BMC Ecology

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Research article

# The effects of weather on fungal abundance and richness among 25 communities in the Intermountain West

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Published: 13 June 2002

*BMC Ecology* 2002, **2**:7

Received: 1 February 2002

Accepted: 13 June 2002

This article is available from: http://www.biomedcentral.com/1472-6785/2/7



## Abstract

**Background:** Because moisture and temperature influence the growth of fungi, characterizing weather conditions favorable for fungi may be used to predict the abundance and richness of fungi in habitats with different climate conditions. To estimate habitat favorability to fungi, we examined the relationship of fungal abundance and species richness to various weather and environmental parameters in the Intermountain West. We cultured fungi from air and leaf surfaces, and collected continuous temperature and relative humidity measures over the growing season at 25 sites.

**Results:** Fungal richness was positively correlated with fungal abundance ($r = 0.75$). Measures of moisture availability, such as relative humidity and vapor pressure deficit, explained more of the variance in fungal abundance and richness than did temperature. Climate measurements from nearby weather stations were good predictors of fungal abundance and richness but not as good as weather measurements obtained in the field. Weather variables that took into account the proportion of time habitats experienced favorable or unfavorable relative humidity and temperatures were the best predictors, explaining up to 56% of the variation in fungal abundance and 72% for fungal richness.

**Conclusion:** Our results suggest that the abundance and richness of fungi in a habitat is limited by the duration of unfavorable weather conditions. Because fungal pathogens likely have similar abiotic requirements for growth as other fungi, characterizing weather conditions favorable for fungi also may be used to predict the selective pressures imposed by pathogenic fungi on plants in different habitats.

## Background

Fungal pathogens can be important selective forces on plants in habitats favorable to fungal development, but estimating the magnitude of selection by fungal pathogens in nature is difficult. The development of fungal disease in plants has at least three important control points: the prevalence of fungal inoculum, the environment during infection, and disease development as modified by plant defenses [1,2]. Most field studies on wild plants have not measured pathogen abundance but have focused on disease expression [3–6]. Atmospheric moisture is generally the single most important environmental factor influencing the incidence and severity of fungal diseases on plants [4,7–10]. High relative humidity and several hours

of free surface water are critical for both spore germination and successful infection [11–13]. In addition, infection (i.e., invasion of plant tissue by the fungus) and disease (i.e., the expression of symptoms such as lesions or necrosis) [14] on plants due to air-borne fungi are favored by temperatures of 15–40°C [12,15]. Field studies on plant pathogens have demonstrated that the growth of fungi is favored by high moisture and moderate temperatures [3,15–18] and that low relative humidity and extreme temperatures inhibit growth and spore germination [13,19]. Other studies on soil fungi also show that prevalence differs among habitats and seasons and correlates positively with moisture and negatively with temperature [13,20]. This apparent positive relationship between moisture and fungal growth and abundance may result from the high surface-to-volume ratio of fungi, making them vulnerable to water loss.

The positive association between habitat moisture and the incidence and severity of disease suggests that the selective pressures imposed on plants by pathogenic fungi may vary among habitats. However, the relationship of habitat characteristics to inoculum abundance, infection and disease is poorly understood. This study focuses on abiotic correlates of inoculum abundance. It is not an attempt to describe the distribution of particular species of fungi, but rather to obtain an independent predictor of the prevalence of fungal inoculi in different habitats. To do this, we examined fungi in the air and on leaf surfaces rather than trying to separate opportunistic and obligate pathogens from non-pathogens. First, it would be impractical to identify all fungi sampled, and second there is no reason to expect that pathogens and non-pathogens differ in their abiotic requirements for growth. The growth and sporulation of many pathogens is favored by high humidity, and temperature requirements are similar to other mesophiles, with ranges between 5 and 50°C and optima between 20 and 30°C [1,12,13]. Thus, characterizing the weather conditions favorable for fungi in general may be useful in predicting the extent of selection imposed by pathogenic fungi on plants in different habitats.

In this paper, we report the relationship of fungal abundance and species richness to abiotic factors such as weather, elevation, geographic location, and soil characteristics in the Intermountain West. Although a geographically restricted area (Fig. 1), the Intermountain West encompasses a diverse array of habitats from desert to alpine habitats. Our goal was to estimate habitat favorability to fungi by relating weather and other environmental conditions to fungal abundance and richness. Given that the distribution and abundance of organisms as a function of environment provides the fundamental basis of many ecological and evolutionary disciplines [21], establishing a better understanding of fungal distributions in natural habitats is central to the study of mycology and plant ecology.

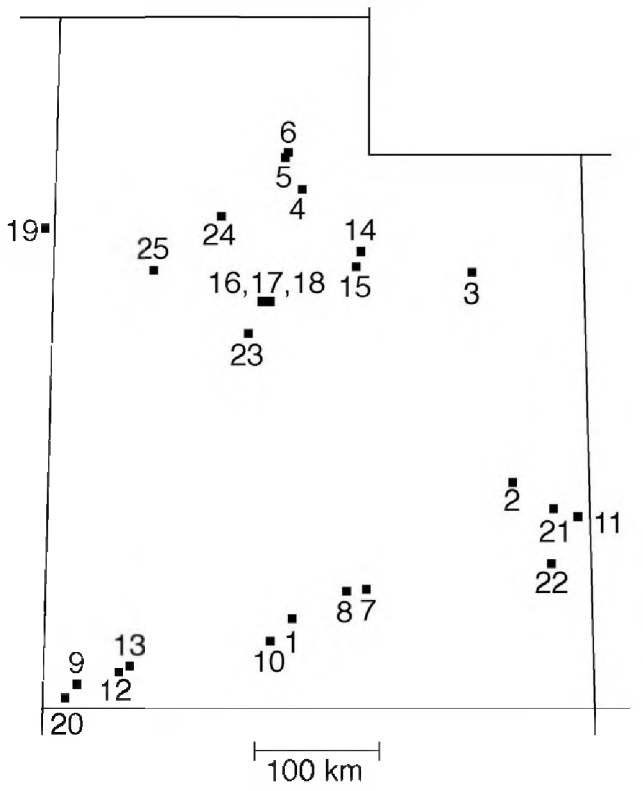


**Figure 1**
**Twenty-five study sites located in the Intermountain West** Topography and elevation separate nearby field sites that are close together.

