	492	372

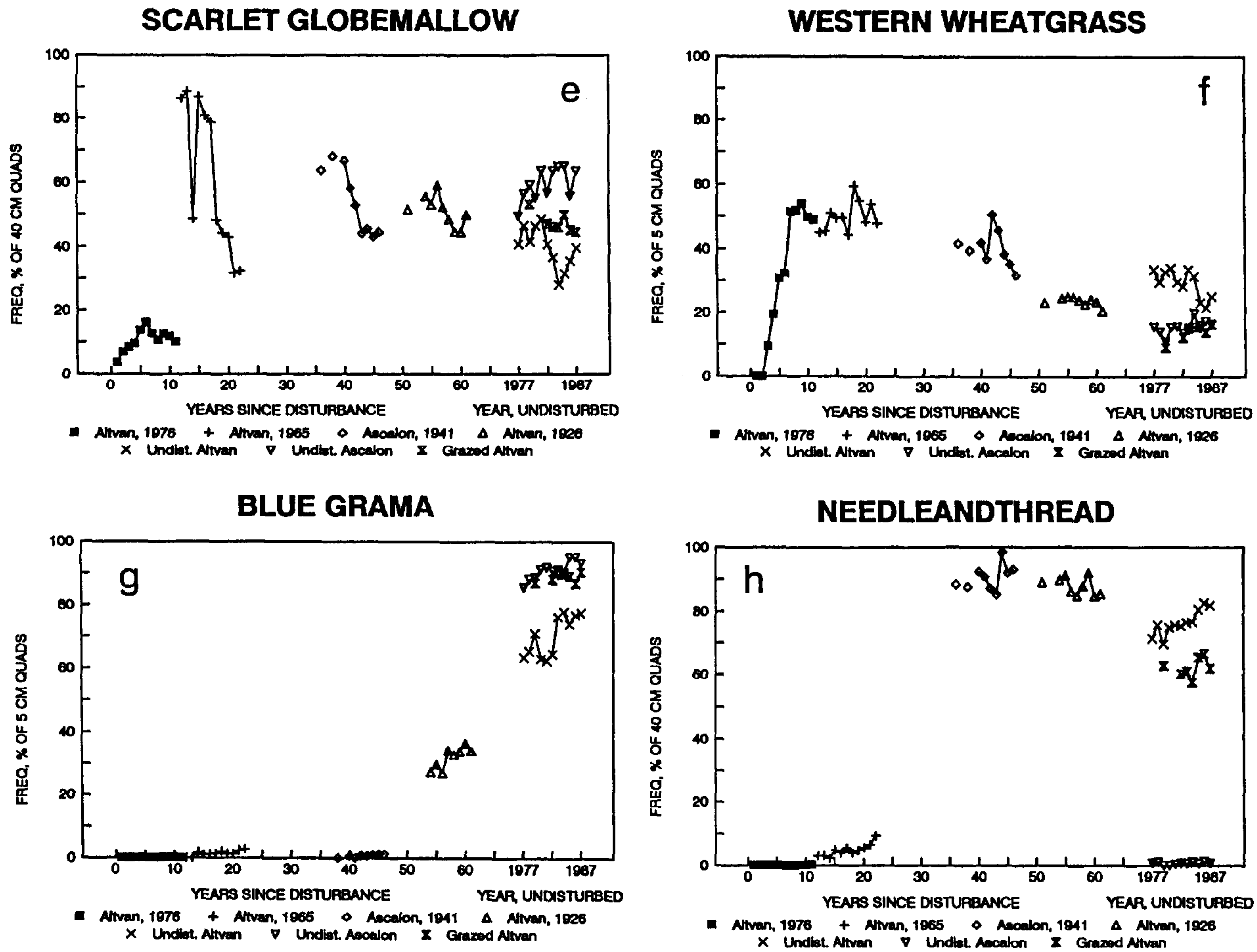

Fig. 2. (continued from adjoining page)

tion contributed by each species or species group was analyzed within each area. Variance was not homogeneous across areas because each area represented a different stage of succession and species contribution varied with stage of succession. When the contribution of a species or species group to peak standing crop was very small or very large, i.e. approached 0 or 100%, the possible range of values was restricted and the variance was low. When the contribution was intermediate the range of values was less restricted and variance was higher. We used analysis of variance with years as treatments and quadrats as samples within years. Because number of samples varied among years, standard errors of means were estimated using the average number of samples.

