Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications

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This study examined small-scale seed distribution using published data collected using the same techniques and the same group of observers in four locations in North American deserts (Curlew Valley, Utah in the Great Basin Desert; Rock Valley, Nevada in the Mojave Desert; Silverbell, Arizona in the Sonoran Desert; and Jornada, New Mexico in the Chihuahuan Desert). The distribution patterns were examined horizontally (under shrub canopy to open areas) and vertically (measured at the soil surface and at four depth intervals) in relation to seed morphology. At all four sites, seed distribution of individual species was positively related to seed abundance. Horizontally, total number of seeds per unit area decreased from under the shrub canopy to intershrub areas. Vertically, total number of seeds declined as soil depth increased. Most species were only present in a small proportion of samples. Small seeds were either abundant and broadly distributed or rare and found in a few samples, but larger seeds were always low in abundance and restricted to a small proportion of samples. For annual species, significantly higher proportions of larger seeds than smaller seeds were found deeper in the soil. However, when much larger-seeded species, i.e. herbaceous perennials and shrubs, were included in the analyses, most very small or very large seeds were found in the upper-most layers of soils and intermediate to large-sized seeds deeper in the soils. Such seed distribution related to seed morphology and soil factors may have significant ecological implications in plant population dynamics and community structure in desert ecosystems.

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Introduction

Seed banks are important elements in desert ecosystems, where annual plants account for a large part of the flora and their seeds can stay viable in the soil for many years, especially in hot deserts (Kemp, 1989; Inouye, 1991; Rundel & Gibson, 1996). In the
last two decades, although considerable progress in seed bank studies have been made in various ecosystems, detailed knowledge of how explicit desert seed distribution patterns (both horizontal and vertical) are affected by seed morphology (e.g. sizes) and soil structure is poor (e.g. Thompson & Grime, 1979; Liddle et al., 1987; Okubo & Levin, 1989). Particularly, the implications of horizontal and vertical distributions of different sized seeds in governing above-ground plant community structure and dynamics have not been given enough attention.

Most studies in desert ecosystems have shown that seed reserves are highly variable in both space and time (e.g. Numata et al., 1964; Reichman, 1984; Thompson, 1987; Rundel & Gibson, 1996). Seed abundance in any particular microhabitat depends on the input of seeds during both phase I (i.e. movement of a seed from the parent to a surface) and phase II (i.e. subsequent horizontal and vertical movements after Phase I; see Chambers & MacMahon, 1994). In deserts, wind, sheet flooding, seed-eating animals, and soil surface microtopography are major factors affecting seed dispersal and distribution (Goodall et al., 1972; Reichman, 1984), thus, seed morphology (sizes and shapes) appears to be important in patterning initial dispersal distances and distributions (Chambers et al., 1991). However, seed distribution and seed bank dynamics after dispersal are functions of several other factors such as predation, germination, local decay, and seed movement in the soil (Chambers & MacMahon, 1994). Desert animals often selectively forage on seeds based on seed size, protein content, and other factors. For example, rodents and birds select larger seeds, whereas ants prefer small seeds (Samson et al., 1992; Guo et al., 1995). The burrowing activities of various non-granivorous animals (e.g. tortoises, peccaries, rabbits; pers. obs.) allow seeds to move deeper into soil through disturbances. These same activities may dig up seeds from far below the surface, and thus increase the possibility of seed germination (Chambers & MacMahon, 1994).

Seed distribution and storage in soil are also related to soil conditions such as particle sizes, structure, and soil chemistry (Larner, 1977; Silvertown, 1981; Coffin & Lauenroth, 1983; Chambers & MacMahon, 1994). In North American deserts, the non-random distribution of seed banks (i.e. different sized seeds at different locations at the soil surface and at different depths) plays an important role in allowing co-existence of many plant species (Reichman, 1984). The distribution of seeds (both horizontal and vertical) may also be important in promoting species diversity of animals that depend on seeds, especially when animal consumers selectively feed on different species and can forage on seeds in different microhabitats or soil depths.

