

The relationship between abiotic factors and species-level self-similarity of
sagebrush, *Artemisia tridentata*

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Abstract

Two of the predominant interests in ecology are patterns in the distributions and abundances of organisms and the interrelationships of organisms with their environment. Many naturally occurring phenomena take on self-similar distributions, appearing the same over different spatial scales. I tested to see if sagebrush, *Artemisia tridentata*, was self-similarly distributed and whether three abiotic factors - slope, aspect and soil moisture, are themselves self-similarly distributed and correlated with the presence or absence of the sagebrush at three sites in the East River Valley, Gunnison County, Colorado. At one of the site there was a significant difference in soil moistures between sites with sagebrush present and those without, and at another site aspect appeared to have a significant impact on the presence of sagebrush. The power law exponent, y' , related to the fractal box counting dimension, of the abiotic factors were the same as the y' values for the distribution of sagebrush at each site. Semivariogram analysis also indicated a self similar distribution of many of the abiotic factors. It is unclear why the y' values of the abiotic factors would be related so closely to those of the sagebrush.

Introduction

The field of ecology encompasses a great deal of theory and can be quite broad in its scope. Reduced down to a simple definition ecology is “the study of the natural environment, particularly the interrelationships between organisms and their environments” (Ricklefs 1973) or “the study of the relationships between organisms and

their environments.” (McNaughton and Wolf 1973). These interactions and relationships can be very complex, and they are the source of intense study. Species and individuals interact not only among themselves but with the abiotic environment as well.

Competition can be fierce for the limited resources required to sustain life such as light, water and chemical nutrients. The biotic components – plants and animals, as well as others – influence these abiotic components, but they are strongly influenced by them at the same time.

In addition to the interrelationships of biotic and abiotic, much of the research in ecology is focused on the appearance of patterns over space and time. In many cases the natural world, abiotic and biotic, is anything but random, nor is it uniformly distributed (Legendre and Fortin 1989). Patterns can be very subtle and hard to detect or as obvious as day and night. The search for patterns can lead to a more mechanistic understanding of the natural world (Harte pers. comm). These patterns can be expressed mathematically in simple or complex equations. Some of these can take on power-law functions. The first ecological pattern that was described with a power-law function was Arrhenius’ (1921) species-area relationship (SAR):

$$S \propto A^z.$$

The SAR applies to communities of species and it has been shown that the SAR can be derived from an assumption of self-similarity (Harte and Kinzig 1997, Harte et al 1999). A thing is self-similar if it does not vary over spatial scales. Self-similarity is strongly linked to fractal mathematics. Many natural phenomena have been shown to exhibit self-similarity such as landscapes, coastlines, clouds, and the distributions of species. Self-similarity does not have to exist over all spatial scales. Many data show self-similarity

over a limited range of scales (Burrough 1981). Individuals of a species of British plants have been shown to be distributed in a self-similar fashion by Kunin (1998) who characterized what is known as the range-area relationship (RAR) that is the species level equivalent to the SAR:

$$R \propto (A/A_0)^{y'}.$$

Where A is the size of the census window, A₀ is the entire area and R is the range as described below in the statistical methods section. Other studies have been performed that also indicate a self-similar distribution of individuals of certain species of plants (Green et al 2001, Harte et al 2001).

What underlying factors could be influencing the self-similar distributions of individuals? Is it purely biological, relating to how seeds are propagated, for example? Or is it due to some distribution of abiotic factors such as nutrients, slope, aspect, water availability etc? Many environmental variables have been shown to vary over very small spatial scales. The range of variation of soil measurements within one square meter can be more than half the total range of variation of a whole farm field (Beckett and Webster 1971). Most of the variation of phosphorus levels has been shown to exist within five meters (Webster and Butler 1976). However others have found that there is no clear maximum to the amount of variation over larger spatial scales (Bell et al 1993). Abiotic factors can influence each other as well. For example, soils may be dryer where the slope is greater since water will tend to run over or through a steeper gradient faster.

Intuitively it would be expected that there would be a correlation between environmental factors; as one gets farther and farther away from the value of a parameter at a particular location one would expect to see increasing variance. This spatial correlation can be

measured using semivariograms, originally developed for geologic and mining purposes (Rossi 1992) but subsequently demonstrated to have increasing applicability to biological and ecological studies.