Table 3. Standard errors of mean frequencies of occurrence of plant species and of peak standing crop on rangeland, 1-61 years after disturbance, and on undisturbed rangeland.

	----Last disturbed in:----				—Undisturbed— —Ungrazed—		Grazed
Plant species	1976	1965	1941	1926	Ascalon	Altvan	Altvan
Frequencies				Standard errors, %			
Fixweed	13.7	0.5	4.3	–	2.4	5.3	–
Yellow sweetclover	10.7	5.4	–	–	0.8	–	–
Slimleaf goosefoot	8.0	4.3	10.6	5.4	15.6	13.7	5.8
Fringed sagewort	3.3	3.5	10.4	13.7	8.2	12.4	11.6
Scarlet globemallow	4.6	5.3	4.0	7.8	4.3	4.1	7.0
Western wheatgrass	5.2	7.8	5.0	5.9	3.0	3.1	6.0
Blue grama	–	0.5	0.5	5.2	1.6	3.1	2.0
Needleandthread	–	2.6	6.0	4.7	0.7	5.8	1.4
Peak standing crop	194	218	198	188	194	206	–

Frequency of occurrence was subjected to analysis of variance within each area, with years as treatments and plots within years as samples. Again, variance was not homogeneous across areas.

Dominance indices were calaculated from 1977 and 1987 data from each area by the method of Simpson (1949); diversity indices are the reciprocal of dominance indices. Frequency of occurrence in 40 × 40-cm quadrats was used as the "importance value" of each species.

Results and Discussion

Peak Standing Crop

Mean peak standing crop was calculated for the years 1978–1981 and 1984–1986, years in which all treatments were clipped. Peak standing crop was 1.33, 1.44, 1.36, and 1.63 Mg/ha on areas last disturbed in 1926, 1941, 1963–65, and 1976, respectively (Fig. 1). Peak standing crop was 1.23 Mg/ha on undisturbed Altvan and 1.09 Mg/ha on undisturbed Ascalon. Peak standing crop on the area last disturbed in 1976 was significantly more than that on all other areas except that last disturbed in 1941, and peak standing crop on undisturbed Ascalon was less than that on all except undisturbed Altvan.

Frequency of Occurrence and Contribution to Peak Standing Crop by Species as Succession Proceeded

It was not feasible to determine by clipping the contributions to peak standing crop of each species that occurred on the study areas. There were too many of them, and many of these contributed so little that it would have been necessary to clip a great many samples. Therefore contribution to peak standing crop, with the exception of that from western wheatgrass and blue grama, is reported by species groups. On the other hand, frequency of occurrence by other then individual species is meaningless. Therefore the progress of succession will be tracked by the contribution of the 2 major grasses and the species groups to peak standing crop, and by frequency of occurrence of individual species.

The annuals flixweed (*Descurainia sophia* [L.] Webb), summercypress (*Kochia scoparia* [L.] Schrad.), povertyweed (*Monolepis nuttalli* [Schultes] Greene), dooryard knotweed (*Polygonum aviculare* L.), and Russian thistle (*Salsola kali* L.), and the biennial sweetclover (*Melilotus officinalis* L.) dominated the vegetation in the first few years after disturbance. Povertyweed was present in 71% of 40-cm quadrats in year 1 but in only 2% in year 3, and totally disappeared after year 6. Flixweed (Fig. 2a), knotweed and Russian thistle were seldom seen after the first 10 years; sweetclover (Fig. 2b) and summercypress persisted into the second 10 years.

Annual and biennial forbs provided nearly all the peak standing crop in the first 3 years but then dropped to less than 10% on all areas, except in 1979 on the area last disturbed in 1941 (Fig. 3a). Yellow sweetclover, dooryard knotweed, povertyweed, and Russian thistle appeared to provide most of the peak standing crop derived from forbs in the early years. These are "pioneering" species which appear early in succession but are rare in climax communities. Slimleaf goosefoot (*Chenopodium leptophyllum* [Moq.] Wats.) is a natural component of climax communities on the Northern Great Plains. Its frequency fluctuated widely from year to year (Fig. 2c), but no correlation with weather was apparent.

