



## Seed Predation, Seed Dispersal, and Disturbance in Grasslands: A Comment

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## NOTES AND COMMENTS

### SEED PREDATION, SEED DISPERSAL, AND DISTURBANCE IN GRASSLANDS: A COMMENT

Seed dispersal provides many advantages to plants, including (1) movement of the seed away from the parent plant where predation rates may be highest (Janzen 1970) and where parent-offspring competition is severe (Cook 1980); (2) placement of seeds in suitable germination microsites (Harper et al. 1965), which may be unpredictable in both space and time; and (3) movement of seeds to recently disturbed sites (Baker 1974). As Howe and Smallwood (1982) stated, however, these selective factors are not mutually exclusive; thus, one objective of studies of dispersal must be to determine the relative importance of each factor. Because dispersal is so important, plant diaspores have physical structures that promote dispersal by wind, water, or animal fur (van der Pijl 1972), or some type of fleshy nutritive reward that promotes consumption of part (Beattie and Culver 1981) or all (McKey 1975) of the diaspore. Nevertheless, seed shadows are skewed, and most seeds fall beneath or near the parent (Cook 1980).

At the community level, the importance of animals as seed dispersers increases along a xeric to mesic gradient (Howe and Smallwood 1982). In arid environments such as grasslands, wind- and ballistic-dispersal mechanisms predominate. Recently, Janzen (1984) suggested that large grazing mammals may have been the common dispersers of many grassland plants previously considered to be wind-dispersed. He proposed that some plants, at least, may offer foliage as a "fruit" to attract seed dispersers. As a result, some characteristics of plant morphology and phenology may have evolved to promote the consumption of ripe seeds, minimize seed destruction by herbivores, and encourage dispersal away from the parent plant. Janzen noted that this hypothesis is very difficult to test. Therefore, the veracity of his idea must be determined on the basis of available evidence derived from relatively natural grassland ecosystems.

Our purpose is to address Janzen's hypothesis by assessing the importance of the selective factors outlined by Howe and Smallwood (1982) in relation to grassland environments. Although the data are inferential, we believe that Janzen misinterpreted the true nature of many grassland communities. As a result, we feel that current evidence supports the notion that seed dispersal of prairie plants by large mammals is a potentially important but purely facultative event. Our comments are based on a series of studies concerning grassland disturbance, seed

dispersal, and plant species diversity (Collins and Uno 1983; Polley and Collins 1984; S. Collins and S. Barber, MS) in the Wichita Mountains Wildlife Refuge, southwestern Oklahoma. The refuge contains a 24,000-ha mosaic of forest (Buck 1964; Dooley and Collins 1984) and grassland (Crockett 1964) vegetation which was established in 1935 to support managed populations of about 700 buffalo (*Bison bison*), 600 elk (*Cervus canadensis*), 600 deer (*Odocoileus virginianus*), 400 longhorn cattle (*Bos taurus*), and 200 prairie dogs (*Cynomys ludovicianus*). In addition, a prescribed burning program was recently initiated such that grasslands are burned at approximately 5-yr intervals. Overall, the populations of native herbivores and the prescribed burning program produce a disturbance regime that generally reflects presettlement conditions. Additional support for our arguments comes from research conducted by Risser et al. (1981) as part of the Grassland Biome studies of the U.S. International Biological Program on the Osage Site, a tallgrass prairie in north-central Oklahoma.

#### SEED PREDATION

Evidence indicating that seed predation is severe in grasslands is equivocal. As Janzen (1984) aptly acknowledged, many of the seed characteristics of grassland plants may have evolved under selective pressures other than increased efficiency of dispersal. In particular, escape from predation or enduring environmental vagaries may account for the small and durable seeds of many prairie plants. Unfortunately, little is known about seed demography of temperate grassland plants. Platt (1976) reported that predation on seeds of *Mirabilis hirsuta* was high on badger mounds but low in adjacent undisturbed prairie. A much larger number of seeds resides in the seed rain than in the soil bank (Rabinowitz and Rapp 1981; Uno, unpubl.). The causes of this decrease are uncertain, but seed predation would seem to be an obvious source of mortality. Janzen correctly noted that seed predation may be severe in some ecosystems, but he cited evidence from deserts (Hay and Fuller 1981), not grasslands. Such evidence is inappropriate because small-mammal populations in deserts are very different from those in grasslands (Grant and Birney 1979). Desert rodents are primarily granivores, whereas most grassland taxa are herbivores (French et al. 1976). In addition, French et al. (1976) indicated that small mammals at the Osage Site consume only a small percentage (< 10%) of available seed and herbage production. Thus, although seed predation may at times be severe, the overall impact on seed populations appears to be minimal.