This project is an attempt to describe the variation in three abiotic factors and try to relate their spatial distributions to the distributions of a single species, *A. tridentata*, the sagebrush that is so abundant throughout much of the western United States and possibly set to become more so under global climate change models are accurate (Harte and Shaw 1995).

Study Sites

This research was performed at the Rocky Mountain Biological Laboratory, located in Gothic, Colorado (38° 53' N, 107° 02' W). Three field sites were used for this project: the lower, middle and upper site. The upper site is located at 3150 m above sea level and is southeast of the RMBL, on the slopes of Red Rock Mountain. It is in an extremely rocky area with aspen surrounding the site and generally faces southwest. The middle elevational site is located above the townsite of Gothic, near the trailhead for the Copper Creek trails at 2970 m above sea level. It lacks the large rocks characteristic of the upper site but has very rocky soil. Like the upper site, the average aspect is toward the southwest. The sagebrush at the middle site tend to be the smallest of the three sites. The lower site is located off of Brush Creek Road on the south side of Crested Butte at 2770 m above sea level. It is in a very grassy meadow, and the soil is much less rocky than either of the other two sites. This site is much closer to typical range of sagebrush,

and the individuals tend to be much larger than at either of the other two sites. The average aspect of the site is toward the east. The sites were chosen because they offer three different elevations and types of terrain and soil, as well as varying densities of sagebrush.. The upper site had 84 sagebrush, the middle, 29, and the lower site had 35.

Methods

Field and Laboratory Methods

Grids 16 m x 16 m were layed out at each site and marked in 1 m increments, and the resulting 256 grid cells were marked using colored flags. Each sagebrush within the grid was marked with a flag, arbitrarily placed on the downslope side of the sagebrush stem. Each sagebrush was measured along the the longest axis of its foliage and along the widest axis perpendicular to the long axis to give a rough estimate of the size of each plant.

Soil samples from the center of each of the 256 cells at each of the three sites were collected. If the rockiness of the soil or the presence of a plant inhibited the collection of a soil sample at the center then the nearest location within the cell that was conducive to the collection of a soil sample was used. The soil cores were 10 cm deep and the soil was immediately put into plastic bags and tied shut to seal the moisture inside. A wet weight was obtained immediately upon return to the laboratory. Soil samples were filtered using a standard 2 mm sieve to remove rocks and large organic materials, weighed and then dried in a drying oven at 100°C for 24 hours. The weight of

the rocks and large organic debris was subtracted from the original wet weight to determine the wet weight of the soil only. Soil moisture was then determined using the standard equation, $(\text{wet weight} - \text{dry weight})/(\text{dry weight})$.

Slope and aspect were measured in degrees using a compass and clinometer. As with the soil cores, measurements were taken as near the center of each grid cell as possible. To prevent very small rocks and microscale variations in soil surface from affecting measurements the slope was measured by placing the clinometer on a 9"x12" clipboard to even out the surface. The steepest slope was recorded and then the aspect of the steepest slope.

Statistical Methods

The RAR that was obtained from the distribution of sagebrush at each of the three sites is easily plotted. The natural logarithm of the range, R , is plotted against the natural log of the area of the census window, A_w . R comes from the equation:

$$R = A_w * W$$

where W is the number of census windows occupied. A linear relationship is indicative of fractal or self-similar behavior and the slope of the line, y' , is the fractal dimension of the distribution of individual species.

The RAR curves for abiotic data are different since they can not be based simply on presence or absence like the species-RAR curve. Instead, the general trend, whether it

was significant or not, of what the sagebrush preferred at each site and the number of grid cells occupied by the sagebrush was used. For example at the upper site sagebrush tended to favor steeper slopes, more easterly aspects and dryer conditions. Seventy-six grid cells had sagebrush. Therefore the 76 steepest slopes, 76 smallest aspects, and 76 dryest soils were marked on a 16x16 grid and counted in the identical presence or absence manner of the sagebrush.

From all the abiotic data a t-test was performed to see if there was any significant difference between abiotic components of cells that had sagebrush present and those that did not.

The semivariograms were computed using the abiotic data and the standard equation:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2$$

where N is the number of values obtained from each particular distance, or lag, h. The natural log of the semivariance was then plotted against the natural log of each lag, h.

