Probabilities of Seedling Recruitment and the Stability of Crested Wheatgrass Stands

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ABSTRACT: Crested wheatgrass seedings in the western United States have persisted as virtual monocultures for over 50 years following their establishment. Such stability typically is attributed to superior competition by crested wheatgrass, but this explanation assumes that native propagules are available for recruitment. Data on seedling emergence from undisturbed topsoil samples show that there is a paucity of native propagules within crested wheatgrass stands. For two stands that were near monocultures, the probability of a seedling being crested wheatgrass was over 85%. Recruitment probabilities favor the maintenance of a monoculture rather than its successional replacement.

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INTRODUCTION

Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn. and *A. desertorum* (Fisch.) Schult.) often has been seeded and managed in North America under the assumption that without continued intervention by man the stand will eventually revert to a native climax community (Lewis 1969). Implicit in the assumption is the concept of only one stable climax for any particular site, and that succession will follow a directional, predictable course toward that stabilized community. Clements (1935) wrote, "the grasses of a particular climax are the best adapted to its climate and have a distinct advantage in terms of competition over the introduced ones. ... Crested wheatgrass (*Agropyron cristatum*) has often been cited as a warrant for such a procedure (introduction), but all evidence available indicates that it can persist in the face of the competition of the indigenous grasses only when man aids it by cultivation or otherwise." The life expectancy of crested wheatgrass seedings is usually placed at 20 years or less (Bartolome and Heady 1978), although some investigators consider that to be a conservative estimate (Sonnermann et al. 1981).

Contrary to these views of crested wheatgrass forming unstable, temporary stands, it is now generally recognized that the species spreads quickly by seed and is capable of invading native, undisturbed habitat (Hull and Klomp 1967, Hull 1971). When sown in a mixture with native species, crested wheatgrass frequently becomes the dominant species in the stand (Heinrichs and Bolton 1950, Hull 1971, Holechek et al. 1981). Several investigators considered crested wheatgrass to be competitively superior to dominant native species (Hubbard 1957, Eckert et al. 1961, Robertson et al. 1966, Robertson 1972, Holechek et al. 1981). Recent studies by Caldwell et al. (1981, 1983) have elucidated some physiological and morphological attributes that contribute to the superior competitive ability and greater grazing tolerance of crested wheatgrass in comparison to bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Love).[1]

Crested wheatgrass seedings in the western United States have resisted invasion by native species for as long as 30 to 50 years (Hull and Klomp 1966, Looman and Heinrichs 1973, Sonnermann et al. 1981), which simply indicates the length of time for which data are available rather than the

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[1] Nomenclature follows Hitchcock and Cronquist (1973) except for grasses of the Triticeae tribe. For bluebunch wheatgrass, we have used the taxonomic revision proposed by Love (1980); nomenclature for other members of the Triticeae follows Dewey (1983).

longevity of the stands. Soils beneath some seedings are not converging to their original condition even after 50 years and may be evolving toward a different equilibrium point than undisturbed soils (Dormaar et al. 1980). In its native habitat, crested wheatgrass is known for its ability to establish on disturbed sites and persist in virtual monocultures (Looman and Heinrichs 1973). Thus, rather than crested wheatgrass eventually being replaced by native species, it may inhibit or even preclude the recovery of native vegetation. It is, therefore, desirable to understand the factors responsible for the stability of crested wheatgrass stands.

Succession ultimately depends on whether a species replaces itself on a given site or is replaced by members of other species (Grubb 1977, McIntosh 1980). This replacement process is a function of two factors (Gleason 1926, Poore 1964, Harper 1977, Whipple 1978): 1) the availability of propagules on the site, and 2) whether those propagules find a suitable environment for germination, growth, and ultimately, survival.

Dispersal of native propagules into crested wheatgrass seedings is usually assumed to occur. Shepherd (1937 cited by Weldon et al. 1959) concluded that "a supply of viable seed is probably never a limiting factor for the aggression of sagebrush." Looman and Heinrichs (1973) surmised that "Over the years, a considerable reservoir of seeds of native and introduced species has built up, and the chances that a given crested wheatgrass plant will be replaced by its own kind after death are lessened with increasing age." Thus, it is typically assumed that the stability of a crested wheatgrass seeding is a function of the superior competitive ability of crested wheatgrass which renders the site unsuitable for the establishment of other species.