Perennial forbs and suffrutescents, mainly fringed sagewort (*Artemisia frigida* Willd.; Fig. 2d) and scarlet globemallow (Fig. 2e), increased after the first few years. Globemallow did not appear as early as it did on the fields studied by Reichhardt (1982). Canada thistle (*Cirsium arvense* [L.] Scop), milkvetches (*Astragalus* spp.), and curlycup gumweed (*Grindelia squarrosa* [Pursh.] Dunal) were occasionally and locally abundant, and dozens of other perennial species were present. Fringed sagewort tended to increase from 1980 to 1987 on all areas. Peak standing crop from perennial forbs and suffrutescents reached a maximum of 51% of the total in year 10 after disturbance (Fig. 3a). However, in some years they provided a substantial fraction of the peak standing crop on undisturbed rangeland; in 1986, they contributed 43% of the peak standing crop on undisturbed Ascalon and 30% on undisturbed Altvan.

Western wheatgrass peaked at 62% of the total peak standing crop in year 9, although it reached 48% on undisturbed Altvan in 1983 (Fig. 3a and 3b). Frequency of occurrence peaked in year 20 (Fig. 2f). Peak standing crop from western wheatgrass in years 51–61 (1977–1987) was 17% of the total, intermediate between that on undisturbed Ascalon (12%) and undisturbed Altvan (23%). Because western wheatgrass is much the largest component of cattle diets on the Wyoming High Plains (Samuel and Howard 1982), early stages of secondary succession may be superior to climax vegetation for cattle grazing.

Blue grama did not exceed 5% of the total peak standing crop until year 54 and never approached the levels on undisturbed rangeland (Fig. 3a and 3b). Blue grama provided an average of 35% of the peak standing crop on undisturbed Altvan and 66% on undisturbed Ascalon vs only 8% on disturbed rangeland in years 51–61 after disturbance. Frequency of occurrence in 5 cm quadrats on the latter averaged 31% vs. 70% on undisturbed Altvan and 91% on undisturbed Ascalon (Fig. 2g).

There is some indication that establishment of blue grama was retarded on the areas last disturbed in 1941 and 1976. These areas were cultivated for 8–10 years and scraped for 11 years, respectively, while the areas last disturbed in 1926 and 1965 were disturbed for only 1 year. Fluctuations are more obvious when frequency of occurrence in 40-cm, rather than 5-cm, quadrats is examined. Blue grama was found in 56.1, 3.0, 7.7, and 0.5% of the 40-cm quadrats last disturbed in 1926, 1941, 1965, and 1976, respectively. The slowness of blue grama to re-establish in areas disturbed for several years probably occurred because fewer of the pre-existing plants survived the longer disturbance. Some blue grama seedlings appeared on the area last disturbed in 1976, representing years 1–11 after disturbance. They appeared only in the vicinity of a pre-existing blue grama plant and only when other perennials, particularly western wheatgrass, were not established in the area. Such seedlings result from the rare combination of a seed source, suitable amount and timing of precipitation, and absence of competition (Wilson and Briske 1979, Samuel and Hart 1992).

One would expect that other perennial species might also be slow to establish and would provide less competition to blue grama seedlings in areas disturbed for several years. On the contrary, frequencies of occurrence of fringed sagewort, needleleaf sedge (*Carex eleocharis* Bailey), prairie junegrass (*Koeleria cristata* Pers.), western wheatgrass, scarlet globemallow, and needleandthread (Fig. 2h) showed no such pattern.

Sedges increased rapidly in year 36 and peaked at 26% of peak standing crop in year 43 (Fig. 3a). Sedge production in years 51–61 was 8% of peak standing crop, still higher than that on undisturbed Altvan or Ascalon, both at 5% (Fig. 3b).

Among other graminoids, annual bromes (*Bromus* spp.) dominated in the early years after disturbance. Sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray] appeared somewhat later; tumblegrass (*Schedonnardus paniculatus* [Nutt.] Trel.) and threeawns (*Aristida* L. spp.) arrived at about the same time. These species were replaced by prairie junegrass and needleandthread in later years. Junegrass increased throughout the study on all areas except that last disturbed in 1976. Sixweeks grass (*Vulpia octoflora* Rydb.), usually present in small disturbed areas within the climax community, was present from year 40 but was never abundant and contributed little to peak standing crop. In years 51–61, other graminoids provided 47% of the total peak standing crop vs 25% on undisturbed Altvan and only 1% on undisturbed Ascalon (Fig. 3a and 3b).

