



Spatial variation and temporal persistence of grapevine response to a soil texture gradient

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Abstract

Studying the water transport in the soil-plant system requires information on the spatio-temporal variability of both subsystems and the ability to assess the impact of the soil heterogeneity and of the biological responses on the coupling between vegetation and its substrate. This study was conducted for 2 years in a vineyard in the Aude Valley, France, by measuring the particle size distribution of the topsoil, the instantaneous isotopic ratios ($^{18}\text{O}/^{16}\text{O}$, $^2\text{H}/^1\text{H}$) of leaf water, annual shoot biomass production, and interannual persistence of this biomass along a 360 m transect. The resultant spatial series were analysed for their correlations and converted to spectra. Changes in the isotopic ratios along the transect reflect the soil texture gradient, suggesting that the vines root deeper on the gravel layers than elsewhere. This could provide a mechanism for the partial decoupling between soil and vegetation, and thus explain (1) the strong temporal persistence of the vegetation pattern, (2) the low overall correlation between biomass production and soil texture. The spectra show that this correlation concentrates at specific scales which correspond to a minimum variability in the shoot biomass. In this case, therefore, soil texture plays only a minor role in determining the spatial heterogeneity of shoot biomass in grapevine.

1. Introduction

Soil physicists and hydrologists have striven for several decades to apply the theoretical laws of soil water flow developed in the nineteenth century to natural watersheds and agricultural lands (see the review by Sposito, 1986). This has proved difficult because of extensive spatial variation in soil properties. Several authors have described such variation

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using spectral analysis (Webster, 1977; Byers and Stephens, 1983; Kachanoski et al., 1985a, b; Böttcher and Strebel, 1988) or geostatistical methods (see Webster and Oliver, 1990 for a comprehensive account). In some instances investigators have considered both soil and vegetation because variation in soil affects plant functioning through the distribution of nutrients and water (McBratney and Webster, 1981; Burrough et al., 1985; Ruelle et al., 1986; Williams et al., 1987).

Plant responses to the availability of water are complex, which adds to the spatial complexity of the soil. Many species tend to avoid drought, whether edaphic or atmospheric, by reducing the stomatal aperture and thus the instantaneous flux of transpiration. This stomatal regulation involves stress hormones which are released by the roots as soon as the soil water deficit reduces the root uptake (Zhang and Davies, 1989). Stomatal closure in response to air dryness also allows the demand from the canopy to decouple from the evaporative demand (Schulze, 1986a). Both mechanisms controlling the plant's water use contribute to maintain the soil-water resources for longer than they otherwise would (Schulze, 1986b) and, hence, delay and lessen the impact of the soil on the plant productivity. On longer times, plant roots which, in perennial woody species, grow each year from an already established framework and pervade a large volume of soil, may also help the plants to overcome local stresses that result from lateral as well as vertical heterogeneity in the soil.

The question then arises whether the various adaptations of a perennial plant to drought tend to smooth the effect of soil variation on plant growth. The answer could be important for building distributed models of water transport in the soil-plant system, indicating to what extent local soil-water parameters remain relevant, and are therefore needed, for such application. More theoretically, addressing this question could bring insights on how spatial structures emerge in such a system, how they are nested and aggregated as one moves through successive levels of integration, from the plant or the soil sample to the field as a whole.

The temporal scale of water transport from soil to plant and to atmosphere ranges from minutes (stomatal reactivity) to years (crop yield), and even longer with woody perennials. In the latter case, the moisture regime of a given year determines the production of buds and the storage of carbohydrates that support the regrowth of the plants in the subsequent year. The persistence of structural organs (main roots and shoots) from year to year might also ensure some stability in the spatial pattern of the canopy. The spatial variation of the biomass is dependent on the scale of consideration, and one could ask to what extent the temporal stability of the biomass also depends on this scale. The answer would require accurate indices of the factors influencing the changes in biomass production through space at the appropriate scales.

This paper is aimed at evaluating the effects of a soil texture gradient on the functioning of the plant canopy at increasing time-scales, viz. instantaneous transpiration flux, annual biomass production, and the persistence of this production from year to year. We accomplished this by sampling a transect across a vineyard in the south of France.