Although earlier studies addressed the remarkable heterogeneity in seed distribution, relationships between seed abundance/distribution and seed morphology (e.g. size) have not yet been given thorough attention (Nelson & Chew, 1977; Reichman, 1984; Rundel & Gibson, 1996), especially when both horizontal and vertical distributions of seeds and their relations with above-ground plant communities are considered as well (Chambers et al., 1991; Chambers & MacMahon, 1994). The International Biological Program (IBP) Desert Biome Projects on soil seed sampling in early 1970s (Goodall et al., 1972; Childs & Goodall, 1973; Goodall & Morgan, 1974; Kemp, 1989; Inouye, 1991) provide valuable data on seed population density and spatial distribution in four sites in North American deserts, and permit detailed studies on seed distribution. Although seed sizes were also measured during these original studies, there was no effort made to relate the seed abundance and distribution with seed morphology.

In this paper we use data collected using consistent sampling methods during the IBP to examine horizontal and vertical distribution patterns of seeds in the soils in terms of seed sizes in four North American deserts. We ask the following questions: (1) what are the small-scale horizontal and vertical distribution patterns of seed banks and how are such patterns related to seed sizes? (2) What are the similarities and differences in seed distribution among locations? (3) What are the underlying
mechanisms and ecological implications of these distributions? The purpose is to examine the functional roles of post-dispersal seed distribution in North American deserts by comparing the horizontal and vertical distributions of desert plant seeds differing in sizes.

**Materials and methods**

**Study sites**

The IBP study sites range from 42° N to 32° N, and the climatic regimes vary from unimodal precipitation (Curlew Valley in the Great Basin and Rock Valley in the Mojave Desert) to typically bimodal precipitation (Silverbell in the Sonoran Desert and Jornada at the edge of the Chihuahuan Desert) with different temperatures (Fig. 1). The purpose of these original studies was to estimate the soil seed populations in the sites of the IBP Desert Biome Program and to provide information on spatial seed distribution (Goodall & Morgan, 1974).

Unlike the other three sites that are located in hot deserts and are rich in annual species, Curlew Valley is a cold desert. Rainfall is evenly distributed between seasons.
and more than half of the annual precipitation falls as snow (Table 1). The diversity and abundance of annual species at the site are low. Important perennials at the site are Atriplex confertifolia (Torr. & Frem.) S. Watson, and Seriphidium tridentatum (Nutt.) W. A. Weber var. wyomingense (Beetle & A. Young) Y. R. Ling, syn. Artemisia tridentata Nutt. subsp. wyomingensis Beetle & A. Young. Rock Valley is in the Mojave Desert, which is transitional between the ‘cold’ and ‘hot’ deserts. Winter precipitation is predominant, with rainfall and snow falling from November to March. Major shrub species are Larrea tridentata (D.C.) Coville, Ambrosia dumosa (A. Gray) Payne, Lycium spp., and Ephedra nevadensis S. Watson. Winter annuals are abundant and rich in diversity, but very few summer annual species are present. At Silverbell, total winter precipitation (November to March) on average approximates total summer precipitation (June through August; 119 and 111 mm, respectively; Davidson et al., 1984). The site is situated in a typical Sonoran lower bajada habitat (alluvial outwash plain) where the dominant perennial shrubs, Larrea tridentata and Ambrosia deltoidea (Torr.) Payne, together account for about 30% of cover (Inouye et al., 1980). There are a great variety of both winter and summer annual species. The Jornada site also has a bimodal precipitation pattern similar to that at Silverbell, but more rainfall occurs in summer than in winter. This site is located on a sandy alluvial fan (bajada) with dominant perennial species (Larrea tridentata, Prosopis glandulosa Torr., Erionema pulchellum (Kunth) Tateoka) and many winter and summer annuals.

The soils at Curlew Valley are primarily silt loams, which are sedimentary in origin and relatively homogeneous at the study site. In contrast, at the Rock Valley site, soil texture is predominantly fine sands derived from calcareous alluvium, with low clay and silt content. At the Silverbell site, the presence of ramifying streams and rivulets increases spatial variation in soil properties; thus, this site has the most heterogeneous soils with five major soil types. The predominance of gravelly sandy loam and clay loam in the upper horizons results in moderate infiltration and permeability. The Jornada site is located on coalesced alluvial fans with silicate and carbonate accumulations in the upper 60 cm depth (Table 1; Szarek, 1979).