## Results

### *Fungal abundance and richness*

In order to estimate fungal abundance and richness of different habitats, we sampled fungi from the air and the leaf surfaces of the vegetation. We used three different media in case fungi had different growth requirements (potato sucrose agar, casein agar and agar made with extracts of sagebrush leaves). For vegetation sampling, we found no effect of media type on fungal abundance (Kruskal-Wallis nonparametric analysis $\chi^2_2 = 0.60$; $P = 0.74$), or on fungal richness ($\chi^2_2 = 3.50$; $P = 0.17$). Therefore, for the vegetation sampling, we averaged data from the three media types to obtain one value for the abundance and richness at each site. For the air sampling in 1998, we found no effect of media type on fungal abundance ($\chi^2_2 = 1.61$; $P = 0.45$) or richness ($\chi^2_2 = 0.73$; $P = 0.69$), so we averaged data from the three media types. Lastly, for the air sampling in 1999, we averaged the data from the 10 plates.

**Table 1: location, fungal sampling, and weather parameters of the field sites.**

| site # | field site | elevation (m) | latitude | longitude | vegetation sampling | 1998 air-sampling | 1999 air-sampling | average fungal abundance | average fungal richness | average temperature (°C) | maximum # of consecutive days >0°C | average daily maximum RH | average vapor pressure deficit (kPa) | proportion of days between 4 and 40°C and max RH >90% | average # of consecutive days with max RH < 50% | annual precipitation (cm) | annual temperature (°C) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Bramble | 2227 | 37°40.19 | 111°48.33 | x | x | x | 0.99 | 1.28 | 8.8 | 75 | 71 | 1.75 | 0.38 | 4.6 | 26.90 | 9.61 |
| 2 | Canyonlands | 1442 | 38°38.73 | 109°45.06 | x | x | x | 0.75 | 0.85 | 20.0 | 127 | 60 | 1.22 | 0.15 | 5.7 | 22.38 | 12.65 |
| 3 | Duchesne | 1633 | 40°10.57 | 110°06.27 | x | x | x | 1.49 | 1.56 | 14.6 | 142 | 79 | 1.51 | 0.48 | 5.5 | 20.30 | 7.51 |
| 4 | Emigration | 1715 | 40°45.78 | 111°42.60 | x | x | x | 2.28 | 1.94 | 16.5 | 109 | 88 | 0.95 | 0.44 | 2.0 | 60.53 | 8.11 |
| 5 | Farmington | 1433 | 40°59.76 | 111°53.09 | x | x | x | 4.19 | 1.68 | 18.4 | 92 | 76 | 1.42 | 0.45 | 2.1 | 61.93 | 10.72 |
| 6 | Francis | 2900 | 41°01.88 | 111°50.33 | x | x | x | 0.5 | 0.82 | 7.5 | 75 | 86 | 0.57 | 0.18 | 4.9 | 150.14 | 2.17 |
| 7 | Grand Escalante | 2045 | 37°52.14 | 111°06.61 | x | x | x | 0.53 | 0.79 | 12.8 | 84 | 71 | 1.14 | 0.33 | 4.1 | 26.94 | 9.25 |
| 8 | GE Slot | 1726 | 37°51.66 | 111°17.89 | x | x | x | 0.37 | 0.74 | 14.4 | 95 | 71 | 1.56 | 0.4 | 5.2 | 26.94 | 9.25 |
| 9 | Gunlock | 1030 | 37°10.76 | 113°44.85 | x | m | x | 0.23 | 0.3 | 21.8 | 187 | 48 | 2.53 | 0.14 | 7.6 | 20.37 | 16.69 |
| 10 | Kodachrome | 1831 | 37°30.09 | 111°59.62 | x | x | x | 0.28 | 0.63 | 13.2 | 86 | 75 | 1.28 | 0.41 | 5.7 | 25.64 | 9.14 |
| 11 | La Sal | 2554 | 38°23.64 | 109°09.86 | x | x | m | 0.63 | 0.97 | 9.7 | 75 | 87 | 0.69 | 0.62 | 3.5 | 33.01 | 7.94 |
| 12 | Leeds | 1290 | 37°16.20 | 113°22.61 | x | m | x | 0.42 | 0.42 | 21.8 | 184 | 42 | 2.29 | 0.13 | 9.1 | 26.90 | 15.03 |
| 13 | Pintura | 1285 | 37°19.26 | 113°16.77 | m | m | x | 0.04 | 0.15 | 18.8 | 184 | 40 | 2.19 | 0.11 | 11.0 | 30.65 | 12.49 |
| 14 | Racetrack | 3113 | 40°18.70 | 111°08.23 | x | x | m | 1.88 | 1.56 | 5.6 | 52 | 77 | 0.56 | 0.43 | 2.6 | 150.14 | 2.17 |
| 15 | Strawberry | 2245 | 40°12.59 | 111°11.21 | x | x | m | 2.99 | 1.37 | 7.7 | 39 | 97 | 0.68 | 0.51 | 0.0 | 150.14 | 2.17 |
| 16 | Tintic High | 2027 | 39°57.58 | 112°05.27 | x | x | x | 1.42 | 1.04 | 12.6 | 79 | 76 | 1.07 | 0.28 | 3.6 | 43.68 | 7.94 |
| 17 | Tintic Low | 1547 | 39°56.89 | 112°00.78 | x | x | x | 0.1 | 0.56 | 20.5 | 150 | 73 | 1.55 | 0.24 | 3.5 | 27.39 | 10.11 |
| 18 | Tintic Wash | 1649 | 39°57.39 | 112°02.73 | x | x | x | 0.78 | 1.51 | 14.1 | 126 | 75 | 1.36 | 0.34 | 3.0 | 27.39 | 10.11 |
| 19 | Wendover | 1640 | 40°28.99 | 114°09.33 | m | m | x | 0.15 | 0.38 | 15.9 | 128 | 57 | 1.6 | 0.09 | 6.5 | 12.24 | 11.25 |
| 20 | Littlefield | 1220 | 37°05.15 | 113°51.29 | x | m | x | 0.6 | 0.3 | m | m | m | m | m | m | 20.37 | 16.69 |
| 21 | La Loop | 1677 | 38°27.16 | 109°23.86 | x | x | x | 0.16 | 0.5 | m | m | m | m | m | m | 21.59 | 13.69 |
| 22 | Needles | 1984 | 38°03.24 | 109°24.57 | x | m | x | 0.17 | 0.82 | m | m | m | m | m | m | 21.56 | 11.75 |
| 23 | Sahara | 1576 | 39°43.15 | 112°13.08 | x | x | x | 0.26 | 1.03 | m | m | m | m | m | m | 28.37 | 10.22 |
| 24 | Stansbury | 1654 | 40°34.44 | 112°29.09 | m | m | x | 0.65 | 1.15 | m | m | m | m | m | m | 31.01 | 10.39 |
| 25 | Dugway Gate | 1350 | 40°10.83 | 113°06.49 | m | m | x | 1.42 | 1.54 | m | m | m | m | m | m | 32.13 | 10.39 |