Competition can be responsible for the stability of crested wheatgrass stands only if propagules of native species are dispersed into the stands. The purpose of this investigation was to test the assumption that there is sufficient dispersal of native species into crested wheatgrass seedings to result in a store of native propagules available for recruitment. In essence we asked, "If a safe site (sensu Harper 1977) becomes available, what is the probability that it will be colonized by crested wheatgrass as opposed to one of its potential competitors?" Our results suggest that there is a paucity of native propagules available for recruitment within crested wheatgrass stands.

METHODS

This study was conducted on the Idaho National Engineering Laboratory (INEL), which occupied some 2300 km^2 of sagebrush steppe rangeland on the upper Snake River Plain. Vegetation of the area is dominated by big sagebrush (*Artemisia tridentata* Nutt.). Other common shrubs include green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), prickly phlox (*Leptodactylon pungens* (Torr.) Nutt.), horsebrush (*Tetradymia canescens* DC.), and spiny hopsage (*Atriplex spinosa* (Hook.) Collotzi. The most important grasses are bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), thick-spike wheatgrass (*Elymus lanceolatus* (Scribn. & Smith) Gould), bluebunch wheatgrass, needle-and-thread (*Stipa comata* Trin. & Rupt.), and Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker).

Average annual precipitation for the INEL is about 21 cm, with 40% typically falling during April, May and June (Anderson and Holte 1981). Mean annual temperature is about 5.5°C; the frost free period averages 91 days. The topography is flat to gently rolling, with occasional lava outcrops. The soils are primarily shallow, calcic aridisols of aeolian origin lying over basalt.

Four crested wheatgrass stands and adjacent native communities were studied during the summers of 1978 and 1979. Three stands, located on a remote section of the INEL known as Tractor Flat, were established following plowing and seeding in the fall of 1956. They are referred to as TFA, TFB, and TFC. They have been grazed by sheep, primarily in the spring, since 1959. The fourth stand (PBF), located near the INEL Power Burst Facility, was seeded in 1960 and has never been grazed by domestic livestock. This stand and TFB were near monocultures; the other two areas were selected because re-establishment of native species (primarily big sagebrush) within the seeding was evident. All study areas were selected so that the main interface between the native community and the adjacent seeding was approximately perpendicular to the prevailing wind direction. At PBF, TFA, and TFB, the seedings were downwind from the native communities, which was assumed to represent the maximum potential for wind dispersal of propagules from the native communities.

At each study area, crown cover of shrubs and basal cover of grasses and forbs were estimated using a 0.5 m^2 sampling frame that was subdivided into dm^2 grids (Floyd and Anderson 1982). The frame was systematically placed at 2- to 4-m intervals along three parallel transects that extended from the native stand into or across the adjacent crested wheatgrass seeding. Transects were 23 m apart; their lengths varied from 115 to over 500 m, depending on the layout of the seeding and adjacent native community. Seed reserves were sampled in March of 1979 by driving cylinders cut from #10 cans into the soil to a depth of 6 cm and removing the intact soil core by passing a trowel under the cylinder. Paired samples from bare and littered areas were taken at systematic intervals along the vegetation transects, sampling both the crested wheatgrass stands and the native community. Between 130 and 180 samples from each study area were placed in a greenhouse or environmental chamber where they were watered regularly with distilled water. Emerging seedlings were identified, counted, and removed. We refer to these counts as seed reserves, but it should be noted that the data actually represent seedling emergence from undisturbed topsoil, except where natural disturbances occurring in the field were sampled. Further details about the study areas and sampling regimes can be found in Marlette (1982).

RESULTS

Vegetal Cover

Native communities at all four study areas were dominated by big sagebrush; green rabbitbrush was also common at the Tractor Flat study areas (Tables 1-4). Crested wheatgrass contributed from 2% (Table 2) to over 17% (Table 4) of the plant cover in the native communities, showing that it had indeed moved from the original seedings into the native communities.

Total plant cover was generally higher in the native communities than the crested wheatgrass stands at Tractor Flat (Tables 2-4), but not at PBF (Table 1). Total cover was remarkably similar (about 36%) among the four crested wheatgrass stands (Tables 1-4).