Data collection

Data for species composition in 1970–76 in plant communities at each study site were available in the IBP annual reports (Curlew Valley: MacMahon, 1976 and literature therein; Rock Valley: Rundel & Gibson, 1996 and literature therein; Silverbell: Thames, 1976 and literature therein; Jornada: Whitford, 1976 and literature therein). Although these data were not collected from the exact locations as those used for seed bank sampling, they are from nearby areas and give an accurate description of the overall plant community structure.

Table 1. Geographic locations and climatic and soil conditions at the four study sites*

<table>
<thead>
<tr>
<th>Sites</th>
<th>Geographic location</th>
<th>Elevation (m)</th>
<th>Precipitation (mm year⁻¹)</th>
<th>Soil texture (main components)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curlew Valley</td>
<td>41°52' N, 112°45' W</td>
<td>1200</td>
<td>260</td>
<td>silt loam</td>
</tr>
<tr>
<td>Rock Valley</td>
<td>36°40' N, 116°05' W</td>
<td>1050</td>
<td>165</td>
<td>fine sand (60%)</td>
</tr>
<tr>
<td>Silverbell</td>
<td>32°40' N, 111°50' W</td>
<td>700</td>
<td>277</td>
<td>sandy and clay loam</td>
</tr>
<tr>
<td>Jornada</td>
<td>32°37' N, 106°44' W</td>
<td>1300</td>
<td>314</td>
<td>clay and fine sand</td>
</tr>
</tbody>
</table>

*Data from Szarek (1979). Data for Curlew Valley and Jornada are 3-year means (1972–74) and for Rock Valley and Silverbell are 2-year means (1972–73).
Soil seed bank studies were initiated in 1971. The Rock Valley site was sampled in November 1971, and the other three sites (Curlew Valley, Silverbell, and Jornada) were all sampled in June 1972. At the Jornada site, replicate samples were taken from three locations: playa, playa fringe, and bajada. These data were reported in Goodall et al. (1972), Childs & Goodall (1973), and Goodall & Morgan (1974).

Soil samples were collected at different distances from locations under the canopies of shrubs and bunchgrasses, as well as intershrub (or interbunchgrass) areas. At each site, samples were collected from soil profiles in four depth increments, 0–1, 1–2, 2–5, and 5–10 cm. Each sample was a cubic decimeter in volume. Samples of surface litter were also included where it was present. In the case of the surface litter samples, the seed counts refer to the number of seeds per 100 cm². In the deeper samples, a subsample of 100 g of air-dried soil was analysed; hence, the seed number was multiplied by the bulk density and by the thickness (in cm) of the soil layer to calculate an area estimate (Goodall et al., 1972). Soil samples were double floated using potassium and then zinc chloride solutions supplemented by sieving to make sure that seeds with different weights would not be missed.

During the sampling years, samples of seeds from growing plants were also collected for species identification of the seed banks and for germination tests. Seed germination tests were performed but not successful because seed dormancy is very prevalent in desert plants and only part of the seed population germinated in a range of conditions used. Tests for seed recovery were very successful and gave results around or well above 90%, indicating the poor recovery is probably not a serious problem in seed counts. Seed identification for the four sites received assistance from S. Bamberg, J. Beatley, A. Holmgren, J. Nelson, J. Reichman, R. Spellenberg, and W. Whitford. For some species in the Jornada site, supplies of seeds for recovery tests were not available, therefore seeds of the same genus and comparable in size to the species in question were used.

There were no data on seed size for Curlew Valley (Goodall et al., 1972). Also, no effort was made to test the viability or germinability of seeds at any site. Some seeds remained unidentified or identified only to genus. The separation of seeds from soils might affect their viability, so a test of germinability was thought of little value. There was no satisfactory means of distinguishing death from dormancy. Therefore, the number of seeds counted is an overestimate of the number of germinable seeds. In this study, we use seed weight as an estimate for seed size. For additional information on seed bank sampling, seed extraction, and seed identification, see Goodall et al. (1972), Childs & Goodall (1973), and Goodall & Morgan (1974).

Results

Total seed population during the sampling period was highest on the playa at Jornada, with nearly 40,000 seeds m⁻², but total seed biomass was highest at Silverbell (8.31 kg ha⁻¹). As expected at all four sites, small seeds were more abundant than larger ones, and were also found in more samples. However, small seeds of some species were also rare and occurred in very few samples. Larger seeds were always low in abundance and found in a small number of samples (Fig. 2). At all sites, most species were present in a very small number of samples whereas only one or two species were present in almost all samples (Fig. 3).