2. Materials and methods

2.1. Description of the study site

The vineyard studied is in the Aude Valley in southern France at 43°13'N, 2°50'E. It has a Mediterranean climate, with a potential evaporation rate of about 1100 mm yr⁻¹, and a

mean annual rainfall of 600 mm (Canet, 1983). The vineyard stands on a nearly level Quaternary terrac e (W rm) between the Aude and the Orbieu rivers. Its brown calcareous soil consists of a silty clay to silty clay loam topsoil covering a discontinuous gravel layer that is more or less hard. This discontinuous layer represents the main source of variation in the vineyard. On the west side of the field the soil is coarse textured with numerous stones. The size of sand and stones gradually decreases from west to east suggesting that the gravel layer deepens or disappears entirely.

The vineyard was uniform in planting: the six year old vines were of a single cultivar (*Vitis vinifera* cv. Shiraz, grafted on RI 10), cordon trained with 1.5 m between plants along the rows. These were 2 m apart and ran from west to east. Tillage as well as pest and weed control were uniform throughout. The vines had received no irrigation since planting, and hence it could be assumed that possible variations in biomass production reflect the variability in soil and in the availability of soil water in particular.

2.2. Data

A transect, 360 m long, was laid across the whole vineyard, parallel to a vine row, in the west–east direction. Soil and plant were sampled at equispaced points at intervals that depended on the type of property.

Isotopic composition of water was used as a tracer of the instantaneous flow of water in the soil–plant continuum (Bariac et al., 1989; see also Ehleringer and Dawson, 1992). Due to evaporation at the soil surface, water in the upper soil layers is generally enriched in heavy isotopes (^{18}O and ^2H). In plant tissues, since there is no isotopic fractionation due to water uptake by the roots, the isotopic composition of the water reflects that of the soil layer from which the plant removed water (F rstel, 1978; Bariac et al., 1989; Stringer et al., 1989). The isotopic ratios $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/^1\text{H}$ were measured in samples of leaves collected on 10 September 1987 between 12:00 and 14:00 (Local Solar Time, LST). We cut three sunny leaves off every other vine, giving a sampling interval of 3 meters. The samples were immediately stored in vessels to avoid transpiration and subsequent artificial isotopic fractionation. Isotopic ratios were measured by mass spectrometer analyses following the method described by Bariac et al. (1989), and expressed in the "delta" notation relative to the international standard V-SMOW (standard mean ocean water). These analyses were performed on randomized batches of leaf samples to prevent any systematic concentration of measurement errors in the series. The delays and costs of the analyses in the laboratory, as well as the necessity to work quickly in the field, limited the sample to 90 (between positions 0 and 267 meters). Nevertheless, as leaf sampling took 2 hours, the series of isotopic data showed trends, and statistical analyses were performed on detrended series (i.e., on the residuals of the linear adjustment to the series).

The dry biomass of the total one-year-old shoot, which is a function of the cumulative transpiration of the vine (M eriaux et al., 1979), provided an index of the plant–water functioning over the whole growth season. The biomass of the shoot was weighed in the field after cutting off the one-year-old stems produced on each vine of the transect, i.e., at an interval of 1.5 meters. The biomass measured on 3 February 1988 and 20 February 1989 represents the annual shoot production per vine for 1987 and 1988, respectively.

Particle size distribution (clay: $< 2 \mu\text{m}$; fine silt: $2\text{--}10 \mu\text{m}$; coarse silt: $10\text{--}20 \mu\text{m}$; fine sand: $20\text{--}200 \mu\text{m}$; coarse sand: $0.2\text{--}2 \text{mm}$) and the gravel percentage ($2\text{--}10 \text{mm}$) were determined for 61 soil surface samples ($0\text{--}20 \text{cm}$ depth) taken along the transect at 6 m intervals. Cultivation has mixed the soil to 40 to 60 cm, and so these samples were representative of the topsoil pervaded by the roots. This soil layer generally contains 60 to 90% of the root biomass of a grapevine (Huglin, 1986). The soil was sampled between two rows of vines (viz. 1 m apart from the vines) and sieved through a 10 mm sieve to remove clods and large stones. The soil samples were sieved again in the laboratory at 2 mm and the coarse fraction ($2\text{--}10 \text{mm}$) expressed as a proportion by weight. The particle size distribution of sand, silt and clay, was determined by sieving and pipette analysis. The samples were analysed in random order to avoid systematic errors within the series.

2.3. Time stability of spatial patterns

Kachanoski and De Jong (1988) discuss the definition of the stability of a spatial process in time and show that it could be tested by simple regression on paired series of spatial observations taken at consecutive times. In the case of a change affecting uniformly all spatial positions between consecutive times, the regression slope will be not significantly different than 1, and the intercept will represent the change that has occurred.