Relative cover of crested wheatgrass was 95% and 93% in the two "monocultural" stands (Tables 1 and 3). A rhizomatous grass, beardless wildrye (Leymus triticoides (Buckl.) Pilger), was the only other species contributing over 1% relative cover in the crested wheatgrass seeding at the PBF study area (Table 1). Big sagebrush and green rabbitbrush, with 2.7% and 1.1% relative cover respectively, were the next most important species at TFB (Table 3). Thirty species were identified on the vegetation transects in the PBF native community compared to only 14 within the crested wheatgrass seeding. At TFB, species richness was 20 in the native community and 17 in the crested wheatgrass seeding.

The TFA and TFC study areas were chosen because there appeared to be considerable re-establishment of native species within the seedings. Relative cover of crested wheatgrass in both cases was 73% (Tables 2 and 4). Big sagebrush, threetip sagebrush (Artemisia tripartita Rydb.), and green rabbitbrush contributed the bulk of the remaining cover within the seeding at TFA (Table 2). Big sagebrush green rabbitbrush and two annuals also having relative cover greater than 1% (Table 4).

Table 1.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the PBF study area.

Species	Relative Cover[1] Native Community	Relative Cover[1] Wheatgrass Stand
	------percent------	
Artemisia tridentata	52.1	0.05
Agropyron cristatum	15.7	95.2
Elymus elymoides	8.4	
Elymus lanceolatus	6.9	0.05
Stipa comata	3.3	
Opuntia polyacantha	1.8	0.05
Descurainia pinnata	1.6	0.03
Leymus triticoides	1.4	3.5
Poa sp.	1.4	
Lappula redowskii	0.9	
Astragalus filipes	0.7	0.6
Carex douglasii	0.1	0.3
Other species	6.6 (n=18)	0.2 (n=6)
Total absolute cover	27.1	36.7

[1]Relative cover is the cover of species i divided by the total cover of all vascular plants, expressed as a percentage. The absolute cover for a species equals relative cover for species i times total absolute cover divided by 100.

Table 2.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand the the TFA study area.

Species	Relative Cover[1] Native Community	Relative Cover[1] Wheatgrass Stand
	-------percent-------	
Artemisia tridentata	48.9	9.6
Pseudoroegneria spicata	14.9	
Chrysothamnus viscidiflorus	14.0	8.1
Phlox hoodii	12.9	0.5
Elymus elymoides	4.2	0.03
Agropyron cristatum	2.4	72.7
Poa sp.	0.6	0.2
Eriogonum microthecum	0.5	0.2
Oryzopsis hymenoides	0.5	
Halogeton glomeratus	0.3	
Artemisia tripartita		8.0
Astragalus filipes		0.4
Gilia congesta		0.1
Leptodactylon pungens		0.1
Other species	0.8 (n=7)	0.5 (n=4)
Total Absolute Cover	39.0	35.9

[1]See Table 1 for definition.

Species richness was 15 and 18 in the native and crested wheatgrass communities respectively at TFC, and 17 vs. 15 at TFA. Despite the similarities in richness, there were large differences in structure between the native and crested wheatgrass stands. Simpson's index of dominance concentration, a measure of the probability that two individuals drawn at random from a community will belong to the same species (Poole 1974), was 0.30 for the TFA and TFC native communities, but 0.55 and 0.56 for the TFA and TFC seedings respectively.

Seed Reserves

Over 17,000 seedlings representing some 46 taxa emerged from the 612 topsoil samples taken from the four study areas. On the average, three to four times as many seedlings emerged from samples of littered areas than from those of bare areas (Marlette 1982). Crested wheatgrass and big sagebrush each contributed about 6500 seedlings to the total count. Bottlebrush squirreltail, with 680 seedlings, was the next most abundant perennial species. Lappula redowskii (Hornem.) Greene was the most common annual, with over 1160 seedlings; halogeton (Halogeton glomeratus Meyer.) and tansymustard (Descurainia pinnata (Walt.) Britt.) were also common, having 457 and 446 emergent seedlings respectively. Ten of the taxa identified among the emerging seedlings were not found in the vegetal cover samples. Likewise, ten of the 46 taxa identified along the cover transects were not represented in the seedling emergence data. Thus, 64% of the taxa were common to both data sets.