In general, the total number of seeds per unit area (combining all depths) decreased from the shrub canopy center to intershrub areas (Fig. 4). This trend was especially striking at Rock Valley, where most seeds were found under shrub canopies. However, exceptions were observed in all four sites for some species, and inconsistent patterns were also observed for some shrub species (Childs & Goodall, 1973). At Curlew Valley, for example, bunchgrass and shrub species such as Agropyron cristatum (L.)
Gaertn. and Atriplex confertifolia did not show any trend at all. Both increasing and decreasing trends of total number of seeds with distance from canopy center were observed in Serrhipodium tridentatum. At Rock Valley the number of seeds also increased with distance from the center of Krameria (Fig. 4). While in most cases more seeds

![Graph showing relationships between seed distribution and seed size in soil samples at three desert sites. Note that seed size data for Curlew Valley are missing. Each symbol represents one species.](image_url)
were found under shrubs, the tendency for seeds of two species of Bouteloua at Silverbell was in the opposite direction, the highest density being recorded in the intershrub areas.

There were significant positive relationships between seed distribution (number of samples present) and seed abundance (number of seeds of the species) at both the soil surface and the four depth intervals. Seed density in litter is extremely variable across the four sites and there was a general decline in number of seeds from upper soils to greater depths (Fig. 5). Curlew Valley had the highest proportion of seeds found at the soil surface, while all Jornada sites had the highest proportion in 1-2 cm. Most seeds were found in the upper 2 cm of soils, and only 10-3% of seeds at Curlew Valley, 3% at Rock Valley, 18% at Silverbell, and 11% at Jornada were found below 5 cm depth.

Similar to horizontal distributions, different species differed in their vertical distribution. At Curlew Valley, for example, some species (e.g. all grasses and Collinsia parviflora Douglas) had most seeds on the soil surface, whereas others, such as Polygonum douglasii Greene, had more than half of the seeds below 2 cm depth. Among annual species, larger seeds tended to be deposited at greater depths than small ones (Fig. 5). Significantly higher proportions of larger seeds of annual species were found in deeper soils than smaller seeds, but there was no such pattern found at the bajada and playa sites at Jornada, where virtually all species found in the seed banks had small seeds. The proportions of larger seeds of annuals on the soil surface and at 0-1 cm depth were significantly lower than those of small seeds. Seeds of perennials, mostly shrubs, however, even if larger in size, were found most frequently in the litter, soil surface or shallow layers. Thus, when herbaceous perennial and shrub species were included in the analyses there was a hump-shaped relationship between proportion of seeds and seed size at the fourth depth (5-10 cm) in the soil profile, i.e. most very small or very large seeds were found in the upper soil layers and medium to large-sized seeds were in deeper soils. This is especially apparent at the Rock Valley site (Fig. 6).

**Discussion**

There are clear non-random patterns of seed bank distribution in the south-west deserts and these patterns are similar to patterns in plant communities. For example, horizontal distributions of seeds of many species are strongly associated with shrub distribution and there is a significant positive relationship between seed abundance and distribution (number of samples present on the soil surface or in any depth intervals). In addition, most species were found in a few samples, and very few species were common and distributed in all or most samples. Similar abundance-distribution

**Figure 3.** Frequency distribution of number of samples where seeds were present at (a) Rock Valley, (b) Silverbell, and (c) Jornada (playa fringe) sites.
patterns and spatial associations of abundant annuals with shrubs were frequently reported for plant communities (Parker et al., 1989). Vertical distribution patterns were also significantly related to seed size. However, the causes of these observed patterns may be complex, and both seed size and soil particle size may be critical in forming these non-random patterns.