2.4. Principles of spectral analysis

The variation of a series of observations through space can be described as a family of sinusoidal waves of different frequencies and amplitude (Platt and Denman, 1975). Spectral (or harmonic) analysis splits the variance of such a series into contributions from all the frequencies present in the observational window. Let Z_j ($j = 1, 2, \dots, N$) be a series of N measurements made at equally spaced points, the power (or variance) spectrum $\hat{I}(f_k)$ of this series can be estimated by (Kachanoski and De Jong, 1988):

$$\hat{I}(f_k) = (2m+1)^{-1} N^{-1} \sum_{l=-m}^m (a_{k+l}^2 + b_{k+l}^2) \quad (3)$$

where:

$$a_{k+l} = \sum_{j=1}^N Z_j \cos(2\pi f_{k+l} j)$$

$$b_{k+l} = \sum_{j=1}^N Z_j \sin(2\pi f_{k+l} j)$$

$$f_k = k/N \quad k = 0, 1, 2, \dots, N/2$$

and m is the coefficient of the moving average filter. The power spectrum is defined from the fundamental frequency $1/(NS)$ to the Nyquist frequency $1/(2S)$. These two frequencies define the observational window allowed by the length of the series N and the sampling interval S . Peaks of the power spectrum show the frequencies of the dominant cycles in the series. Its integral equals the total variance of the series. The choice of the smoothing

Table 1

Data number (N), sampling interval (S), fundamental frequency (f_i), Nyquist frequency (f_n), and smoothing filter used for the spectral analyses of shoot biomass and soil texture between positions 60 and 360 m along the transect

Parameter	Unit	Value
N		50
S	(m)	6
$f_i = 1/(NS)$	(m^{-1})	0.0033
$f_n = 1/(2S)$	(m^{-1})	0.083
Smoothing filter		{1/3, 1/3, 1/3}

coefficient represents a compromise between the search for the largest number of periodic components and the retention of a sufficiently stable spectrum.

Concerning two series of spatial data, their correlation can also be analysed in the frequency domain by means of the coherency spectrum estimated in an analogous way to the power spectrum. In the case where both series consist of the same property measured at two different times, the coherency spectrum characterizes the distribution of the temporal persistence of a spatial pattern throughout the frequency domain (Kachanoski and De Jong, 1988). The significance level of the coherency can be estimated from equations given by Brockwell and Davis (1988).

In our study, power and coherency spectra were calculated for (1) the two series of the biomass produced in 1987 and 1988, (2) the 1987 biomass and the soil fractions series. Table 1 gives a summary of the spectral analyses performed on these series. The analyses were limited to the portion of the transect between positions 60 m and 360 m to avoid the segment of soil directly affected by the gravel layer, and thus fulfil the condition of spatial stationarity required by spectral analysis. To smooth the erratic variation in biomass from one vine to the other the measured values of biomass were averaged for each set of four successive vines. This means that the interval of this variable became 6 m instead of 1.5 m and that it agreed with the interval used for sampling the soil. To smooth the power and coherency spectra, after experimenting moving average filters with a range of smoothing coefficients, the most satisfactory spectra were obtained by applying the filter {1/3, 1/3, 1/3} (i.e., $m = 1$ in Eq. 3).

3. Results and discussion

3.1. Description of the whole transect

Figs. 1 to 3 present the soil and plant data plotted against distance with the origin of the transect located at the west side of the field. Fig. 1 shows two contrasting soil segments, separated by a transition zone of about 20 m long. The first segment (between 0 and 40 m) is characterized by a large percentage of stones (> 30%) and sand (> 35%) corresponding to the gravel layer near the surface. Between 40 and 60 m, the coarse fraction declines rapidly, and the soil texture makes a transition to a silty clay loam.

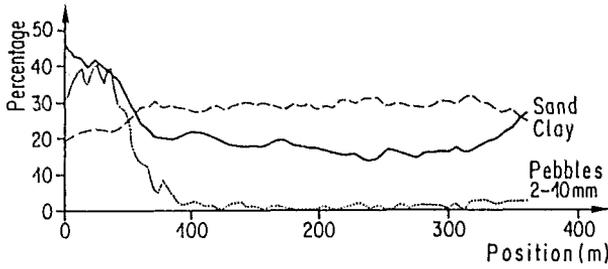


Fig. 1. Variations in sand and pebbles along the transect (sand content is expressed in weight percentage of the < 2 mm soil fraction, pebbles content in weight percentage of the soil sieved at 10 mm).