Crested wheatgrass contributed from 84% to 99% of the total seedling density within the crested wheatgrass stand at the PBF study area (Fig. 1). For seed reserve samples from the seeded area as a whole, 92% of the seedlings were crested wheatgrass, 3% were big sagebrush, and the remaining 5% represented 11 species, of which nine were annuals or biennials. For samples taken at the interface, 51% of the seedlings were crested wheatgrass, whereas only from 2% to 18% of the seedlings in the PBF native community were crested wheatgrass. From 12% to 35% of the seedlings emerging from samples from the PBF native community were big sagebrush; the remaining 50% to 80% represented a variety of native species. Seedlings of 29 species emerged from samples of the PBF native community; only 13 species were represented among seedlings from samples of the crested wheatgrass stand.

At TFB, the second study area where the seeding appeared to be essentially a pure stand of crested wheatgrass, from 1% to 34% of the seedlings in the native community and from 67% to 96% of those in the seeding were crested wheatgrass (Fig. 2). In the native community, big sagebrush contributed from 26% to 76% of the total seedling count, but sagebrush seedlings were virtually absent in samples from the crested wheatgrass seeding (Fig. 2). Seedlings of 17 species emerged from samples from the native community, but only 11 species were recorded for samples from the seeding. Of 1778 seedlings that emerged from topsoil samples from the TFB seeding, over 1500 (84.7%) were crested wheatgrass; 10% of the seedlings were Lappula redowskii and 3% were halogeton. None of the other eight species contributed over 1% to the seedling total.

Table 3.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the TFB study area.

Species	Relative Cover[1] Native Community	Wheatgrass Stand
	------percent------	
Artemisia tridentata	41.5	2.7
Pseudoroegneria spicata	12.9	
Chrysothamnus viscidiflorus	11.7	1.1
Agropyron cristatum	10.7	93.4
Phlox hoodii	7.6	0.3
Elymus elymoides	5.3	
Artemisia tripartita	4.1	0.3
Oryzopsis hymenoides	2.1	0.4
Eriogonum microthecum	1.8	0.3
Poa sp.	0.8	0.5
Halogeton glomeratus	0.1	0.5
Tetradymia canescens		0.3
Other species	1.4 (n=9)	0.2 (n=7)
Total Absolute Cover	38.4	36.0

[1]See Table 1 for definition.

Table 4.--Cover of the more important plant species in the native community and adjacent crested wheatgrass stand at the TFC study area.

Species	Relative Cover[1] Native Community	Wheatgrass Stand
	------percent------	
Artemisia tridentata	48.2	16.3
Chrysothamnus viscidiflorus	18.6	2.3
Agropyron cristatum	17.6	73.1
Elymus elymoides	9.5	
Phlox hoodii	2.4	
Halogeton glomeratus	1.9	3.1
Poa sp.	0.8	
Lappula redowskii	0.5	4.1
Descurainia pinnata	0.3	
Oryzopsis hymenoides	0.2	0.3
Leymus cinereus		0.6
Salsola kali		0.1
Opuntia polyacantha		0.1
Other species	trace (n=7)	0.05 (n=9)
Total Absolute Cover	34.5	34.1

[1]See Table 1 for definition.

At TFA, one of two areas where significant numbers of native species appeared to be re-established, crested wheatgrass seedlings were rare in samples from the native community but made up from 40% to 95% of the totals from the seeding (Fig. 3). Sagebrush seedlings dominated samples from the native community, and were common in samples from the center of the crested wheatgrass seeding. Two additional points should be emphasized concernig the data in Figure 3. First, sagebrush seedlings were uncommon at the interface between the native community and the crested wheatgrass seeding. Thus, the re-establishment of big sagebrush within the seeding was not taking place as a sort of wave out from the native community. The second point is that within the crested wheatgrass seeding, species other than crested wheatgrass and big sagebrush (n = 11) contributed only about 4% to the total seedling pool. The area was essentially a biculture of crested wheatgrass and big sagebrush.