Winter bird populations are largely granivorous (Grzybowski 1980) and may account for reduced seed numbers in the soil. Risser et al. (1981) indicated that grassland bird communities consume only about 0.04% of seed biomass per week during the peak of the breeding season. Birds consume about 2% of the total seed production annually. Finally, seed consumption by lygaeid bugs may be significant, but it is difficult to quantify at the community level and was not estimated for the Osage Site (Risser et al. 1981).

Evidence that a large number of seeds in grasslands escape predation is provided by analyses of seed pools. Estimates of seed pools in prairie soils range from

TABLE 1  
 PERCENTAGE OF GRASS AND FORB SPECIES THAT PRESENT THEIR SEEDS  
 ABOVE OR WITHIN THEIR OWN FOLIAGE

GRASSLAND TYPE	GRASSES			FORBS*		
	Above	Within	<i>N</i>	Above	Within	<i>N</i>
Ungrazed . . . . .	90.0	10.0	10	47.1	41.2	34
Burned + ungrazed . . . . .	100.0	0	10	37.5	43.7	16
Grazed . . . . .	93.3	6.7	15	61.4	29.5	44
Burned + grazed . . . . .	92.8	7.2	14	69.4	19.4	36

NOTE.—Composition of each grassland type was estimated using 100 randomly located 0.5-m<sup>2</sup> quadrats within a 0.5-ha area (S. Collins and S. Barber, MS).

\* Values do not total 100 because species with obvious adaptations for ectozoochory were not included in either category.

600 m<sup>-2</sup> in a Kansas prairie (Lippert and Hopkins 1950), to 6000 m<sup>-2</sup> in a Missouri prairie (Rabinowitz 1981), to over 36,000 m<sup>-2</sup> in the Wichita Mountains Wildlife Refuge (G. Uno, unpubl.). Therefore, small seeds may represent a successful means of escaping predation. Alternatively, seed size may simply be a function of allometry (Rabinowitz and Rapp 1981), and predation may not be the primary selective force shaping seed characteristics. In summary, escape from predation does not appear to be an important selective advantage of seed dispersal in some grasslands.

#### DISPERSAL TO SUITABLE MICROSITES AND DISTURBANCES

We do not deny the possibility that large herbivores may serve as important dispersal agents for some grassland plants. We have germinated seeds in *Bison* dung collected from the Wichita Mountains Wildlife Refuge. Samples from four buffalo chips collectively weighing 472 g dry weight contained 219 seeds that germinated. Of these, 195 (89%) were monocots, most of which were of the nonnative weedy annual *Bromus japonicus*.

Evidence favoring the use of foliage as "fruit" is sparse, at best. In contrast to Janzen's hypothesis, a majority of prairie grasses (*Andropogon*, *Panicum*, *Sorghastrum*, *Schizachyrium*) bear their seeds on stalks held above the herbage (table 1). Wind pollination of elevated flowers is an obvious selective advantage. The dispersal distance of grass seeds, however, does not appear to be affected by height (Rabinowitz and Rapp 1981). A higher percentage of forbs present their seeds within their own foliage (table 1). Counter to Janzen's hypothesis, however, this percentage was higher on ungrazed grasslands (no mammalian herbivores) than on grazed grasslands. Many of the forbs that present seeds above or within their own foliage also place their seeds among the foliage of neighboring grasses. The patchy distribution of prairie grasses would be unlikely to promote coevolution of this phenomenon; thus, it probably reflects a facultative relationship. Sacrificing aboveground biomass may significantly affect reallocation of nutrients

and reduce asexual reproduction by perennial grasses (Adams and Wallace 1985). If consumption does occur after reallocation of nutrients to seeds and below-ground parts, the aboveground foliage would be less nutritious and, therefore, a less suitable "fruit" to attract dispersers. Additionally, grass foliage is most nutritious in the spring, and intense grazing occurs when the foliage is highly nutritious. Regrowth foliage is more nutritious than that of ungrazed plants. Thus, regrowth foliage is selectively grazed later in the year. Grazing reduces flowering, however; grazed grasses therefore would provide few seeds for consumption and dispersal by large herbivores (J. K. Detling, personal communication). If seed consumption were desirable, placing seeds in neighboring foliage would seem to be a more clever approach than sacrificing one's own leaves and stems for dispersal.