Diversity

Diversity appeared to peak about 10–20 years after disturbance, as indicated by the minimum dominance and maximum diversity indices in 1987 on the area last disturbed in 1965; values for 1977 were similar (Table 4). Diversity at this stage was substantially higher than that on undisturbed prairie, whether grazed or ungrazed. In the absence of disturbance, diversity of ungrazed prairie appeared to be somewhat higher than that of grazed prairie. Additionally, diversity appeared to be higher in 1987 than in 1977; favorable spring precipitation in 1987 (Table 2) resulted in a greater frequency (Fig. 2) and a greater contribution to peak standing crop (Fig. 3) of a greater variety of forbs.

Dominance indices were lower than those of 0.12 and 0.18

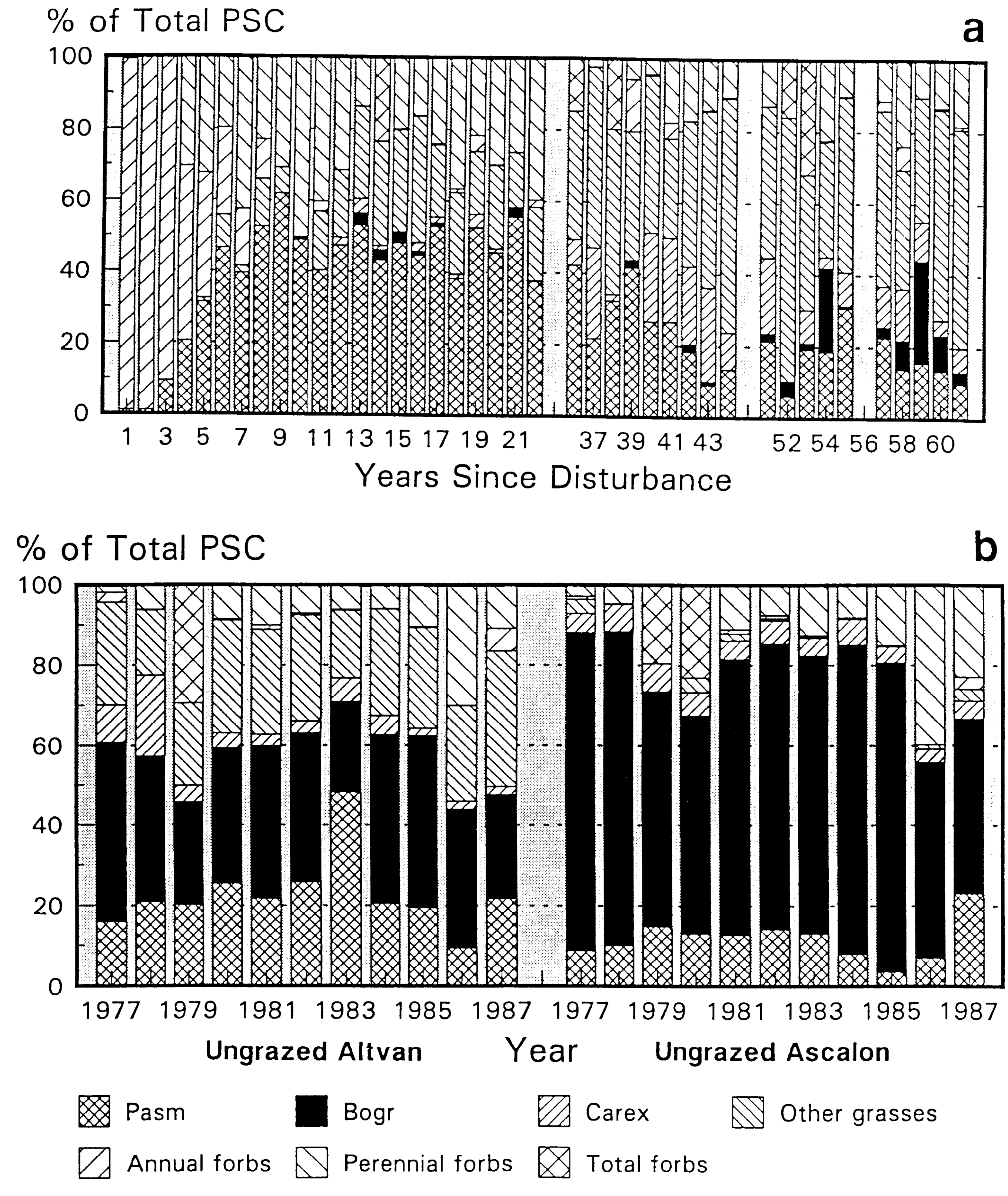

Fig. 3. Botanical composition of peak standing crop by plant species and species groups on disturbed rangeland, 1–61 years after disturbance (a), and on undisturbed rangeland on 2 soil types (b). Pasm = Western wheatgrass *(Pascopyrum smithii)*; Bogr = blue grama *(Bouteloua gracilis)*; Carex = Sedges (*Carex* spp.).

reported for 2 Smoky Mountain cove forests (Whittaker 1965), indicating a lower concentration of dominance and greater diversity in prairie than in even these species-rich ecosystems. However, basing dominance and diversity indices on frequency in 40 × 40-cm frames, rather than on density or production, may underestimate dominance. The maximum value of frequency is 100%; this level of occurrence may be reached well below the maximum level of production or density for dominant species, and thus underesti-

Table 4. Dominance and diversity indices of vegetation on rangeland, 1-61 years after disturbance, and on undisturbed rangeland.

Treatment	Soil	Dominance –indices– 1977	1987	Diversity –indices– 1977	1987
Undisturbed, ungrazed	Ascalon	0.102	0.071	9.83	13.99
Undisturbed, ungrazed	Altvan	0.099	0.067	10.10	14.93
Undisturbed, grazed	Altvan	0.139	0.079	7.18	12.59
Last disturbed 1976	Altvan	0.083	0.095	11.92	10.56
Last disturbed 1965	Altvan	0.058	0.057	17.27	17.52
Last disturbed 1941	Ascalon	0.106	0.084	9.40	11.95
Last disturbed 1926	Altvan	0.092	0.068	10.82	14.81

mate their dominance.

Soils and Grazing Effects on Undisturbed Areas

On the undisturbed and ungrazed areas, more western wheatgrass, annual bromes, prairie junegrass, and needleandthread were present on Altvan soil, and more grama and needleleaf sedge on Ascalon. Fringed sagewort was more plentiful on Altvan and scarlet globemallow on Ascalon, but other species and total annual and perennial forbs differed little.