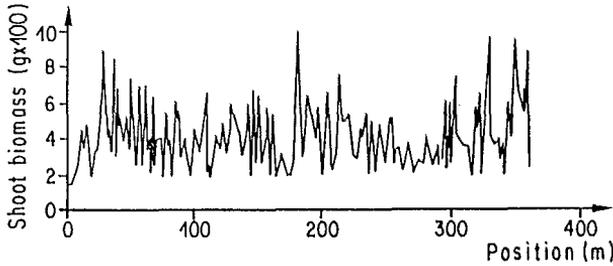


Fig. 2. Variations in shoot biomass per plant produced in 1987 along the transect.

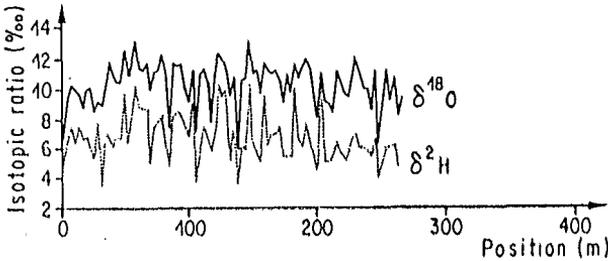


Fig. 3. Variations in leaf water isotopic ratios along the transect.

Patterns in total shoot biomass do not show any similarity with the spatial distribution in soil: shoot biomass increases slightly over the first 40 m, and then oscillates with three main local minima at 80, 170 and 270 meters (Fig. 2). Conversely, the spatial pattern of soil texture appears clearly through the changes in isotopic ratios of the leaf water: mean values of isotopic ratios were significantly smaller over the first 40 m of the transect than over the remainder of the transect (*t*-test, $P < 0.02$) (Fig. 3). This variation cannot be attributed to changes in weather or leaf water. In fact, while we were collecting leaves the temperature of the air and its humidity measured 2.7 m above the ground over 15 minute periods remained fairly constant, at $25.8^{\circ}\text{C} \pm 0.25$ and $55.5\% \pm 0.77$, respectively. The leaf water potential measured on 11 September at 11:30, 13:00 and 14:20 hours (LST), sampling three vines at a time, had a mean value of -1.9 ± 0.1 MPa, characteristic of the midday plateau commonly observed on vines growing outdoors (Katerji and Daudet, 1986; Grimes and Williams, 1990). This enabled us to interpret variations in isotopic ratios along the transect in relation to the soil texture gradient. Considering that water on the upper soil layers is enriched in heavy isotopes, our data show that within the same vineyard vines growing on

Table 2
Statistical parameters concerning the shoot-biomass per vine produced in 1987 and 1988 along the whole transect

Year	Statistical parameters		Coefficient of correlation r	Regression parameters 1988 = $a * 1987 + b$	
	Mean (g)	CV (%)		Slope a	Intercept b
1987	368	48	0.80	1.01	119.9
1988	494	45		(0.05) ^a	(20.3)

^aValues in parentheses are the standard errors of estimation.

the gravel layer extracted water from deeper layers than those on a more favourable soil. This implies that during the early growing phase (6–8 years after planting) the root system could extend through the gravel (in places 90 cm thick) to the more humid layers beneath. Soil water profiles measured on this portion of the transect using a neutron moisture gauge show that this was actually so (Winkel and Rambal, 1993), and confirm the considerable rooting power of the grapevine as described by Seguin (1981).

3.2. Temporal persistence of biomass patterns

Results of the statistical analyses on the biomass data are given in Table 2. The large linear correlation coefficient between the 1987 and 1988 data indicates a significant persistence of the spatial pattern observed during those years. The coefficient of determination reveals that about 64% of the spatial variation observed in 1988 can be explained by the variation in the previous year. The slope and intercept of the regression, about 1 and 120 respectively, show that, year by year, each vine on the transect retained approximately the same deviation from the mean, and that biomass increased by 120 g/vine on average, probably because of more rain during the 1988 growth season (April–July): 213 mm against 113 mm in 1987. The coefficients of variation were similar in both years, so the drought of 1987 did not increase the variability in the production of biomass. This correlation analysis demonstrates the stability of the variation in the total shoot biomass across the vineyard from year to year. However, only spectral analysis reveals the relation between temporal persistence and spatial scale and, at the same time, enables one to look for the possible deterministic link between biomass production and soil properties.