The average fungal abundance and richness were calculated using two or three fungal samplings when present. Sites in which vegetation and air were sampled for fungi are noted by an "x". Missing data are noted by an "m". All analyses of weather parameters except annual precipitation and temperature were carried out using records for the growing season (March to October, 1999).

Because one time sampling may not adequately estimate fungal abundance and richness in the community, we combined the vegetation values and the two air sample values to give one index of fungal abundance from each site and one index of fungal richness from each site (Table 2). To calculate this index, we standardized the values for the vegetation sample by dividing the value at each site by the mean for all sites. This gives an average index of 1. We repeated this procedure for the two air samplings using their respective means. For each site, the one vegetation and two air samples were averaged to obtain an index of fungal abundance. Fungal richness was calculated the same way. The resultant average fungal abundance positively correlates with the average fungal richness across sites ($r = 0.75$, $P < 0.0001$).

We compared habitat differences for each of the fungal sampling techniques in question independently. For fungi sampled on vegetation, field sites differed in fungal abundance (Kruskal-Wallis nonparametric analysis $\chi^2_{20} = 127.33$; $P < 0.0001$) and richness ($\chi^2_{20} = 114.52$; $P < 0.0001$). For samples from air, field sites differed in fungal abundance ($\chi^2_{16} = 30.87$; $P < 0.01$) and richness ($\chi^2_{16} = 34.29$; $P < 0.005$) in 1998 and in 1999 (fungal abundance $\chi^2_{21} = 129.37.87$; $P < 0.0001$ and richness $\chi^2_{21} = 130.86$; $P < 0.0001$). Fungal measures obtained from vegetation and air sampling in 1998 were not correlated (abundance, $r = 0.17$, $P = 0.49$; richness, $r = 0.10$, $P = 0.69$). Fungal abundance in air was positively correlated between years ($r = 0.81$, $P < 0.0007$), but this relationship was not significant for fungal richness ($r = 0.40$, $P = 0.18$).

### *Weather*

Two years of data (1998 and 1999) were compared for seven sites, and weather patterns were similar between years (data not shown). The weather within the two field sites with duplicate dataloggers had no detectable within-site differences (data not shown). Conversely, the weather across field sites had a broad range of temperatures and moisture regimes (Table 2). With the exception of the seasonal maximum and minimum relative humidity, all weather variables differed considerably among sites. The average temperature for the growing season ranged from 5.6°C to 21.8°C. The average relative humidity ranged from 30% to 72%, and the average diurnal maximum in relative humidity ranged from 40% to 97%. The duration of unfavorable periods, expressed by the average number of consecutive days with maximum diurnal relative humidity less than 50%, ranged from 0 to 11.0 days. While relative humidity is a measure of available moisture in air, the VPD is an absolute measure of the moisture deficit of air. Therefore, temperature has a negative effect on relative humidity and a positive effect on VPD. During the growing season, the average VPD ranged from 2.53 kPa at the hottest site (Gunlock, 21.8°C) to 0.56 kPa at the coolest site (Racetrack, 5.6°C). Sites with a high VPD had a higher variance in VPD than sites with low values of VPD; the standard deviation in VPD explained 45% of the variance in average VPD ($P < 0.002$).

### *Relationships of fungal abundance and richness with weather variables*

Fungal abundance and richness of the field sites were related to many of the weather variables; however, single weather parameters averaged over the season, such as temperature or moisture, generally explained less variance than composite weather variables such as the average number of consecutive days with a maximum diurnal relative humidity less than 50% (Table 1). Temperature was negatively related to fungal richness ($r^2 = 0.26$, $P < 0.05$), but not to fungal abundance. The relationships of the average relative humidity of the growing season with fungal abundance ($r^2 = 0.30$, $P < 0.05$) and richness ($r^2 = 0.35$, $P < 0.01$) were stronger than the relationships with temperature. An even stronger negative relationship was observed with VPD and fungal abundance ($r^2 = 0.30$, $P < 0.05$) and richness ($r^2 = 0.44$, $P < 0.01$; Fig. 2).

