

Wind dispersal and subsequent establishment of VA mycorrhizal fungi across a successional arid landscape

Michael F. Allen¹, Lawrence E. Higgs² and Gene L. Wooldridge²

¹*Department of Biology and Systems Ecology Research Group, San Diego State University, San Diego, CA 92182 USA;* ²*Department of Soil Science and Biometeorology, Utah State University, Logan, UT 84322-4840 USA*

Keywords: mycorrhizal fungi, wind dispersal, landscape, establishment, mesoscale wind patterns, landscape ecology, desert

Abstract

Wind is an important vector in the dispersal of microorganisms to new habitats. However, wind dispersal is generally assumed to be random or logarithmically related to distance. We assessed the wind dispersal and subsequent establishment of an important group of plant symbionts, VA mycorrhizal fungi, across a 74 Ha recontoured surface mine. Winds were predominantly westerly aloft, but due to complex north-south ridges, up-valley, thermally-driven air flows developed. Patterns of spore dispersal were tested by a combination of released spore mimics from the potential source areas and by assessing the composition of species deposited across the site and in the putative source areas. Survival of the fungi was assessed two years after the dispersal patterns were monitored.

The spore mimics moved in predictable but complex patterns across the site depending on the interactions of surface and upper winds. Mimics from the valley sources moved up the valleys in the lower flows and occasionally over the ridges in the upper winds. Those from the ridge approximately 2 km distant were entrained in the upper air flows and deposited all across the site. The VA mycorrhizal fungal species compositions from the soils correlated with the deposition patterns measured with the mimics.

Fungal survival showed a pattern similar to dispersal; the fungi often survived in habitats not resembling the habitat of origin although some selection in both more favorable and less favorable sites occurred. These data suggest that microbial dispersal even by wind is predictable if the wind characteristics are known, that the VA mycorrhizal fungi from the site can survive in habitats different from their habitats of origin, but that some selection among species may occur after deposition.

Introduction

Terrestrial ecosystems depend upon microorganisms for critical processes such as nitrogen fixation and decomposition, but the dispersal and establishment of microorganisms are poorly understood. To understand the migration potential of a natural or engineered microorganism and its ability to find an open habitat for re-establishment, descriptions of sources, sinks and vectors of diaspore migration are

essential. Models of microbial migration (other than those that assume specific animal vectors) generally assume that dispersal is random and unpredictable (*e.g.*, Lippincott and Lippincott 1984), have described sources or sinks measured at large scales (up to hundreds of hectares), or have described deposition as a simple numbers versus distance relationship (*e.g.*, Burdon 1987) with abiotic vectors presumably mixing propagules as they move across a landscape.

Vesicular-arbuscular (VA) mycorrhizal fungi regulate resource allocation among plants (*e.g.*, Chiarello *et al.* 1982; Caldwell *et al.* 1985; Allen and Allen 1986) and thereby affect plant community composition (Grime *et al.* 1987; Allen and Allen 1988, 1989). These fungi frequently are lost following severe disturbance (*e.g.*, Allen and MacMahon 1985). Because they cannot be grown in mass culture for re-inoculation, their invasion from neighboring habitats or as escaped inoculants affects the rates and patterns of plant re-establishment (Allen 1988a). Also, different fungi have differing physiological effects on their hosts and are considered prime organisms for genetic modification for applied uses (Hayman 1984; Allen 1988b).

Previously we demonstrated that spores of *Glo-mus* spp. (the fungi that form VA mycorrhizae with most plants at this site) migrated via wind up to two km from the disturbed site of interest, primarily during the autumn drought (Warner *et al.* 1987) and in high winds (Allen 1988b). Moreover, the wind dispersed approximately two orders of magnitude more spores than did animals, the other potential vector for fungal immigration (Allen 1988a). However, despite the general westerly direction of the prevailing winds, the north-south ridges (500 m high) created complex mesoscale wind dynamics. Across the ridge there was no reduction in numbers of spores or mimics with distance from source area Warner *et al.* 1987). Our objectives were to describe the immigration patterns of the wind-borne spores based on the wind dynamics around these complex terrains, and to determine whether the surviving species represented the wind immigrants.