Results

The range-area curves obtained for the three sites from the sagebrush locations can be seen in Figure 1. All three sites show a very strong linearity over the smallest four census window sizes, 1 m², 2 m², 4 m², and 8 m². The figure does not show the remaining census window sizes because they all begin to level out and approach the same

asymptote as the census windows become larger and every window shows the presence of sagebrush. The best fit lines for the RAR curves over four A_w size classes as shown in Figure 1 are as follows: for the upper site, $y = .5055x + 4.353$, $r^2 = .9851$; for the middle site $y = .8085x + 3.262$, $r^2 = 1$; for the lower site, $y = .7553x + 3.5667$, $r^2 = .9811$.

The abiotic RAR curves for the same four scales can be seen in Figure 2. These, like those of just the sagebrush, are very linear, indicating a self-similar distribution pattern over these four scales. They, too, begin to reach the same asymptote as the census windows become saturated with the presence of sagebrush. It is interesting to note that the slopes for each abiotic component are very similar within a site, and they are equal to those of the slopes of the RAR curves of the sagebrush within the same site. This relationship is represented graphically in Figure 3 and the equations for the least squares regression lines are summarized in Table 1.

The semivariograms showed several interesting relationships. Five of the nine showed strong relationships, especially over the smaller scales, indicating that the variation does indeed increase as the distance between sampling locations increases. These five can be seen in Figures 4 through 8. The relationships were all strongest below about eight meters. Beyond that point the scatter increases indicating that the relationship between two points has been reduced or eliminated. The other four semivariograms showed no relationship between variance and distance, exhibiting very small slopes and low r^2 values. Figure 9 shows a semivariogram over the entire range of scales. It demonstrates first, a slope of zero over smaller scales and second, the increased scatter that occurs at larger scales. A summary of the slopes of the best fit regression lines and r^2 values can be seen in Table 1.

The t-tests showed few significant differences between cells with sagebrush and cells without. The only significant differences occurred with the moisture at the middle site ($p < 0.02$) and aspect at the upper site ($p < 0.01$). While not significant statistically, at all three sites the sagebrush tended to favor steeper slopes and lesser aspects (those tending toward south and east). At two of the sites, the middle and lower, sagebrush were more commonly found on cells with higher soil moisture contents. A summary of t-test results can be seen in Table 2.

Discussion

Sagebrush do appear to exhibit a self-similar distribution over smaller spatial scales. This is consistent with other data from individual species of plants. The sagebrush could be self-similarly distributed over larger scales as well but a much larger sampling grid would be needed to test this. Y' values at the three sites varied from about .5 to about .8. The abiotic factors also appeared to exhibit self-similar distributions, both from the RAR curves as well as in the semivariograms, over the smaller range of scales. Like with the sagebrush they may be self-similarly distributed over larger scales, but the grid size did not allow this to be seen. It is especially interesting that the y' values for the abiotic RAR curves appear to be the same as for the sagebrush RAR curves, and yet no strong and robust relationship between sagebrush and the abiotic factors was seen. It isn't clear why there would be such a strong relationship between the biotic and abiotic y' values. This is especially puzzling given the general lack of connection between the abiotic factors and the presence or absence of sagebrush.

From the data it appears that not one of the three abiotic factors tested stands out as a strong determinant of the location of sagebrush. Even taken together using multiple regression analyses they do not strongly relate to the locations of sagebrush individuals. While it is true that there were significant differences in soil moisture levels between cells with sagebrush and those without at the middle site and differences in aspect at the upper site, it is unclear why those would be significant and others would not. Soil moisture levels tended to be higher in cells with sagebrush present. This could lead one to believe that sagebrush prefer wetter soils or it could be that the sagebrush alter the habitat and lead to more moisture in the soil since their litter could hold more water than soil that is not laden with as much organic litter. Rosenzweig (1995) suggested a similar idea, that biotic components will influence the abiotic, leading to more habitat and abiotic diversity.