A greater proportion of the variance in fungal abundance and richness was explained by the proportion of time conditions were favorable for growth (Table 1). The favorability indices were the proportion of days and the average number of consecutive days with temperature between 4 and 40°C plus a maximum relative humidity greater than 90%. Both measures were positively related to fungal abundance ($r^2 = 0.41$, $P < 0.01$; $r^2 = 0.21$, $P < 0.05$, respectively) and richness ($r^2 = 0.54$, $P < 0.001$; $r^2 = 0.12$, n.s., respectively). Variables based on maximum diurnal relative humidity greater than 90% consistently had stronger relationships than variables based on relative humidity greater than 75% (data not shown).

Measures of unfavorability explained even more of the variation in fungal abundance and richness among sites. Both the proportion of days and the average number of consecutive days with maximum diurnal relative humidity less than 50% were negatively related to fungal abundance ($r^2 = 0.43$, $P < 0.01$; $r^2 = 0.56$, $P < 0.001$, respectively) and richness ($r^2 = 0.70$, $P < 0.001$; $r^2 = 0.72$, $P < 0.001$, respectively). In fact, the average number of consecutive days with a maximum diurnal relative humidity less than 50% was the best climatic predictor of fungal abundance and richness (Table 1; Fig. 3). Most weather variables were highly correlated with each other, so combining variables through stepwise multiple regression explained no more of the variance in fungal abundance and richness than did the average number of consecutive days with relative humidity less than 50%.

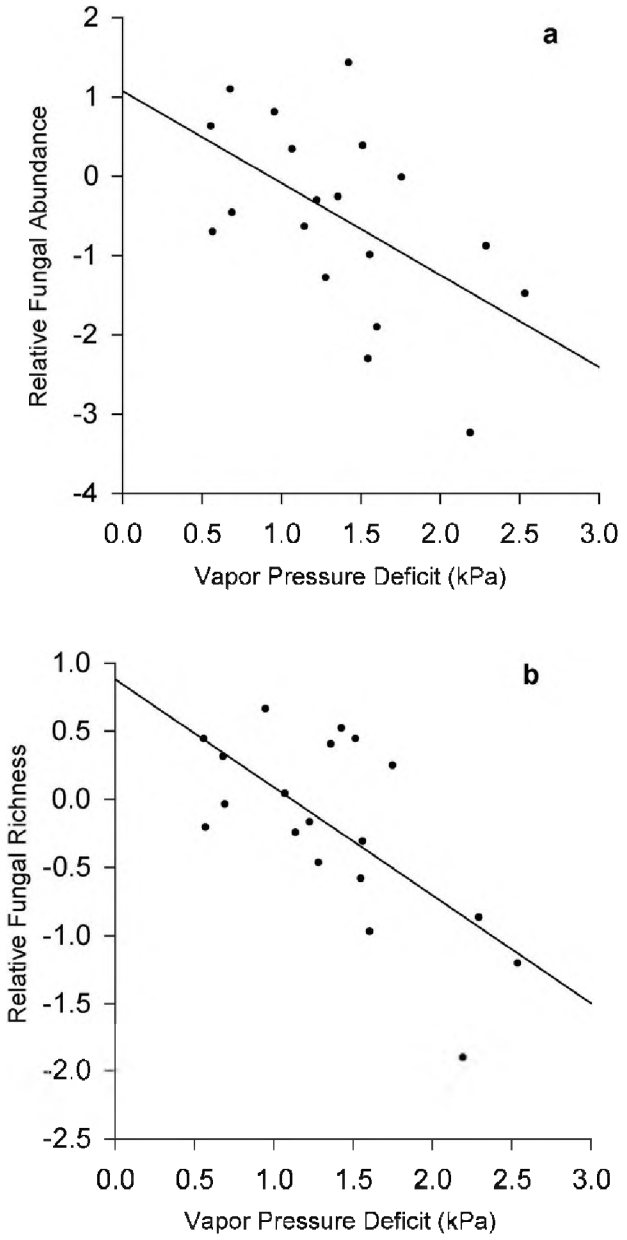


**Figure 2**
**The relationship between fungal abundance and richness and the average vapor pressure deficit (VPD)a** Natural logarithm of fungal abundance = 1.08 - 1.16 × VPD ($r^2$= 0.30, $P < 0.05$). **b** Natural logarithm of fungal richness = 0.88 - 0.79 × VPD ($r^2$= 0.44, $P < 0.01$).

### *Weather stations*

Fungal abundance and richness, when regressed against climate records from nearby weather stations, displayed a positive relationship with precipitation (abundance, $r^2$= 0.21, $P < 0.05$; richness, $r^2$= 0.14, n.s.) and a negative relationship with temperature (abundance, $r^2$= 0.22, $P < 0.05$; richness, $r^2$= 0.37, $P < 0.001$). The trend for fungi to be less abundant and diverse as temperatures increase and moisture decreases is consistent with the results obtained from the direct weather measurements (Table 1).

### *Geographic pattern*

The fungal abundance and richness of the habitats has a geographic and elevational pattern (Table 1). Fungal abundance and richness were positively related to latitude ($r^2$= 0.22, $P < 0.05$; $r^2$= 0.35, $P < 0.01$, respectively) and elevation ($r^2$= 0.09, n.s.; $r^2$= 0.18, $P < 0.05$, respectively). A negative relationship was found between fungal richness and longitude ($r^2$= 0.17, $P < 0.05$), but this relationship was not significant for fungal abundance ($r^2$= 0.03, n.s).

### *Site-specific factors*

There was a positive relationship between the presence of streams or lakes at a site and fungal abundance ($r^2$= 0.26, $P < 0.01$) and richness ($r^2$= 0.16, $P < 0.05$). However, the presence of water at a site was not related to the average temperature ($r^2$= 0.15, $P < 0.10$) or the relative humidity ($r^2$= 0.15, $P < 0.10$) of the site. The associated vegetation indicative of moisture also explained a significant portion of the variance in fungal abundance ($r^2$= 0.49, $P < 0.001$) and richness ($r^2$= 0.40, $P < 0.001$).