The same general patterns were found at the second sagebrush re-establishment area, except that there were few seedlings of either crested wheatgrass or big sagebrush in samples from the native community (Fig. 4). Again, crested wheatgrass seedlings strongly dominated samples from the interface, and sagebrush seedlings became most numerous in the middle of the crested wheatgrass stand. We believe that the most probable explanation of this pattern is that some big sagebrush plants survived the original revegetation treatment and that they provided the original seed source for re-establishment within the seeded area. At TFC, from the interface to 360 m into the seeding, less than 2% of the seedlings were species other than crested wheatgrass and big sagebrush (Fig. 4). Thus, succession on this area, like the

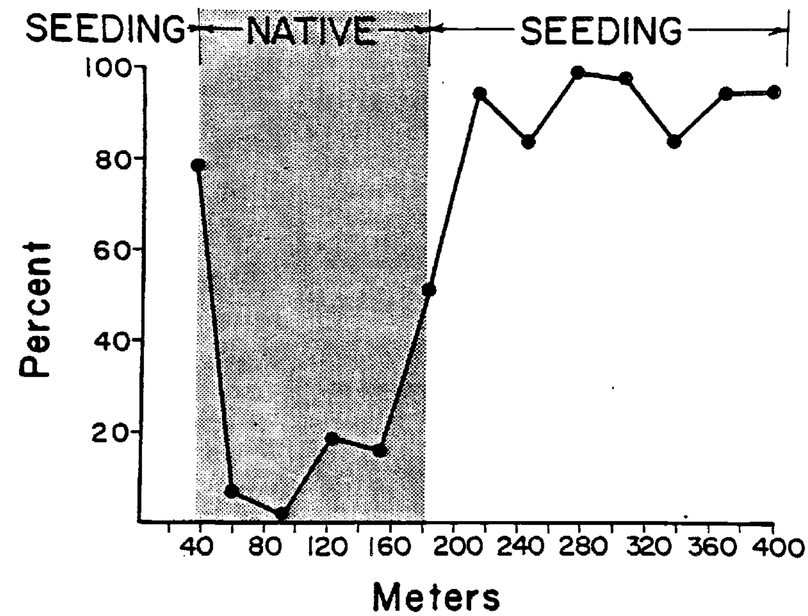

Figure 1.--Percentage of total seedlings emerging from topsoil samples from the PBF study area that were crested wheatgrass vs. distance along the sampling transects.

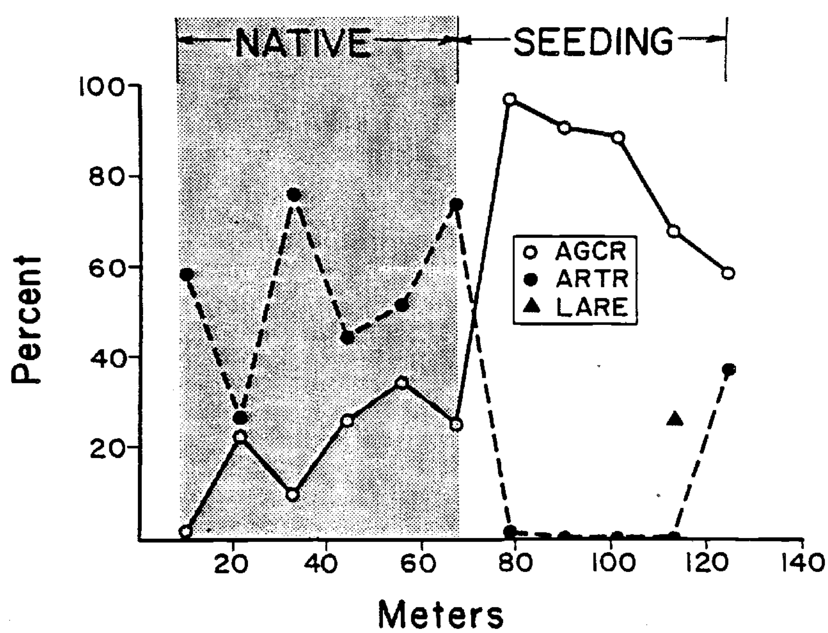

Figure 2.--Percentage of total seedlings emerging from topsoil samples from the TFB study area that were crested wheatgrass (AGCR) or big sagebrush (ARTR) vs. distance along the sampling transects. LARE = *Lappula redowskii*.