Blue grama and needleleaf sedge were found more frequently on grazed than on ungrazed Altvan, and annual bromes, prairie junegrass, western wheatgrass, and needleandthread were recorded less frequently. From 1982 to 1987, more scarlet globemallow was found on grazed Altvan, but frequency of other forbs showed no effects of grazing.

Weather Effects

Hyder et al. (1975) concluded "Due to the great effects of weather, conventional range condition classification on shortgrass plains serves no useful purpose...range condition standards that included the annual plant species would lead alternately to dismay and pride in range condition because the annuals come and go with the weather." We saw wide fluctuations from year to year in frequencies of several annual plant species but it was seldom possible to relate them to weather. Annual precipitation during the 11 years of the study ranged from only 3% below the 116-year average of 372 mm to 65% above average, with the 11-year mean 25% above average (Table 2).

Frequency of slimleaf goosefoot was near maximum on all sites in 1982, when precipitation was 40% above average, but not in 1983 when precipitation was 65% above average. Sweetclover, present in significant amounts only on the 2 most recently disturbed sites, reached its highest frequency on these sites in 1986 and 1987; precipitation was 32% above average in 1987 but only 1% above average in 1986. Sweetclover frequency slumped in 1981, with precipitation 20% above average. Samuel (1986) noted that frequency of bluebur stickseed (*Lappula redowskii* [Hornem.] Greene) and slimleaf goosefoot increased enormously following a year with above-average precipitation, but no such correlations of frequency of annual species with preceding year's precipitation was noted in this study.

Succession: Traditional or Non-traditional?

Succession seemed to follow traditional patterns, with annual forbs dominant in the early years, followed by annual grasses and perennial forbs, then short-lived perennial grasses, and finally long-lived perennial grasses. No clear-cut stages were detectable; frequencies of individual species followed smooth curves with no obvious discontinuities between soils or types of disturbance. Collin and Adams (1983) found that only the first (pioneer weeds) and last (mature prairie) stages of secondary succession were identifiable on Oklahoma tallgrass prairie; "The intervening vegetation development was heterogeneous and unpredictable." As in their study, a general convergence toward mature prairie was seen on all sites in our study.