3.3. Spatial and spectral relations between biomass production and soil surface properties.

The coherency between both the series of biomass exceeds 0.62 (significant at $P < 0.05$) over most of the frequency spectrum (Fig. 4a). The mean value of the coherency spectrum is related to the correlation coefficient between the series. Fig. 4a shows that the coherency oscillates around 0.80, in agreement with the overall correlation coefficient (Table 2). Coherency is maximum in a frequency domain ranging from 0.04 m^{-1} (period = 25 m) to 0.055 m^{-1} (period = 18 m), and minimum near 0.08 m^{-1} (period = 12 m). Thus, stability in time in biomass production depended on the spatial scale, being smaller for small distances than for larger ones.

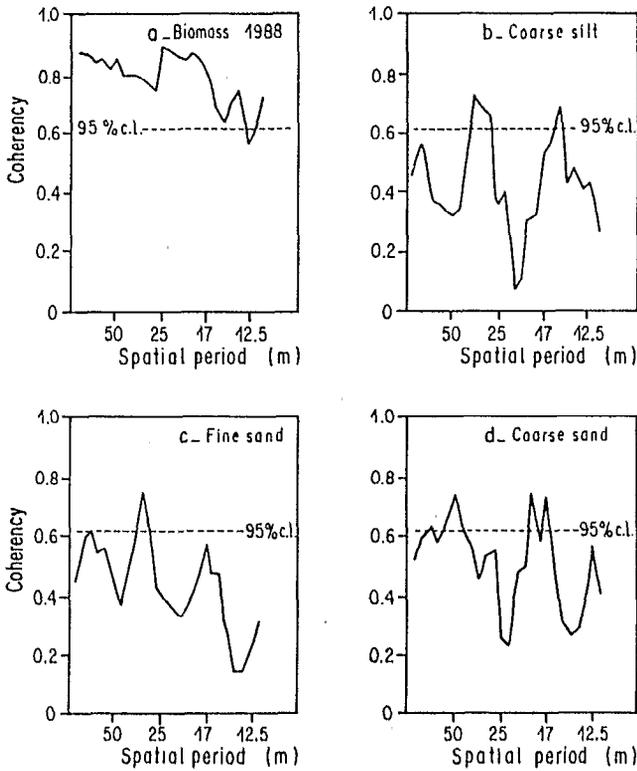


Fig. 4. Coherency spectra of the biomass produced in 1987 with the biomass of 1988 (a) and the main soil fractions (b–d) between positions 60 and 360 m along the transect (dashed lines show the 95% significance level).

The possible impact of the soil substrate on this pattern of stability can be seen by studying the spatial dependence of shoot biomass on soil texture. Fig. 5 shows that the biomass production fluctuated in a roughly periodic way with relative maxima at each 20–30 meters. Changes in the various soil fractions are more difficult to describe. All correlated with biomass production, positively for the sands, negatively for the silt and clay (Table 3).

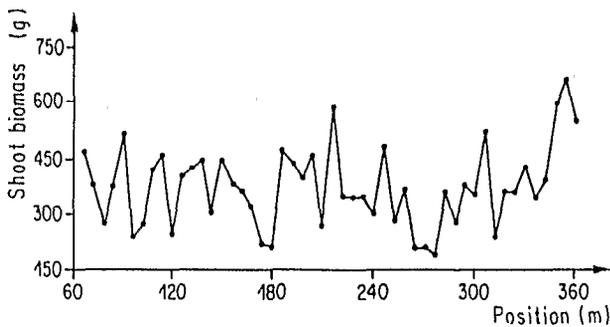


Fig. 5. Variations in the shoot biomass produced in 1987 between positions 60 and 360 m along the transect (each point is the mean of 4 neighbouring vines).

Table 3

Correlation of the biomass produced in 1987 to the soil fractions between positions 60 and 360 m along the transect (*, ** significant at $P < 0.05$ and 0.01 , respectively; " not significant)

Sand			Silt			Clay
fine	coarse	total	fine	coarse	total	
0.35**	0.32*	0.39**	-0.30*	-0.24"	-0.39*	-0.21*

Their power spectra show many peaks, different from one fraction to the other (Fig. 6b–d). Also they all show a higher spectral variance at scales greater than 50 m, which could reflect a trend in the data or edge effects. Although the power spectrum is no longer defined in the presence of a trend, Kachanoski et al. (1985a) outlined that, in practice, the spectral analysis could still be used, particularly because the frequencies of interest are in the medium to high range while trend affects the low frequencies. Böttcher and Strebel (1988) also present power spectra of data affected by trend.