### *Soil*

We found no significant correlation between soil properties and fungal abundance and richness (% organic carbon in soil, % nitrogen in soil, pH of soil, % sand in soil, % silt in soil, or % clay in soil). However, we noted trends for fungal abundance and richness to be positively related to soil organic carbon, nitrogen, clay, and silt and negatively related to soil pH and sand.

## Discussion

### *Abiotic predictors of fungal prevalence*

Fungal abundance and richness were clearly affected by weather, showing large differences among habitats. Weather parameters differed considerably in the amount of variance they explained in the fungal abundance and richness of the habitat. As demonstrated by previous studies, both temperature and moisture were important in explaining the fungal abundance and richness of the habitats. All three of the humidity variables averaged over the growing season (VPD, relative humidity, and the average maximum diurnal relative humidity) were highly positively related to both measures of fungal prevalence (Table 1). These data are consistent with studies of crop plants that suggest dew duration, relative humidity and temperature are critical parameters for predicting the extent of disease [22–27]. Of the three humidity measures in our study, the average maximum diurnal relative humidity was the best predictor, explaining 43% and 65% of the variance in fungal abundance and richness, respectively. Because most mesophilic fungi fail to grow at less than

**Table 2: The relationship of fungal abundance and richness to weather.**

| Direct climate measurements | Fungal abundance | Fungal richness |
|---|---|---|
| average temperature | (-) 0.18 | (-) 0.26[a] |
| standard deviation of temperature | (+) 0.01 | (+) 0.02 |
| average relative humidity (RH) | (+) 0.30[a] | (+) 0.35[b] |
| standard deviation of RH | (+) 0.27[a] | (+) 0.33[b] |
| average daily maximum RH | (+) 0.43[b] | (+) 0.65[c] |
| average vapor pressure deficit (VPD) | (-) 0.30[a] | (-) 0.44[b] |
| standard deviation of VPD | (-) 0.15 | (-) 0.16 |
| # of consecutive days above freezing | (-) 0.38[b] | (-) 0.45[b] |
| proportion of time with RH > 94% | (+) 0.37[b] | (+) 0.36[b] |
| proportion of days with max RH >90% | (+) 0.41[b] | (+) 0.54[c] |
| average # of consecutive days with max RH >90% | (+) 0.21[a] | (+) 0.12 |
| proportion of days with max RH <50% | (-) 0.43[a] | (-) 0.70[c] |
| average # of consecutive days with max RH < 50% | (-) 0.56[c] | (-) 0.72[c] |
| Climate parameters from weather stations | | |
| annual precipitation | (+) 0.21[a] | (+) 0.14 |
| annual temperature | (-) 0.22[a] | (-) 0.37[c] |
| Site-specific parameters | | |
| elevation | (+) 0.09 | (+) 0.18[a] |
| latitude | (+) 0.22[a] | (+) 0.35[b] |
| longitude | (-) 0.03 | (-) 0.17[a] |
| presence of water at site | (+) 0.26[b] | (+) 0.16[a] |
| associated vegetation indicative of moisture | (+) 0.49[c] | (+) 0.4[c] |

a: $P < 0.05$, b: $P < 0.01$, c: $P < 0.001$. The relationship of fungal abundance and richness to parameters derived from direct climate measurements (calculated from the relative humidity and temperature of the habitat), annual climate records from nearby weather stations, and site-specific factors. Values are coefficients of determination ($r^2$) with the sign of the slope in parentheses. Direct weather parameters were analyzed using records for the growing season, March to October, 1999.

96% humidity [12], it is not surprising that the maximum relative humidity was a better predictor of fungal prevalence than the average.

Because extreme temperatures below freezing and above 40°C likely impede the growth of most mesophilic fungi regardless of moisture conditions [12,15], one might predict that the length of the growing season would be positively correlated with fungal abundance. However, in our study, we found that fungal abundance and richness decreased as the number of consecutive days without freezing increased. Furthermore, there was a weak negative relationship between fungal abundance and richness and average temperature. These negative relationships may result from the fact that our field sites with a longer growing season are hotter and drier than sites with a shorter growing season.

Although direct weather measurements almost always explained more of the variance (Table 1), data on temperature and precipitation obtained from weather stations were significantly related to fungal abundance and richness and had similar trends as data obtained in the habitat. Hence, in the absence of direct weather measures, weather station data may be of value in predicting fungal abundance and diversity [25].

***Proportion and duration of favorable or unfavorable days***

All weather variables expressing the proportion of time with favorable conditions in a habitat (high relative humidity with moderate temperatures) had a positive relationship with fungal abundance and richness (Table 1). Although previous work has emphasized using favorable conditions to explain fungal distribution [3,10] in our study, the parameter that explained the greatest amount of