However, exceptions were noted. Western wheatgrass was an exception to the rule that long-lived perennial grasses are the last to appear. It appeared very early, rapidly increased to levels several times higher than those on undisturbed rangeland, and then declined to pre-disturbance levels. Our observations confirm those of Tolstead (1941), Judd (1940) and Judd and Jackson (1939). The early appearance of western wheatgrass may reflect the persistence, through the kinds of disturbance applied to the study areas, of rhizomes as propagules. The abundance of seed and other propagules in the soil may be the primary control of secondary succession in grasslands (Kinucan and Smeins 1992 and references cited). The later decline of western wheatgrass to pre-disturbance levels probably reflects increasing competition from other perennial species.

Traditional successional theory or "relay floristics" (Clements 1928, Dyksterhuis 1949) holds that early seral species are better adapted to the conditions following disturbance than later seral species. The early species modify conditions, making them more favorable to establishment of later species. There is some support for the concept that early- and late-seral species differ in responses to environmental variables. Carpenter et al. (1990), Redente et al. (1992) and McLendon and Redente (1992) concluded that addition of N and P favored early seral species and retarded succession in a semiarid *Artemisia tridentata* community. Tilman (1983, 1984) found that early seral plant species which were most productive at high N rates persisted while those which were most productive at low N rates had nearly disappeared by the tenth year after disturbance.

However, experiments and practical experience with range reseeding indicate that many species, regardless of the seral stage in which they occur naturally, are adapted to early establishment on disturbed areas if an adequate number of seeds or vegetative propagules are provided. An alternative explanation of succession is that early seral species are better adapted to rapid and extensive dispersal and quick establishment because of the number, morphology and physiology of their propagules (Connell and Slatyer 1977, McIntosh 1980, Laycock 1991). Other species appear later in succession because they lack these adaptations. These species eventually replace the early seral species because the later arrivals are more competitive (western wheatgrass) or better able to survive stresses of weather and grazing (blue grama). In addition, succession may be interrupted or diverted to alternate pathways by the chance occurrence of rare events which interact with the life histories of plant species (Smith 1988).

Survival of large numbers of propagules from the initial plant communities seems to explain early dominance of western wheatgrass in this study. Some species may not appear for years after disturbance because conditions are seldom favorable for production of propagules and establishment of seedlings (Egler 1954, Coffin and Lauenroth 1989c, Kinucan and Smeins 1992). Hyder et al. concluded (1971, 1975) this was true for blue grama; Reichhardt (1982) concurred. Gap size in stands of pioneering perennial grasses may be so small as to restrict establishment of later-appearing grasses (Coffin and Lauenroth 1988, 1989a, 1989b, 1990; Samuel and Hart 1992).

Conclusions

Succession on the area disturbed 61 years before had not reached the point represented by the undisturbed areas. On the oldest disturbed area, the plowline between plowed and undisturbed range was still plainly visible. Blue grama was much less plentiful; size and distribution of blue grama plants suggested that few had become established since plowing but had instead survived plowing. Other grasses, particularly prairie junegrass, sand dropseed, and needleandthread were more plentiful. Frequency and production of western wheatgrass and needleleaf sedge on disturbed and undisturbed areas were similar, as were production of annual and perennial forbs and frequency of selected forb species. More than 61 years will be needed for plant communities on drastically disturbed rangeland to return to pre-disturbance condition. It has been suggested that blue grama reached its present dominance in a climate differing from that of the present (Wilson and Briske 1979); if this is true, the pre-disturbance community may never completely return.

This is not necessarily undesirable. Rangeland 10–20 years after disturbance may be superior to undisturbed range for cattle grazing. Disturbed range produced more forage in most years (Fig. 1) and had a much higher percentage of western wheatgrass (Fig. 3a and 3b), which is the most important grass in cattle diets on the Wyoming High Plains (Samuel and Howard 1982). Biological diversity also appears to be higher on disturbed range, which is not dominated by blue grama as is undisturbed range, but has a much higher percentage of forbs and other grasses.

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