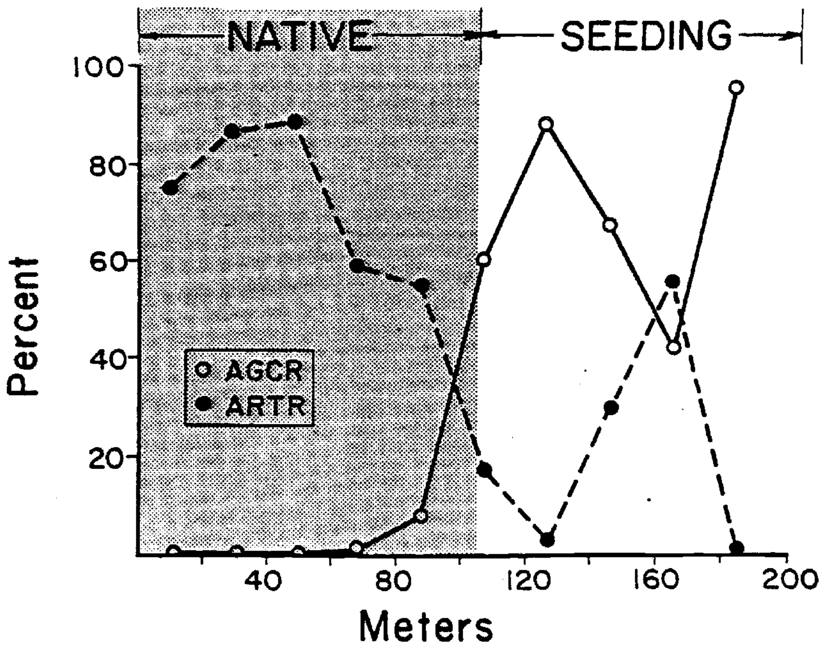

Figure 3.--Percentage of total seedlings emerging from topsoil samples from the TFA study area that were crested wheatgrass (AGCR) or big sagebrush (ARTR) vs. distance along the sampling transects.

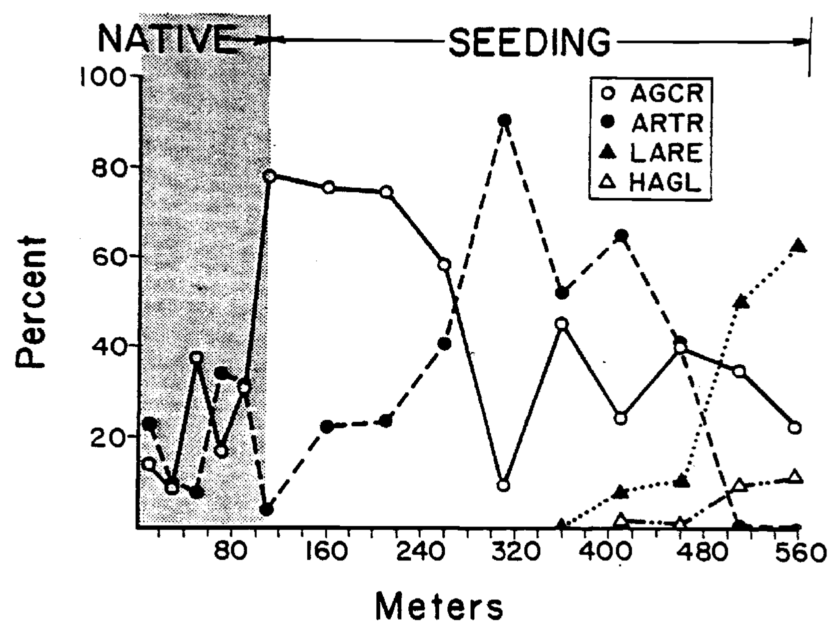

Figure 4.--Percentage of total seedlings emerging from topsoil samples from the TFC study area that were crested wheatgrass (AGCR), big sagebrush (ARTR), Lappula redowskii (LARE), or halogeton (HAGL) vs. distance along the sampling transects.

previous one, was producing a crested wheatgrass-big sagebrush biculture, not a diverse native community. Our seed reserve samples from distances beyond 360 m from the interface produced sizeable numbers of two annuals, Lappula redowskii and halogeton (Fig. 4).