Site characteristics

Since 1981 we have studied successional processes on a disturbed landscape near Kemmerer, Wyoming. The study area is a recontoured surface coal mine (-74 Ha), originally a shrub-steppe cold desert, replanted in 1982 with a mix of local plant species (for details on soils, microorganisms, animals and plants, see Allen and MacMahon 1985; Parmenter *et al.* 1985). The initial disturbance and high precipitation years of 1982 to 1984 contributed

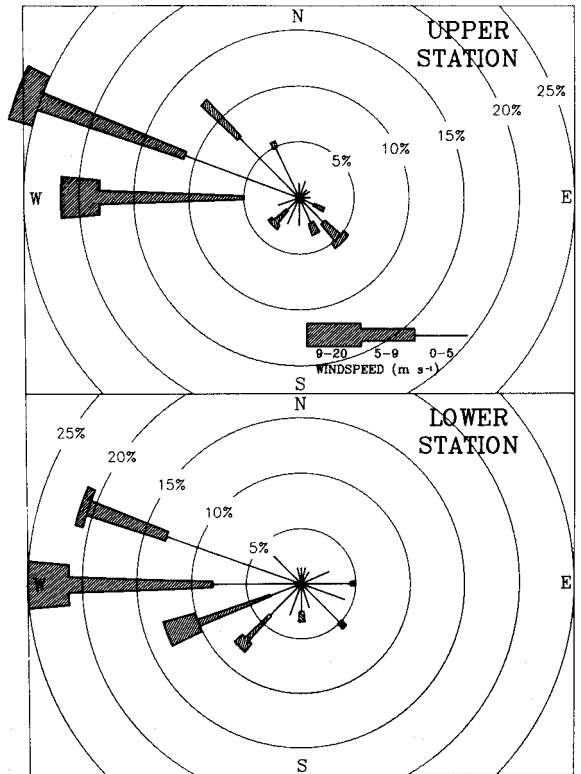


Fig. 1. A wind rose constructed for two locations, 500 m apart, near the top of the lee side of the western-most ridge of the disturbed area for July through September of 1985, when the dispersal studies were conducted. The locations are at sampling sites C (upper station) and F (lower station) (diagrammed in Fig. 3) but are mounted at a height of 5 m to reach into the upper air flows. The winds for both sites were predominantly westerly but the terrain forced a more northerly component to the upper station (near the peak of the ridge) and a more southerly component to the lower station (near the middle of the ridge).

to low VA mycorrhizal fungal activity (Allen *et al.* 1987). Two undisturbed sites up-wind of the disturbed area were identified as likely sources of the VA mycorrhizal fungi, an adjacent undisturbed valley and a more distant (2 km) ridge, the Bear River Divide.

The general wind direction is westerly with wind speeds often ranging up to 10 m/s, 5 min averages, with gusts commonly exceeding 15 m/s. However, the terrain is a complex of north-south ridges altering the wind patterns such that the wind direction and speeds differ even at locations only 500 m apart on the same slope and aspect (Fig. 1).

Methods

Regional upper air flows, both across the ridges and in the valleys, were measured using a series of weather balloons released several times between 1981 and 1985 under varying wind conditions. Wind directions near the surface were also recorded under differing atmospheric conditions with wind socks 1 m high at 23 locations around the site.

To determine source area VA mycorrhizal fungi, surface soils were collected from the two regions upwind that were previously suspected as source regions (Warner *et al.* 1987). Spores of the VA mycorrhizal fungi were identified and counted following differential centrifugation (Ianson and Allen 1986). To determine background levels upwind of the suspected source areas, spin traps (previously described in detail capable of continuous action without power in these high wind conditions, Warner *et al.* 1987) were placed at 4 m height on weather towers for one week collection intervals. Others were suspended at approximately 20 m height above the ground from a dirigible attached with a ground line for two hour intervals during flights of the weather balloons. Both were placed on the Bear River Divide to detect any spores from areas west of the study regions.