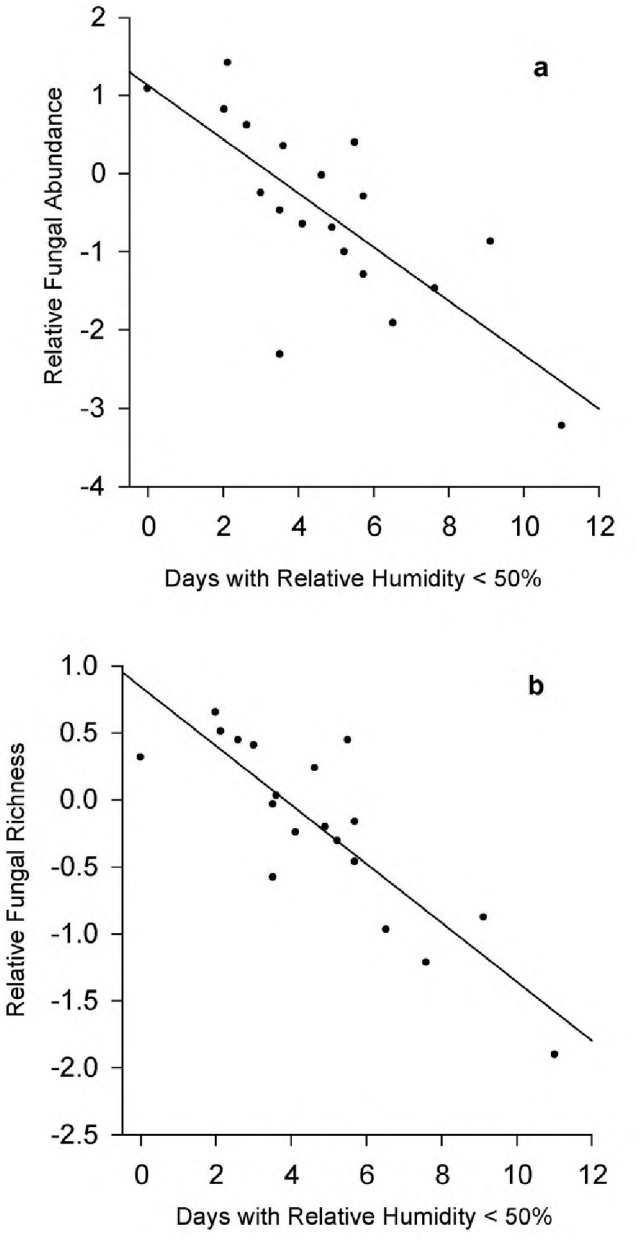


**Figure 3**
**The relationship of fungal abundance and richness to duration of unfavorable weather** The relationship between fungal abundance and richness and an estimate of the duration of unfavorable periods for fungal growth, the average number of consecutive days with maximum diurnal relative humidity less than 50% (arh50). **a** Natural logarithm of fungal abundance = 1.18 - 0.34 × arh50 ($r^2$= 0.56, $P$ < 0.001). **b** Natural logarithm of fungal richness = 0.86 - 0.22 × arh50 ($r^2$= 0.72, $P$ < 0.001).

variance was an index of unfavorable conditions, the average number of consecutive days with maximum relative humidity less than 50% (Fig. 3). It is not entirely clear why unfavorability was such a strong predictor, as most spores are probably capable of surviving these conditions although fungi might not be able to sporulate, germinate or grow [1,12].

### *Habitat and Geographic patterns*

The abundance and richness of fungi were related to the presence of water in a habitat and to vegetation indicative of moisture (Table 1). Drier habitats generally have less vegetation than do moister, cooler habitats, and plant biomass has been shown to accurately predict the microbial biomass of the soil [28]. These observations indicate that the plant community may be a good predictor of fungal abundance and richness.

The geographic trend in Utah of fewer fungi with decreasing latitude and increasing longitude may be explained by more arid weather towards the south and west than towards the north and east (Table 1). Western and Eastern Utah are divided by two biogeographic provinces that differ in precipitation patterns [29]. Western Utah is part of the Great Basin, which receives the majority of precipitation during the winter months when most fungi may be dormant. Conversely, Eastern Utah is part of the Colorado plateau and receives a substantial amount of precipitation during the growing season.

## Conclusions

Our data indicate that microclimate strongly influences the abundance and diversity of fungi in the Intermountain West. Even though both measures of fungal prevalence were strongly correlated across habitats, we propose that fungal richness is a better indicator of habitats favorable to most fungi than is fungal abundance. In other words, a high fungal richness may be a superior indicator that conditions of the habitat are broadly favorable to fungi. Because a few species may produce abundant spores during periodic conditions of high moisture and moderate temperatures, sporadic sporulation events may affect fungal abundance measurements and overestimate the habitat favorability to most fungi.

A surprisingly large proportion of the variation among sites in fungal richness was explained by the proportion of days with favorable conditions of temperature and high humidity ($r^2$= 0.54). The number of days with unfavorable periods was an even better predictor ($r^2$= 0.72). Because fungal pathogens appear to have similar abiotic requirements for growth as most fungi [1,13,15,16], it is likely that fungal pathogens would show correlations with climate that parallel those reported in this study. This suggests that moister habitats will have a greater inoculum

potential from pathogenic fungi than drier habitats. An elevated inoculum by pathogens could be largely responsible for the increased incidence of fungal disease documented in moister habitats. We would also predict that a high prevalence of pathogens would select for greater levels of anti-fungal defense by plant species adapted to moist habitats. Thus, weather factors identified in this study as being important predictors of fungal abundance and diversity in general, may also shed light on the distribution of fungal pathogens and the extent of selection on plant defenses.

## Materials and Methods

### *Study sites*

The Intermountain West is topographically and climatically diverse and provides many different habitats to study the relationship between weather and fungal abundance and species richness. We selected 25 field sites (approximately 1 hectare in area) in and near Utah that differ in factors that influence weather such as elevation, longitude and latitude, proximity to permanent water sources, and topography. To eliminate comparing habitat extremes, all 25 field sites share a widely distributed species of shrub, sagebrush, *Artemisia tridentata* (Asteraceae). Community types include arid grasslands with cacti, riparian communities characterized by cottonwoods, and subalpine areas with tall forbs and aspen stands.

The Intermountain West consists of two biogeographic provinces, the Great Basin and the Colorado Plateau, that differ in precipitation patterns and drainage [30]. While both the Great Basin and the Colorado Plateau share weathers with cool wet winters and relatively dry summers, they differ in that the Colorado Plateau has wetter summers and drier winters than the Great Basin [29]. There is also a trend for sites to have lower total annual rainfall towards the south and west.