A much more thorough sampling of abiotic factors could lead to a better picture of how the abiotic influences the biotic world and vice versa. Given time and resources I was unable to perform all the tests that would have been done under ideal circumstances. It could be especially enlightening to look at the distributions of soil carbon, nitrogen and phosphorus to see what kind of distribution they have and how their spatial arrangement relates to that of the sagebrush. Another factor to consider is that of the date of snowmelt. It has been shown that sagebrush does very well in areas of earlier snowmelt (Harte and Shaw 1995, Perfors and Harte 2001). Perhaps the sagebrush are favoring locations that have earlier snowmelts, and perhaps these regions of snowmelt exhibit a self-similar distribution like the other abiotic factors. This would have to be looked at in the spring over the course of the next several years.

It is unclear what the theoretical relationship is between y' and the slopes of the semivariograms. This is an unexplored question. It may be that there is no relationship but since they are both related to fractals and self-similarity one would expect that some relation could be found. This is another area worthy of further investigation.

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Table 1. Summary of RAR abiotic data, comparison of y' values within sites and semivariogram (SV) slopes through 8 m with r² values.

	y'	Regression equation	r ²	SV slope	SV r ²
Upper moisture	.4927	Z = .4927x + 4.3751	.9871	.325	.945
Upper aspect	.4689	Z = .4689x + 4.3777	.9861	.268	.916
Upper slope	.5293	Z = .5293x + 4.4254	.9748	.007	.006
Upper mean y'	.4969				
y' for sagebrush	.5055				
Middle moisture	.7931	Z = .7931x + 3.3103	.9993	.134	.496
Middle aspect	.7285	Z = .7285x + 3.3571	.9983	.167	.824
Middle slope	.8797	Z = .8797x + 3.3192	.9988	0	0
Middle mean y'	.8004				
y' for sagebrush	.8085				
Lower moisture	.8167	Z = .8167x + 3.5215	.9983	.007	.012
Lower aspect	.734	Z = .734x + 3.5738	.9927	.14	.85
Lower slope	.7162	Z = .7162x + 3.5383	.991	.034	.115
Lower mean y'	.7556				
y' for sagebrush	.7553				

Table 2. Summary of t-test results for 3 sites and 3 abiotic factors. Values shown represent p-values. The aspect at the upper site and the moisture at the middle site were significantly different between cells with sagebrush and those without (p<0.05).

	Upper	Middle	Lower
Slope	.185	.072	.566
Aspect	.003	.587	.120
Moisture	.126	.017	.123

Table 3. Summary of data from all three sites (mean +/- standard error).

	Upper	Middle	Lower
Slope (in degrees)	19.5 +/- .348	15.1 +/- .313	15.7 +/- .313
Aspect (in degrees)	217.0 +/- 1.14	214.9 +/- 1.40	88.3 +/- .963
Moisture	.232 +/- .00522	.0618 +/- .00096	.136 +/- .00296

Figure 1. Range-area relationship for sagebrush over smallest four A_w size classes.