Dispersal patterns of VA mycorrhizal fungi were described using two methods. First, soil was collected from the surface 3 cm at 11 sites across the disturbed area in 1985. All soils were collected from areas between plants to exclude inoculum produced *in situ*. Spores of VA mycorrhizal fungi present in the various soils were identified and counted as above. Second, a tracer experiment was performed simultaneously (1985) with the wind trajectory measurements and soil spore counts. Spore mimics were used that duplicated the size (60 to 90 μm in diameter), shape (spherical), and density (0.7 g/cm^3) of VA mycorrhizal fungal spores found dispersing (greater detail can be found in Warner *et al.* 1987). These mimics were raked into the surface soil early in the morning before winds developed. Red mimics were placed at eight locations along the Bear River Divide. White mimics were spread up the adjacent valley. During two days mimics were trapped on 1 m high rotating sticky traps (Warner

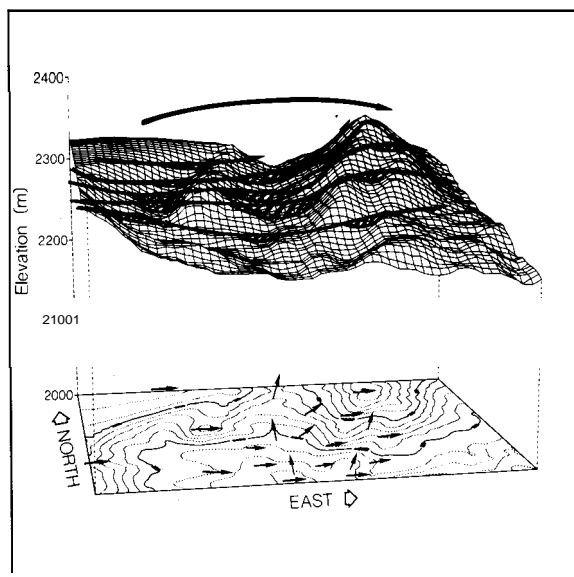


Fig. 2. The topography and predominant wind flows when the propagules are dispersed to the disturbed region. To the west is the Bear River Divide (a ridge), that is parallel to a valley source region (partially bisected by a small ridge). The disturbed region, to the east, is composed of two north-south ridges merging to Mount Cavanaugh, the high point in the northeast corner. Arrows show the upper wind flows, moving from the west to the east over the ridges. Cross-hatching represents the thermally-driven, up-valley flows that move from south to north. Small arrows on the lower topographic map show the surface wind directions when the spores moved across the westerly ridge of the disturbed region onto the study areas.

et al. 1987) at the same 11 locations where the soil samples were taken. Virtually all mimics were trapped by the end of the first day.

In 1987 (five years after disturbance, two years after the immigration studies) survival and reproduction of the different fungal species were determined by isolating and counting spores in the rhizosphere soils of *Agropyron smithii* Rydb., an abundant mycotrophic grass that forms VA mycorrhizae with all of the isolates from the site.

Results

Wind patterns during the windy days when spores migrated across the site (surface speeds $> 5 \text{ m/s}$, Warner *et al.* 1987, Allen 1988b) were relatively consistent. The upper level winds were generally

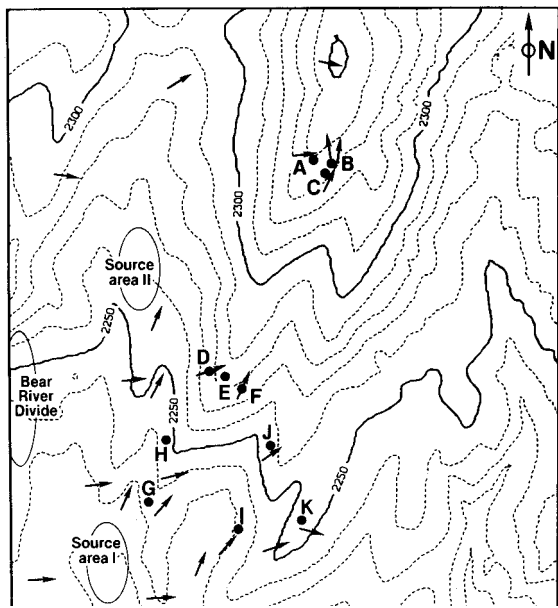


Fig. 3. Topographic map showing diaspore source regions, surface wind directions and sample sites. The source regions are the Bear River Divide, an uplift 2 km to the west of the disturbed area, and the nearby valley labelled source area. The disturbed area extends from the peak in the northeast corner (Mount Cavanaugh) along the middle of the westerly ridge below the locations labelled H and G, and extending eastward. Sites A through K are sampling locations for soil spores and containing wind traps for collecting spore mimics. Arrows represent the surface wind directions (1 m high) during conditions when the spores move across the disturbed area.