One important element of Janzen's hypothesis concerns the nature of grassland environments. When Janzen referred to grasslands as composed of "herbaceous vegetation of long permanence" (p. 340), we believe he did not appreciate the true disturbance regime characteristic of grasslands. For many ruderals, one of the primary objectives of dispersal is to colonize open sites (Baker 1974), which often result from some form of disturbance. Janzen proposed game trails and edges of arroyos as such convenient sites in grasslands, implying that these features are local, unpredictable, and rare in the landscape. Arroyos are practically nonexistent in grasslands of the Great Plains. Such misconceptions of the true prairie environment are perpetuated because, as Janzen noted, few ecosystems today even approximate presettlement grasslands.

Our studies in the Wichita Mountains Wildlife Refuge, however, indicate that animal-mediated disturbances are and were quite common in grasslands (Collins and Uno 1983; S. Collins and S. Barber, MS). Common disturbances in prairies include badger and pocket gopher mounds, buffalo wallows (up to  $24 \text{ ha}^{-1}$  in the Refuge), and prairie-dog towns (which may have extended for kilometers). All provide exposed sites and environments different from that of undisturbed grassland (Platt 1975; Grant et al. 1980; Coppock, Detling et al. 1983; Polley and Collins 1984). Prehistoric estimates of over 50 million bison, 1 billion prairie dogs, 20 million antelope, and untold numbers of elk, deer, badgers, ground squirrels, etc., in the Great Plains (England and DeVos 1969) suggest that animals induced frequent large- and small-scale disturbances in grasslands. Fire frequency of 3–5-yr intervals (Wright and Bailey 1982) further contributed to the commonness of disturbance. Plant species diversity was highest on grasslands subjected to several concurrent natural disturbances (S. Collins and S. Barber, MS). Much of this increase in diversity resulted from an increase of native ruderals (from  $16 \cdot 0.5 \text{ ha}^{-1}$  in ungrazed grasslands to  $25 \cdot 0.5 \text{ ha}^{-1}$  in grazed grasslands) and decreased dominance by perennial grasses (from 81% total cover to < 65% in ungrazed and grazed grasslands, respectively). Seed dispersal to *distant* sites was probably unnecessary in presettlement times. Instead, our evidence suggests that there is a high probability of fire or animal-mediated disruption of the plant canopy at any given point in the grassland. Dispersal to these sites may have been increased via animal dung because *Bison* are attracted to recently burned areas (Vogl 1974),

prairie-dog towns (Coppock, Ellis et al. 1983), and patches where buffalo wallows already exist.

If dispersal by large herbivores has shaped seed characteristics, why are there so few plants with adaptations for external dispersal in animal fur? The risks of seed destruction by chewing, digestion, or predation within dung are significant. In addition, dispersal via dung is a random, although common, process. We observed 86 *Bison* dung piles along 8.2 km of a dirt road in the Refuge. Of 44 wallows observed, however, only 16 (36.4%) contained dung. In contrast, *Bison* commonly move to rest, feed, and wallow at disturbed sites (Coppock, Ellis et al. 1983), and this movement would provide a directional approach favoring ectozoochory from disturbance to disturbance. Perhaps this is not more common because disturbances were frequent enough to reduce the selective advantage of long-distance dispersal. With regard to short-lived forbs, dispersal away from the parent plant may not be advantageous. Werner (1977) and McEvoy (1984) have shown that seeds of *Dipsacus sylvestris* and *Senecio jacobaea* have a higher probability of survival in the area vacated by death of the parent. Therefore, while seed consumption by large mammals may serve to disperse some seeds via dung, the costs of destruction may outweigh the benefits of such a system.

In summary, we believe that the predation and disturbance regimes in grasslands do not provide the selective forces necessary to promote coevolved mammalian seed-dispersal syndromes. Nevertheless, consumption of seeds by large herbivores may be an important method of long-distance dispersal for some small-seeded plants. We believe that this relationship is nearly always facultative. Exceptions such as *Bouteloua gracilis* (Wicklowsky et al. 1984) may exist. Alternatively, such dispersal may result from the accidental consumption of seeds during the grazing of neighboring foliage. In conclusion, we agree with Janzen that prairies are "enormous planar chlorophyllous multispecies" (1984, p. 349) communities, but the time is not yet ripe to consider them or their vegetative components as green fruits.

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