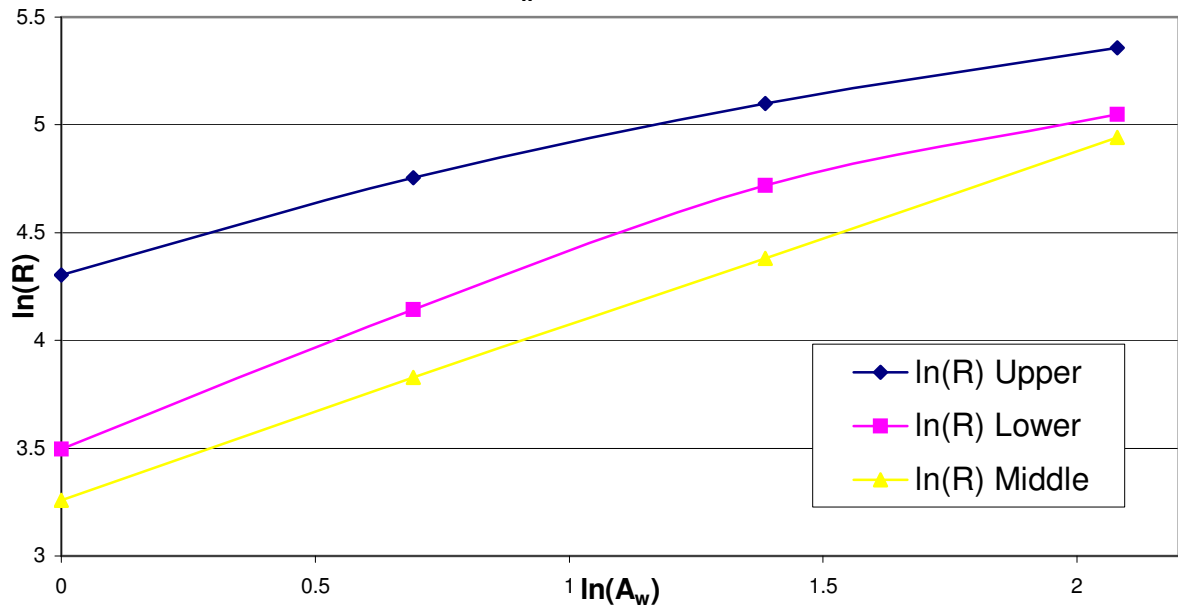


Figure 2. Range-area relationship for all abiotic data over smallest four A_w size classes

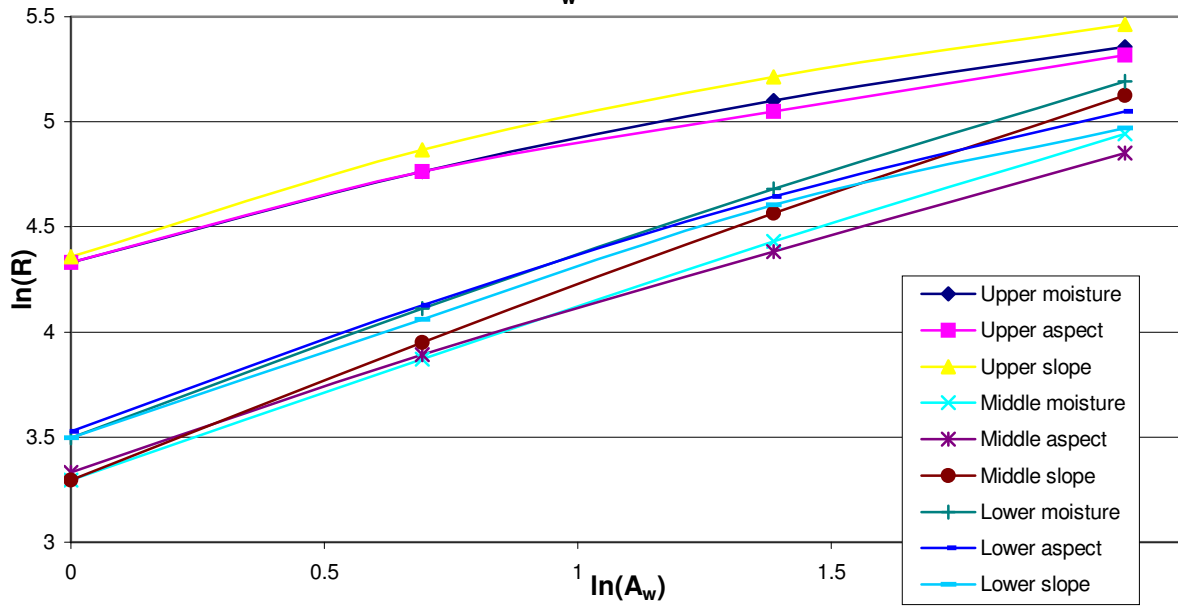


Figure 3. Comparison of y' values from RAR curves for sagebrush and abiotic data.