westerly. This combined with daily heating of the valleys resulted in secondary circulations in the valleys where air flow was orthogonal to the westerlies (Fig. 2). Wind directions at the surface (1 m high) reflected these patterns in that winds were westerly across the ridge tops, up the valleys (south to north) in the valley bottoms, and of various directions (including easterly) depending upon the particular turbulence generated by the interactions of the two dominant flows (Fig. 3).

No spores were trapped in the spin traps suspended from the dirigible and a maximum of only 12 spores were trapped over an entire week on the traps on the Bear River Divide (compared with up to 20 per hour on the site, Warner *et al.* 1987). Spores of the different fungal species from the two predicted source regions were different. The dominant VA mycorrhizal fungi from the Bear

River Divide were almost exclusively *Glomus microcarpum* Tul. & Tul. (92% of all spores observed). In the Valley areas, only 3% of the spores were *G. microcarpum*, the rest being a mix of *G. fasciculatum* (Thaxter sensu Gerdemann) (Gerdemann and Trappe), *G. macrocarpum* Tul. & Tul., and *G. mosseae* (Nicol. & Gerd.) Gerdemann and Trappe.

Table 1 shows the ratios of the various spores found at each sample location and of the mimics trapped from the disturbed region. The data from the traps and the soil spore counts in the disturbed area show close agreement in the proportion of spores found and mimics dispersed from the Bear River Divide compared with the total immigrant counts ($r = 0.84$, significant at a confidence level > 0.99). Spore mimics from the valley moved up the western slope onto the western ridge of the disturbed area with a few coming over the top into the upper trap sites. Also, some mimics were entrained into the secondary circulation south of the western ridge and entered the disturbed valley at locations I and J (Fig. 3). Few spores of the species found in the valley were found at location K. No mimics from the valley were trapped at location K. Apparently no propagules or mimics moved from the secondary valley flows into the upper air stream. Spore mimics and spores of the species of VA mycorrhizal fungi from the Bear River Divide were dispersed across the site.

No correspondence was observed between deposition habitat and habitat of origin. Survival of fungi up to 1987 was highly correlated with initial immigration patterns ($r = 0.78$, significant at a confidence level > 0.99 , Table 1). Exceptions were mostly in the upper ridges of the disturbed area (locations A, C and K). In these sites, spores from the valley apparently were selected against. Only at site I was survival of valley spores greater than *G. microcarpum*.

Discussion

Dispersal of microorganisms across a landscape generally has been assumed to be random and therefore unpredictable (*e.g.*, Lippincott and Lip-

Table 1. Vesicular-arbuscular mycorrhizal fungal spore and mimic dispersal patterns and subsequent survival patterns at sites across the disturbed region. The data shown are the ratio of spores (*Glomus microcarpum*) or mimics (red) originating from the Bear River Divide to the total spores or mimics measured. Collection sites are shown in Fig. 3.

Collection site	1985 mimic ratio (red/total)	Total mimics trapped	1985 soil spore ratio (<i>G. microcarpum</i> /total)	1987 soil spore ratio
A	0.57	114	0.38	0.69
B	0.51	77	0.39	0.44
C	0.73	51	0.42	0.98
D	0.34	138	0.41	0.67
E	0.83	48	0.66	0.85
F	0.79	80	0.54	0.69
G	0.53	117	0.26	0.35
H	0.29	114	0.30	0.38
I	0.64	159	0.33	0.20
J	0.76	49	0.57	1.00
K	1.00	31	0.75	1.00

pincott 1984). Alternatively, others have suggested that dispersal can be described using simple log-log relationships of numbers of deposited propagules versus distance from source (Burdon 1987). These two simple approaches to dispersal currently characterize the limits to describing the potential of microorganisms to migrate and establish in new habitats.