### *Fungal culturing*

Fungi were collected in the air and on the vegetation (see below) and were grown on plates containing growth medium. This method quantifies a portion of the viable propagules that are able to germinate and form visible colonies in the time frame observed unlike visual counts of spores using a microscope. Four types of media containing 2% granulated agar (Difco, Detroit, MI) were used to grow fungi: (1) potato dextrose agar [31], (2) potato sucrose agar (similar to potato dextrose agar except sucrose is used instead of dextrose; [31], (3) casein agar (for 1 L, 5 g casein, 0.5 g NaCl, 20 g sucrose, and 20 g agar), and (4) sagebrush-leaf agar. To prepare the sagebrush-leaf agar, we removed surface secondary metabolites on 80 g of fresh *A. tridentata* leaves by washing them in 400 ml of chloroform for three minutes and washing again in 200 ml of chloroform for 1 minute. Leaves were placed under a hood for one day to remove chloroform and then dried at 70°C to constant weight (1 to 2 days). We homogenized dried leaves in 900 ml of water and then filtered the leaf extract (Whatman #1). We combined 500 ml of leaf extract, 250 ml of $H_2O$, 20 g of agar, and 250 ml of Czapek's minerals [31]; 1 L of Czapek's aqueous solution, contained 2 g $NaNO_3$, 1 g $KH_2PO_4$, 0.5 g $MgSO_4 \cdot 7H_2O$, 0.5 g KCl, 0.01 g $FeSO_4$, and 1 ml of an aqueous solution of 1% $ZnSO_4$ and 0.5% $CuSO_4$). All four media contained ampicillin (60 μg/ ml) to eliminate contamination by bacteria. We used potato-based media because they are commonly used to grow fungal pathogens. We used the leaves of *A. tridentata* in a medium (sagebrush-leaf agar) because this species is common to all habitats.

### *Vegetation sampling*

During September of 1998, we measured fungal abundance and richness in each habitat by culturing fungi found on the vegetation in 21 communities. Because some plants contain secondary metabolites on the leaf surface that inhibit fungal growth, we cultured fungi collected only from leaf surfaces of the species that were not aromatic when their leaf surfaces were rubbed. Using sterilized scissors, we collected one $cm^2$ of leaf material from each of seven haphazardly chosen plants (from three to five species) and combined all seven in a single sterile vial. This was repeated using the same plants. Leaf samples were collected in the late afternoon and stored at 4°C for up to 7 days before culturing. The relationship of diversity and abundance of culturable fungi with storage time was not determined. To remove fungi from leaf surfaces, we soaked and vortexed leaf samples for 15 seconds in 7 ml of a sterile aqueous solution containing a 0.5% sodium chloride, 2.0% casein, and 4.0% sucrose. We spread 250 μl of the inoculated solution onto one 10-cm Petri plates each of potato sucrose agar, casein agar, and sagebrush-leaf agar. Since we collected two vegetation samples per site, there were two plates of each of the three media, or six plates per site.

We incubated the inoculated plates at room temperature (22°C) for 4 days before counting the number of colonies per plate as a measure of fungal abundance. We found little change in the number of colonies after 4 days, presumably due to the proliferation of the aggressively growing fungi. We classified the colonies under a dissecting microscope (10 to 50×) into morphotypes based upon colony morphology (effuse, raised, domed or umbonate), color, transparency, and shape (irregular, crenated, or rhiziod). We scored fungal richness as the total number of morphotypes per plate. We averaged fungal measures from two vegetation samples for each of the three media. We did not attempt to identify species or to compare morphotypes across plates. Although the different media probably favor different fungal species, our goal was not to measure

habitat differences of specific fungi, but to estimate the overall fungal abundance and species richness of the habitats. Furthermore, the fungal measures likely represent the abundance and richness of mesophiles, because the temperature (22°C) used to incubate inoculi falls within the temperature optima of mesophilic fungi.

### *Air sampling*

During September of 1998, we collected air-borne fungi at 17 sites by vertically swiping three agar plates (one each of potato sucrose agar, casein agar, and sagebrush-leaf agar) ten times in the air. During October of 1999, we collected air-borne fungi at 22 sites by swiping 10 potato dextrose agar plates vertically 10 times in the air. At each site the replicate plates were collected at 10 haphazardly chosen locations to obtain an average measure of fungal abundance and richness of the habitat. Samples were collected in the late afternoon. We incubated inoculated plates in a cooler at ambient temperature (approximately 22°C) for 4 days and examined plates in the field. Fungal abundance and richness were scored as above.

### *Direct weather measurements*

We recorded the average temperature and relative humidity every 30 minutes at 19 of the 25 study sites with NOMAD dataloggers (OM-NOMAD-RH-32, Omega Engineering, Inc; Stamford, CT) protected in a weatherproof casing. For all sites, we recorded the weather for a complete growing season, mid-March of 1999 to mid-October of 1999. To compare annual differences in weather, we also recorded weather from June of 1998 to mid-October of 1998 at seven sites. To investigate differences within a habitat, two sites were equipped with two dataloggers each. Using these data, we calculated weather variables that are commonly reported in the literature (see below).

### *Temperature*

We calculated the following temperature parameters in °C for the entire growing season: average, standard deviation (of the 30-minute readings), range, maximum, and minimum. We also calculated a "length of growing season" parameter equal to the maximum number of consecutive days without freezing temperatures.

### *Relative humidity*

The growth and survival of a fungal spore germinating on a leaf depends on the amount of moisture available in the air and the length of time the leaf surface is wet [13]. Dew formation can be critical for spore germination of many plant pathogens, and may be the best indicator of the proportion of time a habitat has weather favorable to fungi. Although the duration of leaf wetness is frequently measured in agricultural studies [1], it is not practical for many ecological studies. However, relative humidity of the air is a good measure of moisture availability [13]. The relative humidity ($RH$) where $RH = (e_a/e_s) \times 100\%$ (the units of $e_s$ and $e_a$ are kPa) is the ratio of water vapor pressure in the air, $e_a$, to the maximum amount of water vapor that air can retain at a given temperature, the saturation vapor pressure, ($e_s$) where $e_s = 0.61365e^{17.502T/(240.97+T)}$ (the units of $e_s$ are in kPa and $T$ is the Celsius temperature; Buck 1981). Using the relative humidity records from the dataloggers, we calculated the following relative humidity parameters for the entire growing season: average and the standard deviation (of the 30-minute readings), average of daily maximums, and the seasonal range, maximum, and minimum.