**Horizontal distribution**

In most parts of North American deserts, microhabitat differentiation causes spatial variation in plant abundance and distribution, through the presence of many island-
like microhabitat types such as shrub, half-shrub, and tussock grass canopies, rodent
and ant mounds, and open areas (Reichman, 1984; Price & Reichman, 1987; Inouye
1991, Pip, 1996). Consequently, desert seed banks also show significant spatial
variation. Comparisons between plant distribution and horizontal distribution of seeds
appear to show positive small-scale feedbacks between above-ground plant densities
and underground seed banks. For example, because seeds of desert plants are
primarily locally dispersed (Ellner & Shmida, 1981), greater seed banks under shrubs
are associated with higher annual plant densities (Parmenter & MacMahon, 1983).
Wind and water are primary dispersal agents in North American deserts and can
directly transport seeds horizontally (Nelson & Chew, 1977; Reichman, 1984). Given
the dense annual vegetation and low wind velocity under shrub canopies, seeds are
logically most abundant under shrub canopies, with a gradual decline from the shrub

Figure 5. Vertical distribution of total seed populations at the five depth categories, measured
in soil samples of equivalent weight.
canopy center to the peripheral areas (Fig. 4; see also Nelson & Chew, 1977; Okubo & Levin, 1989).

Variation in seed densities under shrubs is, however, not clearly related to the size of the shrub canopy at all four study sites (see also Nelson & Chew, 1977; Reichman, 1984). The lack of a close relationship could be due to some other confounding effects of canopy shape, height, or LAI (leaf area index) which may have affected seed dispersal and animal predation (Price & Reichman, 1987; Bower & Brown, 1992). Besides, leaf nutrient content may affect LAI depending on how well leaves of shrubs are protected from microbial degradation (D. Davidson, pers. comm.), and particular chemicals produced by shrub roots may also affect seed viability as well. The relatively low, dense, and flat canopy of Krameria parvifolia Benth., for example, may have restricted seed deposition, led to greater seed predation under its canopies and caused lower seed densities underneath. Temporal microhabitat use by rodents and birds, and selective harvest of clumped seeds by animals clearly reduces the spatial patchiness of seeds in the soil (Nelson & Chew, 1977; Reichman, 1979; Liddle et al., 1987; Inouye, 1991; Bower & Brown, 1992).

With larger numbers of seeds available and usually greater dispersal capacity, small-seeded species may have more chances to reach different microhabitats and to have higher above-ground abundance in favorable years. Temporally, variations in seed reserves were also very different in different microhabitats, with greater variation in open areas than under shrub canopies (Nelson & Chew, 1977).

**Vertical distribution**

For a given set of soil attributes, seeds of a particular size are likely to be found at a particular depth. Vertical movements and final distribution of seeds in the soil profile are determined mainly by seed morphology (e.g. mass and shape), soil structure and

![Figure 6. Comparison of vertical seed distribution in terms of seed size at the soil surface (including litter) and at soil depths (5–10 cm depth) at (a) Rock Valley, (b) Silverbell, and (c) Jornada (playa fringe only). Each dot represents one species. Note that different scales on x-axes were used. At Silverbell, very large seeds, such as that of Larrea tridentata, were absent from the seed banks during the sampling of vertical distributions of seeds, although they were found in other samples at the site (Fig. 2).](image-url)
particle size, animal disturbances or other physical processes (Goodall et al., 1972; Chambers et al., 1991). Gravity can move seeds deeper into soil profiles, and some large-seeded species possess their own structures (e.g. awn) that can facilitate penetration of the soil surface (Harper, 1977). Thus, larger seeds with larger mass would sometimes have greater chances to go deeper into the soil. However, the physical structure of soils may prevent very large seeds from doing so, because the pore spaces or cracks may be too small for them.

Because seeds are most likely to fall on soil surface (phase I dispersal) after they are produced and may thereafter be under the pressure of mass predation, the proportion of seeds on the soil surface would change more dramatically during the year. But different species with different sizes would show significant different responses. For example, selective predation may leave fewer large seeds on the soil surface and therefore proportionally more may be found deep in the soil. But very large seeds may still be proportionally higher on soil surface because they can not move deep in the soil, simply because of their sizes in comparison with soil particle sizes and crack sizes. In contrast, small-seeded species are under lower pressure of predation but are more likely to be redistributed by wind or water. Distribution patterns would also vary among different ecosystems. For example, Chambers et al. (1991) reported that smaller seeds in alpine ecosystems reach greater depths where soils had larger particle sizes. Harper (1977) reported that smaller seeds tend to move downward with rain water in loose textured soils. In contrast to these findings, we found that in North American deserts, medium-large seeds tend to be distributed deeper in the soil and very small and very large seeds tend to stay in the upper layer of soil.