In general, we found a close positive correlation between the cover of a dominant species and its potential for recruitment as estimated by seedling emergence from topsoil samples (Marlette 1982). There was little evidence to suggest any significant dispersal of propagules from the native communities into the adjacent crested wheatgrass stands.

DISCUSSION

These results show that there may be little opportunity for recruitment of native species, especially perennials, within crested wheatgrass seedings. We found no rich store of native propagules within the crested wheatgrass stands. In the four areas examined, the seed bank, as evidenced by seedling emergence from undisturbed topsoil samples, was heavily dominated by crested wheatgrass, or crested wheatgrass and big sagebrush. In the two monocultural areas, the probability of a seedling being crested wheatgrass was between 85 and 92%. Seed reserves on the other two areas reflected the composition of the vegetation; crested wheatgrass and big sagebrush comprised the bulk of emergent seedlings. The only other species contributing sizeable numbers of seedlings were two annuals.

Our results do not support the assumption that competition is the primary factor responsible for the persistence of relatively pure stands of crested wheatgrass. This does not mean that competition doesn't occur between plants within the stand. Competition may well be a factor in the survival of any seedlings that do emerge within a seeding; our data simply indicate that such cases involving native species will be relatively rare occurrences.

The results of numerous studies (Robertson and Pearse 1945, Blaisdell 1949, Hubbard 1957, Cook and Lewis 1963, Frischknecht 1963, 1968, Harris and Wilson 1970, Robertson 1972, Rittenhouse and Sneva 1976, Harris 1977), as well as the observation that native grasses often fail to persist when sown in mixtures with crested wheatgrass (Hull 1971, Holechek et al. 1981), attest to the strong competitive ability of crested wheatgrass. In addition to competing effectively for space and soil resources, crested wheatgrass has an advantage over many of the native grasses in terms of seed production (Frischknecht and Bleak 1957, Harlan 1960). In fact, Cook et al. (1958) found that if the vigor of a crested wheatgrass plant is sufficient for seed production at all, the seed produced is likely to be viable. Thus, crested wheatgrass seems to have an advantage over native grasses in both vegetative and reproductive attributes. Both its competitive ability and the limited availability of native propagules would contribute to the persistence of a crested wheatgrass monoculture.

Our results suggest that adjacent native communities do not serve as significant sources of propagules for the colonization of crested wheatgrass seedings by native species. It is well known that the number of seeds deposited at increasing distance from a parent plant generally falls off exponentially (Cook 1980), and long-range dispersal is rare in semiarid regions (Ellner and Shmida 1981). Even the achene-pappus dispersal of many composites is local and ineffective over long distances (Cook 1980). Frischknecht (1978) reported that 90% of the total progeny of big sagebrush plants were within 9 m of the parents. Johnson and Payne (1968) concluded that sagebrush plants adjacent to seedings were of no practical importance as a seed source for re-establishment.

Succession in crested wheatgrass seedings is consistent with the initial floristics model proposed by Egler (1954) and with the inhibition model of Connell and Slatyer (1977). Succession is primarily a function of what species survive a disturbance (or treatment) and what species become established immediately following the disturbance. Once established, the vegetation tends to inhibit further recruitment of other species. Chance plays an important role in such models because the initial colonization and establishment are dependent upon a number of random factors. Recruitment as the stand ages also depends largely upon probabilistic events associated with the relative abundances of propagules. Our data show that chance favors the maintenance of the monoculture rather than its successional replacement.

These results have several important implications for management. The nature of a disturbance and the differential survival of species on the disturbed area are important factors in determining subsequent species composition on the site. Plants surviving a revegetation treatment are the primary seed source for the re-establishment of their populations. Our results suggest that crested wheatgrass monocultures could be maintained with minimum effort if the existing vegetation (including rhizomes, sprouting roots, and seed reserves) was eliminated from the area prior to seeding. Such a treatment could hardly be recommended except in cases where the native vegetation had been destroyed previously. On the other hand, if the goal is to re-establish a diverse native flora on a site, seeding initially with crested wheatgrass may preclude, or at least delay, the recovery of native vegetation.

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