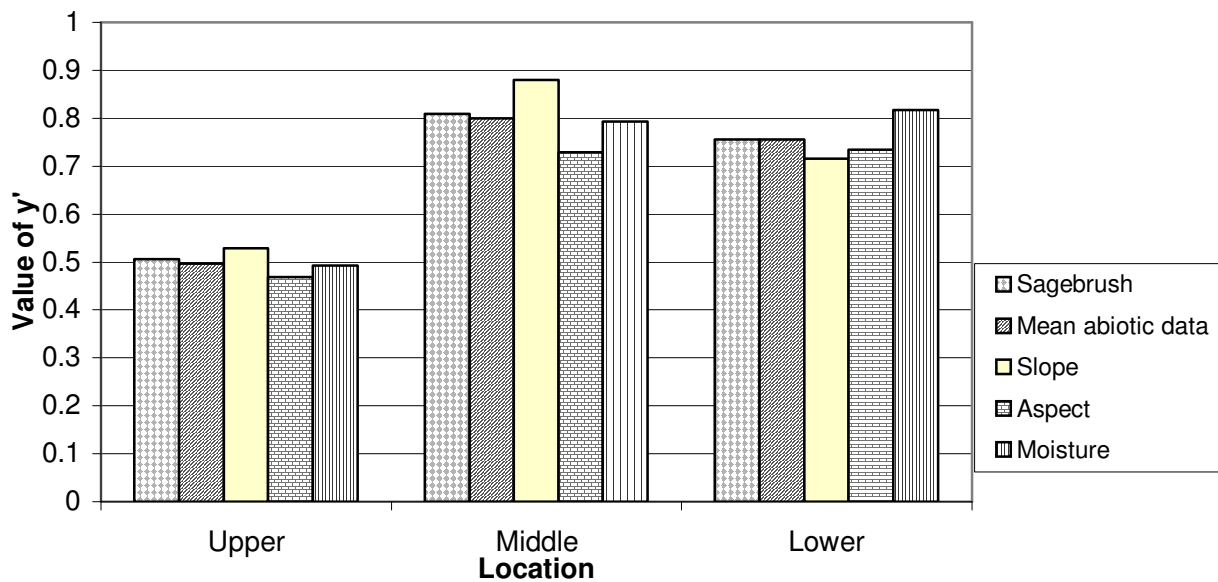


Figure 4. Middle aspect semivariogram over small scales

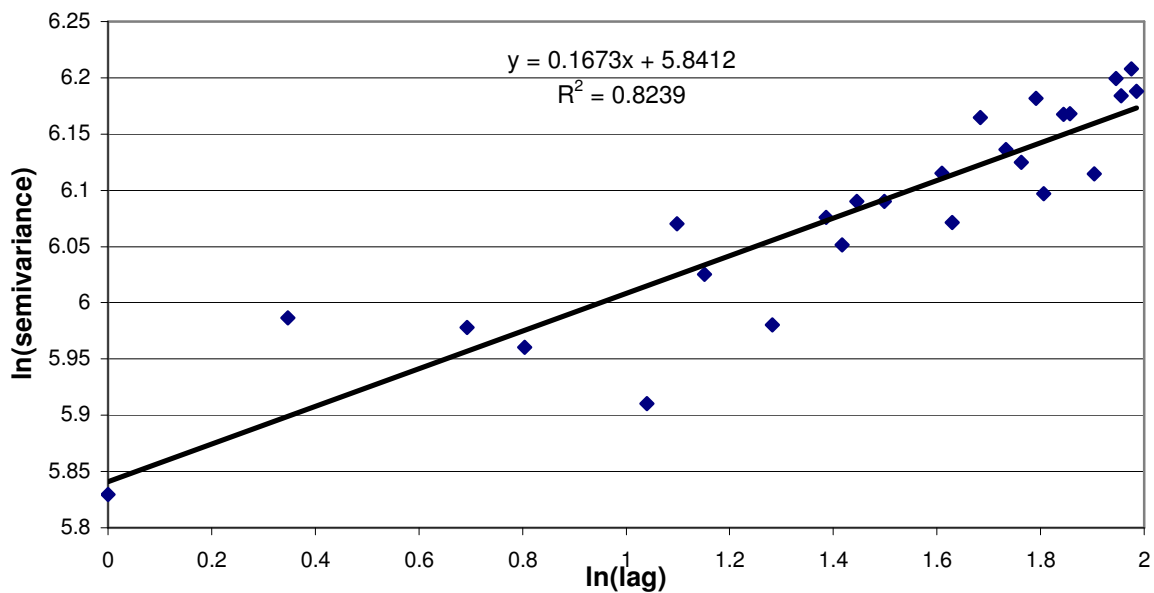


Figure 5. Lower aspect semivariogram over small scales