Implications

The role of seed size in determining above-ground plant distribution can be viewed horizontally and vertically in terms of their abundance and distribution in the soil. The positions of seeds on the soil surface and in the soil columns affect their germination and establishment, and thus the structure of plant communities (Chambers et al., 1991). Both biotic and abiotic factors, in turn, control seed bank distribution, as well as the fate of seeds.

To see how horizontal and vertical distribution of desert seed banks affect plant population and communities, seed ecologists have examined the effects of seed morphology and their positions in the soil on germination, growth, seed predation and further seed redistribution in following generations (Harper et al., 1970; Crawley, 1992; Chambers & MacMahon, 1994). Studies show that, for example, seeds of many desert annual species cannot germinate from depth greater than about 1 cm (Freas & Kemp, 1983), and seeds of desert shrubs cannot emerge from below 4 cm (Williams et al., 1974). Moreover, seed predators do not forage below 7 cm (Reichman, 1979). Large seeds and seeds of many grass species commonly do not require light for germination, and thus may be able to germinate from deeper in the soil, but germination of small seeds is very sensitive to light (Harper et al., 1970; Bazzaz, 1979; Silvertown, 1981; Rice, 1989). In addition, seedlings from the largest seeds emerged most quickly from deep sowing, and those from the small seeds most quickly from shallow sowing, and thus growing season phenology and seed size often show a positive relationship (Baker, 1972; Westoby et al., 1992).

Variation among the four study sites in the proportion of seeds distributed at different depths may reflect the seed size composition and differences in soil particle sizes. While we cannot provide direct evidence that soil particle size alone (independently of nitrogen or water) may to a certain extent control plant community structure, published data showed that soil at the Silverbell site, where a higher proportion of larger seeds were found, had larger particle sizes than other sites (Solbrig...
In an alpine ecosystem, Chambers et al. (1991) reported that the total number of diasporas in the soil increased with soil particle size until a threshold size was reached, above which no seeds were trapped. Their study indicated that small diasporas may have lower rates of establishment in soils with large particle sizes than do species with larger diasporas. All these findings suggest effects of soil texture on the distribution and species composition of the seed banks.

Both horizontal and vertical distribution of seeds are also very important in structuring animal communities (Brown et al., 1986; Price & Reichman, 1987). For example, smaller seeds would attract more ants (Davidson et al., 1984) and the amount of larger seeds at both surface and deeper soils may, to a certain extent, control the species richness and relative abundance of rodents and birds (Price & Podolsky, 1989).

Similar to the patterns found in seed banks, studies in the Chihuahuan Desert have shown that small-seeded species show broader ranges of abundance (i.e. either high or low) whereas large-seeded species were always low in abundance. Temporally, small-seeded species were more frequently observed and more broadly distributed over space in any particular season but the large-seeded species were present in fewer seasons and with restricted spatial distribution in any season.

Finally, it is worthwhile to point out that there are limitations in the data sets. First, since soil samples were collected only once in the sampling year, different results might be achieved if seed maturation of the main common plant species occurs at different times of the year. Ideally, soil samples should be collected several times in a year (i.e. shortly after seed maturation, dispersal, and/or pre-germination) and over several years to obtain more accurate comparative results. Year-to-year variation in seed germination rates, abundance of seed-eaters, and other associated factors may also affect the results. Second, many desert plants produce rain-dispersed seeds which adhere to the soil surface by means of a mucilaginous layer. This strategy may prevent massive seed predation and only small portions of these seeds reach the soil seed bank until they germinate. Although these limitations in seed sampling could not be resolved in our current analyses, they should not violate the general conclusions reached in this study.

In summary, the non-random distribution of seeds in terms of their size may have important effects in promoting species richness by reducing the possibilities of competitive exclusion and mass predation (Chesson, 1989; Crawley, 1992). More importantly, horizontal and vertical seed distributions may play different roles in governing above-ground plant communities (Pulliam & Brand, 1975). Further studies on the similarities and differences in seed distribution and its ecological implications in different ecosystems would greatly improve our understanding of the structure and dynamics of above-ground plant and animal communities.

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