### *Vapor pressure deficit*

The vapor pressure deficit (VPD) where $VPD = e_s - e_a = e_s - (e_s \times RH/100)$ (the units of $e_s$ and $e_a$ are in kPa) is the maximum amount of water vapor that can be retained in air at a given temperature minus the actual water vapor pressure in air [32]. This measure reflects the desiccating capacity of the air. Using the 30-minute readings of relative humidity and temperature from the dataloggers, we calculated the average VPD and the standard deviation for the entire growing season.

### *Proportion of time a habitat has weather favorable or unfavorable to fungi*

We calculated weather variables that reflected the proportion of time a habitat is favorable or unfavorable for fungal growth. We calculated the proportion of time (based on the 30-minute averages over the growing season) that the temperature was between 4 and 40°C [15] and also had a relative humidity greater than 94%. Three other indices were calculated as follows: the proportion of days when the temperature remained above 4°C and below 40°C as well as having a maximum relative humidity that was (i) greater than 90%, (ii) greater than 75%, or (iii) less than 50%. A broad temperature range (4 to 40°C) was used to represent the range of temperatures likely to support most mesophilic fungi [2,12,15,18]. Because the growth of mesophilic fungi can occur between 0 and 50°C with optima from 15 to 40°C, a temperature of 4°C may represent a conservative minimum at which mesophilic fungi grow and a temperature of 40°C may represent a conservative maximum at which mesophilic fungi grow.

### *Duration of periods with a favorable or unfavorable weather*

We calculated weather variables that reflected the duration of consecutive favorable or unfavorable days in a habitat. We estimated the average number of consecutive days during the growing season when the daily temperature remained between 4 and 40°C as well as having a maximum diurnal relative humidity that was (i) greater than 90%, (ii) greater than 75%, or (iii) less than 50%.

The maximum number of consecutive days also was calculated for the same three parameters.

### *Climate estimated by nearest weather station*

We estimated the climate of each site using the monthly average precipitation and temperature collected by weather stations located 4 to 30 km from the study sites. For three of the high elevation sites (Francis, Racetrack, and Strawberry in Northern Utah), we used records from Alta, Utah, a site with similar altitude and location (within 100 km of the three sites). Climate data were obtained from the Western Regional Weather Center and elsewhere [33]. Climate records covered 21 to 58 years, depending on the site.

### *Site-specific factors*

We scored two other site-specific factors, the presence of nearby water sources and vegetation types indicative of moisture [34–36]. For the presence of nearby water sources, we gave a score of zero for none, 0.5 for ephemeral water sources such as washes, and a score of 1.0 for habitats with permanent water sources such as streams and lakes. We listed the five most common plant species at each site (determined visually) and scored sites for vegetation types indicative of moisture. Plant species characteristic of dry habitats such as cacti and yucca were given a zero. Each plant species indicative of intermediate levels of moisture, such as juniper, pinyon pine, scrub oak, and rabbit brush were given a score of 0.5. We gave a score of 1.0 for each plant species characteristic of mesic habitats such as riparian vegetation, tall forbs, aspen, and spruce. Therefore, the highest vegetation score a site could have is 5.0.

### *Soil*

We also measured soil properties that might be indicators of habitat moisture. To control for variation in soil nutrients due to seasonal fluctuations, we collected soil from 22 sites within a month during the spring of 1999. Because overtopping vegetation can affect the nutrients in the soil below, we collected samples away from overtopping vegetation [37]. We discarded the top 5 cm of soil and collected 2 to 3 kg of soil up to a depth of 20 cm. We dried soil samples for 48 hours or until constant weight at 105°C. For particle size analyses, we removed rocks before sieving [38]. We determined the percent silt and clay using a hydrometer. We determined soil pH using 15 g of ground soil in 30 ml of distilled water. To determine percent organic carbon and nitrogen of soil by mass spectroscopy, we first removed the inorganic carbon by bringing soil samples to a pH between 4 and 5 with 5N hydrochloric acid. Soil samples were then flash combusted on an elemental analyzer (Carlo Erba, Milan, Italy) coupled to an isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) operated in continuous flow mode.

### *Data analysis*

We performed univariate and multivariate statistical analyses in SYSTAT, Version 7 [39] and JMP (SAS Institute Inc., Cary, NC). For differences in fungal abundance and richness among media types and sites, we applied Kruskal-Wallis nonparametric analysis. Using simple linear regression, we analyzed the natural log of fungal abundance and richness as a function of the previously mentioned weather variables. For periods when the dataloggers malfunctioned and did not record temperature and humidity, we estimated missing values in SYSTAT by their correlation with data from other seasons at the same sites. For example, spring data were missing from the Canyonlands field site, so we used summer and fall correlations of relative humidity and temperature across all sites to estimate the missing value for Canyonlands. There were three sites with missing values for spring, three for summer, and none for fall. To determine whether two weather variables could explain more than a single variable, we applied stepwise multiple regression analysis.

## Acknowledgements

We thank Drs. Gregg Gilbert, Donald Feener and Dale Clayton for advice, Dr. Steve Krueger for mapping field sites, Jonathan Monsor for field work, Mara Haslam and Sandar Lazar for laboratory work, and Jeffrey Farnsworth and Marie Hickman for soil analyses, and the Stable Isotope Ratio Facility for Environmental Research at the University of Utah for analyzing the carbon and nitrogen content of the soil. This study was supported by NIH, Grant # 5 T32 GM07464, Training Program in Genetics, the University of Utah, and the Gold Scholarship (Department of Biology, University of Utah) to SMT and NSF grant DEB 9419543 to TAK and PDC.

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