Mycorrhizal fungi affect the structure and functioning of communities by regulating the resource allocation among plants (Allen and Allen 1989). In our semiarid site, adding VA mycorrhizal fungi to specific plots altered the succession rates and/or trajectory by altering the growth and competitive interactions among successional seres (Allen and Allen 1986, 1988, 1989). However, in order for the fungi to affect the communities, they must colonize. We previously demonstrated that spores of VA mycorrhizal fungi migrate both by wind and animals at this site (Warner *et al.* 1987). Moreover, the deposition of propagules by wind did not follow a decreasing deposition with increasing distance as hypothesized. Animals appear not to move enough VA mycorrhizal fungal spores to initiate the level of VA mycorrhizal activity that was observed and the animals deposited feces containing spores in an ir-

regular pattern by defecating under some shrubs but not others (Allen 1988a). We therefore hypothesized that the dispersal of VA mycorrhizal fungal propagules was more closely related to the complex wind dynamics created by the strong westerly winds bisected by the north-south ridges and that the landscape-scale dispersal patterns could be predicted if an adequate understanding of the wind dynamics was developed.

If the dispersal patterns of VA mycorrhizal fungal spores were described using traditional spatial statistics, they would be considered random. For example, the variance to mean ratio was 4.0 following arc-sine transformation of the ratio of mimics from the Bear River Divide to the total, suggesting random dispersion (Elliott 1971). However, the wind patterns indicated that the migration of these fungi was not random. Mimics of VA mycorrhizal fungi moved in patterns dictated by the mesoscale atmospheric flow around the terrain. Those from the valley migrated only to the western ridges adjacent to the valley with a few going over the top onto a different habitat and a few being entrained into a secondary flow migrating around the base of the ridge and into the adjacent valley. The upper air flows moved mimics from the Bear River Divide and transported them all across the site. Since the dispersion patterns of the species of VA mycorrhizal fungi correlated with the deposition patterns of the mimics, we suggest that they dispersed in a like manner.

No correspondence was observed between deposition habitat and the habitat of origin. Soil properties and plant species composition were relatively constant across the reclaimed site; thus, the microclimate differences probably were the major agents of selection (Allen *et al.* 1987). At all sites (especially A, C, and K) the survival rates indicated greater survival of the ridge top species, *G. microcarpum*, than valley spores. At sites J and K, harsh ridgetop locations, where some of the valley propagules immigrated, only the *G. microcarpum* survived. At site I, where the ratios changed in favor of the valley spores, the location was on an east-facing slope that received greater moisture due to drifting snow than the other sites (Allen *et al.* 1987).

These data suggest that both immigration and

selection dictate the structure of the VA mycorrhizal fungal community at a particular site and that these cannot always be predicted using the simple epidemiological models currently in vogue. Previously, we demonstrated that the VA mycorrhizal fungal spores are wind dispersed but not deposited in decreasing densities with increasing distance from the source region (Warner *et al.* 1987). The mimic and fungal species composition data presented here suggest that these fungi become wind-borne and disperse in non-random, complicated patterns dictated by the structure of the upper air flows and the thermally-driven valley flows. Although some selection occurred, each fungal species survived in most of the habitats to which it had been dispersed, although these sites did not always have the same apparent environmental conditions as the site of origin. These fungi also have different effects on the host plants (Stahl and Smith 1984; Allen and Friese, unpublished data) including differential host survival when infected by the different fungi.

These data contradict suggestions that soil-borne microorganisms cannot migrate and establish rapidly in new habitats. Moreover, migration is neither random nor unpredictable. By understanding the physical characteristics of a site as well as the biological, prediction of the potential for migration and establishment should be possible. However, survival of specific microorganisms cannot be predicted simply by describing the environment of origin. To understand the establishment and ecological impact of a microorganism, it is also important to understand dispersal and the environmental scale at which selection pressure operates. As with plants and animals, only when an organismal approach to microorganisms is taken, can predictability of their movement in the landscape, essential to field application of biotechnology, be possible.

Acknowledgments

We thank E.B. Allen, D. Freckman, J.A. MacMahon, K.T. Paw U, and J. Smith for reviewing this manuscript and C. Friese, K. Leunk and S. Smith

for technical help. Support was provided by grants BSR 83-17358 from the National Science Foundation, 83-CRCR-1-1229 from the United States Department of Agriculture and R813751-01-0 from the Environmental Protection Agency.

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