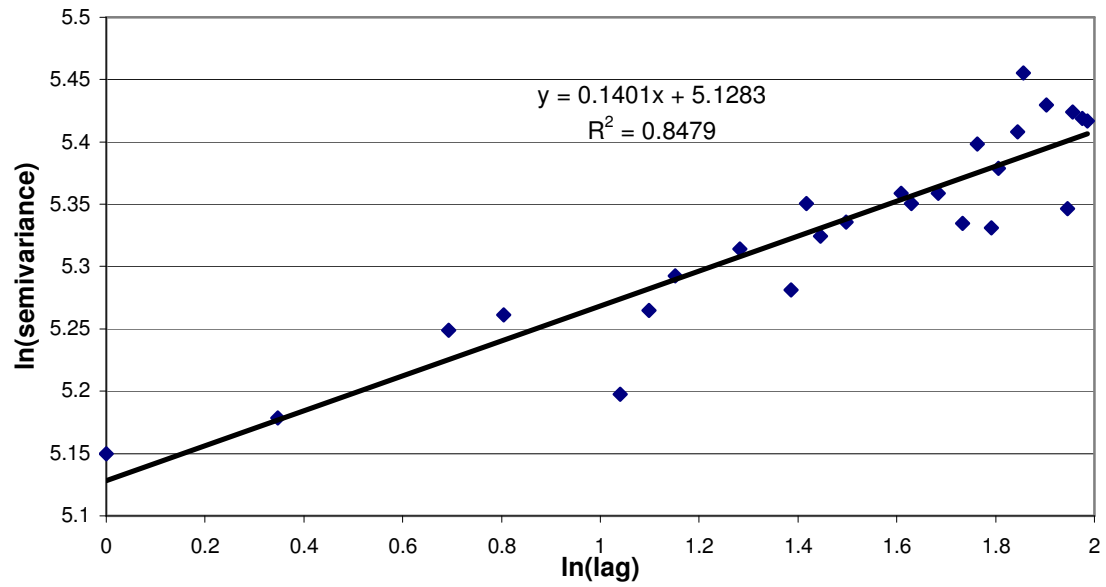


Figure 6. Upper aspect semivariogram over small scales

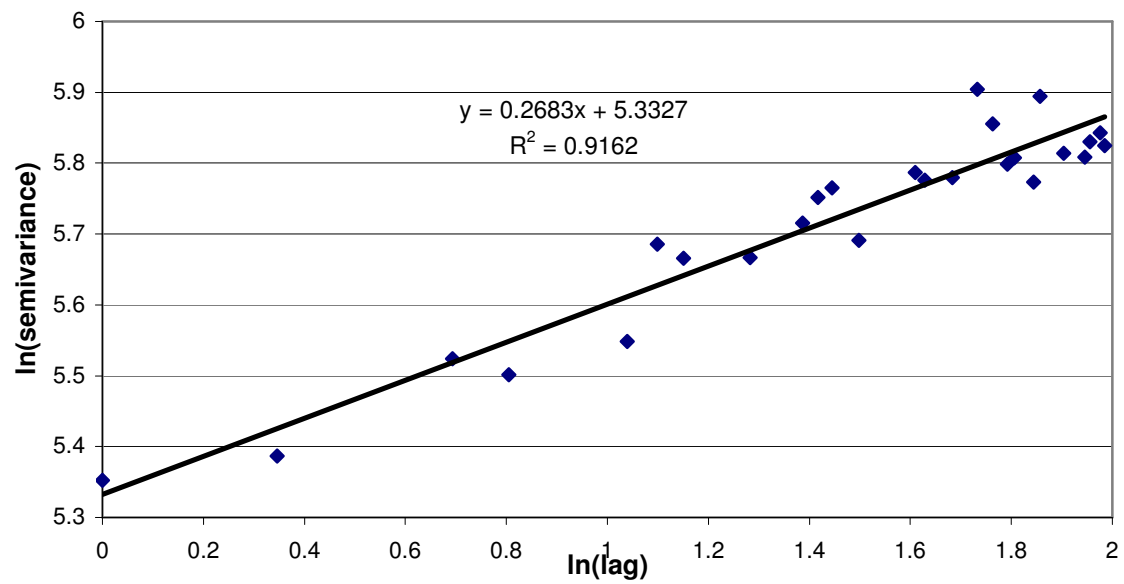


Figure 7. Middle moisture semivariogram over small scales