The power spectrum for biomass shows that the variance was concentrated at the small distances (< 15 m) and between 20 and 25 m (Fig. 6a). Coherency spectra enable the

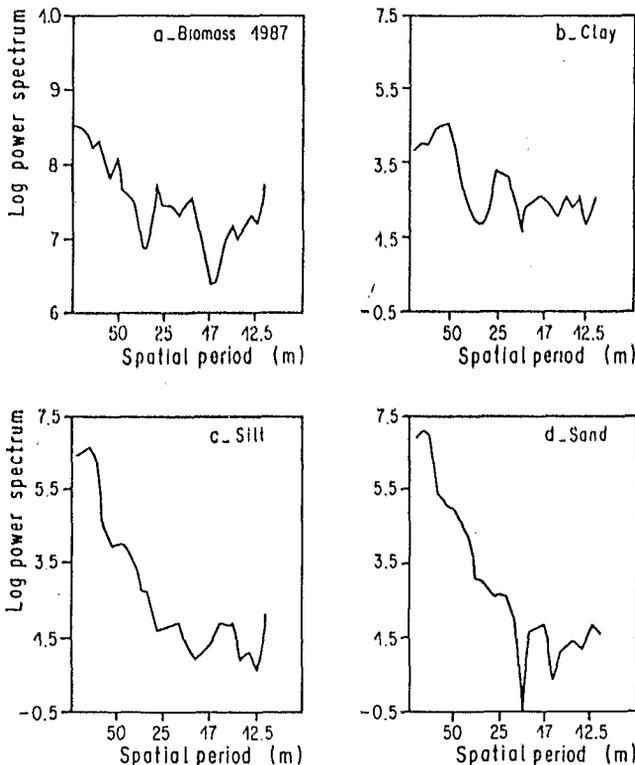


Fig. 6. Spectral variance of the biomass produced in 1987 and of some soil fractions between positions 60 and 360 m along the transect.

distribution of the correlation between biomass and soil texture as a function of scale to be examined (Fig. 4b–d). Biomass shows a significant coherency with the sands (fine and coarse) and the coarse silt for periods at 30 and 17 m, corresponding to the two minima of its own power spectrum. Thus, it appears that scales where the biomass production was more correlated to the soil texture were also those where its variability is the least. This implies that biomass changes, which were large between 20–25 m and beyond 15 m, resulted from sources of variation other than soil texture. Obviously, the topsoil texture only partially reflects the nature of the substrate pervaded by the roots, and other soil factors might influence the biomass production (chemical properties, thickness of the horizons, etc.). Also, systematic or random factors outside the soil–plant complex affect the biomass production, in particular cultivation which, be it even very long ago, can influence the variability in crop production at the field scale (McBratney and Webster, 1981; Böttcher and Strebel, 1988).

4. Conclusion

Spectral analysis enabled us to relate a biological pattern (annual biomass production of the vine) to a physical pattern (soil texture), demonstrating that the large correlation that exists between them is not equally distributed over the whole range of scales. Dismissing the trend or edge effects, significant coherency between biomass and soil texture was concentrated in specific portions of the frequency spectrum which, in the present case, corresponded to a minimum variability in the biomass production. Within the vineyard studied, the vine was particularly variable at small scales and its variation appeared to be dominated by factors other than soil texture.

Power spectra also show that spatial structures were less variable for the biomass than for the soil. This could be interpreted as a smoothing of the effects of spatial variation in soil by the plant canopy, and it supports the hypothesis that vegetation acts as a spatial filter towards its substrate (Warriek and Gardner, 1983; Trangmar et al., 1987). For a perennial plant like the vine the potential for deep rooting provides a powerful damper on the spatial changes in the soil substrate. At the same time variable rooting depth, as supported by our data on the isotopic ratios of the leaf water, allows the vegetation to release itself, at least partly, from local constraints in the soil, particularly local shortages in water. So, it is not surprising that interannual variations in aerial biomass production, essentially due to the seasonal water regime, occurred uniformly throughout the space and that, as a consequence, the spatial organization of the canopy showed a strong temporal persistence.

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