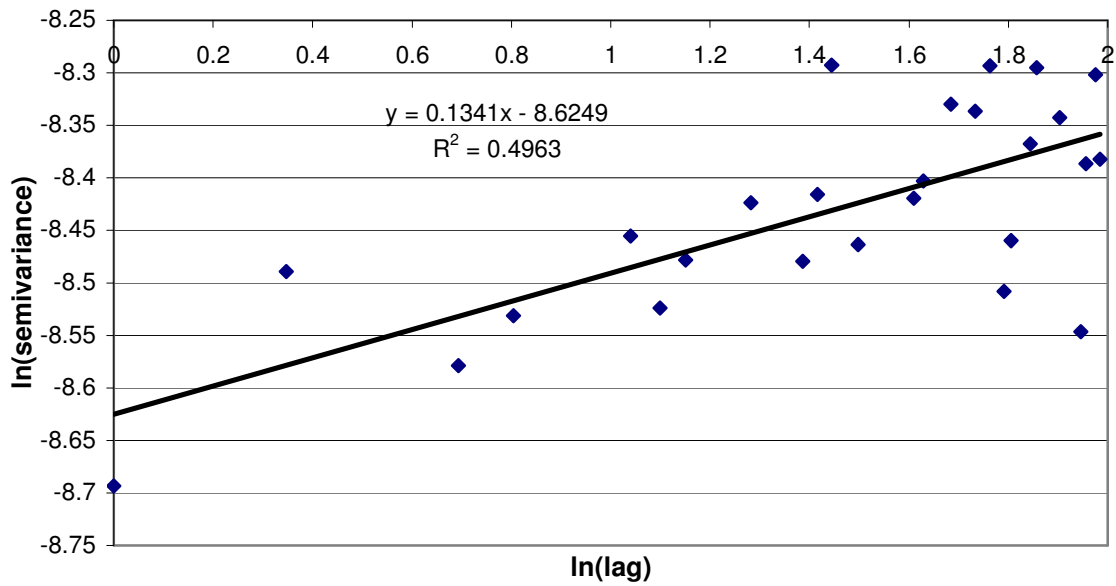


Figure 8. Upper moisture semivariogram over small scales

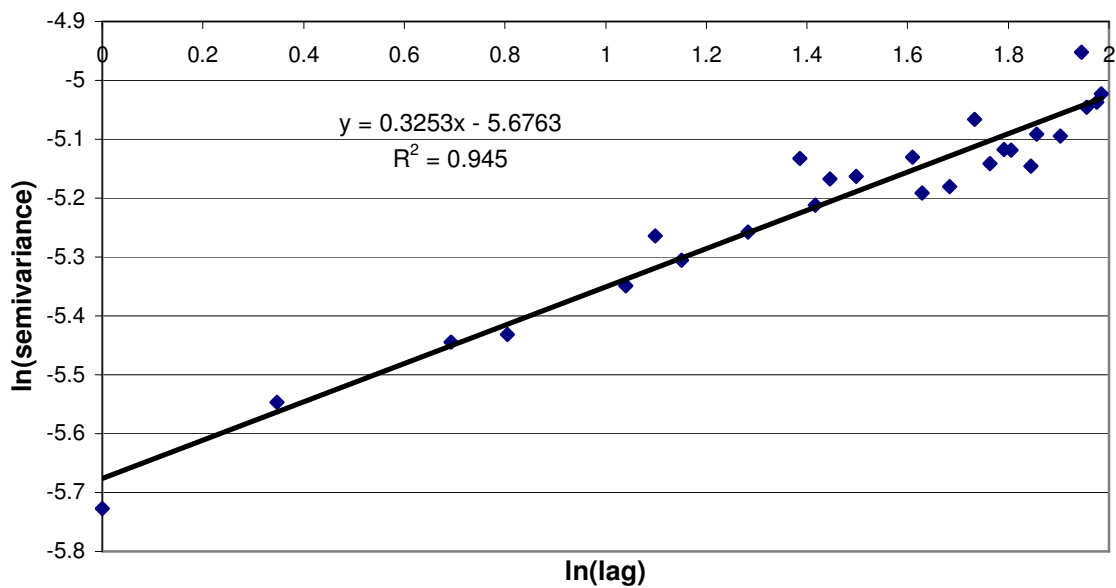


Figure 9. Lower moisture semivariogram over all scales

