

Productivity and modifications of ecosystem processes in gaps of a low Macchia in southern Italy

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Disturbance in Mediterranean shrub lands creates gaps that break up the shrub cover and potentially restrict productivity and other ecosystem processes. Gaps make up to about 20% of the low Macchia area at the Castel Volturno nature reserve (southern Italy). The plant community consists mainly of small annual species (legumes, grasses and forbs) that germinate in November and die out before the onset of summer drought. The inter-annual variability in productivity and the relative abundance of legumes, grasses and forbs were assessed over 4 years (2004–2007) to evaluate main potential modifications of ecosystem processes determined by the occurrence of gaps in the shrub cover.

In the study years, at the peak production, plant mass varied from about 250 to 700 g m⁻²; biomass belowground allocation varied from 23% in the wettest to 44% in the driest year. Belowground/aboveground biomass ratios were negatively related to rainfall and positively related to the length of the dry period, showing that water availability controls biomass allocation patterns. Legumes were the most abundant fraction (about 60%) of the aboveground mass in the wettest year. In the drier years legumes exhibited a shorter life cycle and senesced by mid-spring. Among the three functional groups monitored, legumes were the most sensitive to water shortage and their biomass was positively related to the amount of rainfall and negatively related to the length of the dry period. The higher fraction of legume mass was associated with higher nitrogen content in plant tissues and in the soil. Senesced annual species decomposed more than senescent *Phillyrea* sp. leaves. The stability of organic carbon pool, evaluated through the endogenous mineralization coefficient (CEM), was lower in gaps than in understorey soils.

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Mediterranean-type ecosystems are characterized by an evergreen shrub land cover, called maquis in the Mediterranean basin. Evergreen shrub lands turn into sclerophyllous woodlands at increasing moisture availability and into heath lands at decreasing nutrient availability (di Castri 1981). In heavily degraded woodlands and

shrub lands, trees and shrubs are replaced by annual species which dominate open communities and constitute approximately 15% of the regional flora. Natural and anthropogenic disturbances have an important role in shaping Mediterranean vegetation and landscapes and contribute to the high species diversity in the area, as the

20% of the world's vascular plant species are found in the relatively small area covered by Mediterranean-climate regions (1.2% of the earth's surface, di Castri 1981).

Mediterranean climate presents a marked seasonality with hot dry summer, moist winter and a great inter-annual variability in rainfall. In this climate annuals are most sensitive to drought, being strict drought avoiders with their life cycle tuned to the duration of soil water availability. Their importance in terms of ecosystem productivity is highest in years with wet springs (Troumbis 1985). In contrast, sclerophyllous shrubs and trees have the ability of surviving drought and assimilate carbon also during scattered rain periods in summer. If the dry season begins earlier in spring and lasts too long, annual plants will shorten their life span. Pereira et al. (2007) comparing carbon fluxes in contrasting Mediterranean ecosystem in southern Portugal, found that during two years of severe droughts carbon sequestration was strongly restricted in an evergreen oak woodland whereas a grass land was a net source of carbon dioxide to the atmosphere.

As drought spells in Mediterranean ecosystems are predicted to become longer and more frequent as a consequence of climatic change (Christensen et al. 2007), many studies have focused on how this could affect carbon sequestration in these ecosystems (Serrano-Ortiz et al. 2007, Aires et al. 2008, Allard et al. 2008).

Average plant biomass in Mediterranean shrub lands ranges from 10 to 120 t ha⁻¹ depending on environmental characteristics and type of maquis, i.e. low or high maquis, species composition (Costa and La Mantia 2005), with a pattern of biomass allocation 50% aboveground and 50% belowground (Saugier et al. 2001). Biomass in Mediterranean grass lands at the end of the growing season varies considerably between areas and, in the same area, between years, ranging from 300 to 1200 kg ha⁻¹ in dry grass lands (Osman et al. 1991, Cocks and Osman 1996) to 1000–5000 kg ha⁻¹ in the Negev (Osem et al. 2004). Therefore, Mediterranean grass lands are a minor carbon stock compared to shrub lands. Moreover, herb cover is limited to the wet season of the year, thus only in the moist period grass lands may act as an effective carbon sink. For instance, Aires et al. (2008) found that a grass land in southern Portugal in a dry year produced a peak standing biomass of 1570 kg ha⁻¹ and was a net source of carbon, while in a normal year it produced a peak standing biomass of 5520 kg ha⁻¹, and was a net carbon sink.

In Mediterranean shrub lands, gaps are linked to frequency and size of disturbance and to the recovery of shrub canopy (Trabaud 1994), thus the fraction of gaps in a shrub land may vary in space and time. Plant cover in gaps consists mainly of annual herbs with a short life span. Replacement of drought-adapted sclerophyllous shrubs with drought-sensitive, avoiding annuals, is expected to reduce the amount of biomass and the potential carbon storage. Moreover, the very different traits of sclerophylls with hard, leathery leaves, and herbs with soft leaves, lead

to the production of litter of different quality that influence the rate of decomposition and the organic matter turnover and carbon storage in soil.

Mediterranean grass lands are typically constituted by legumes, C₃-grasses and forbs. Legumes, with symbiotic nitrogen-fixing bacteria, use different nitrogen sources than grasses and forbs, reducing competition and consequently promoting coexistence of plant species. By increasing the nitrogen content in the soil, legumes increase productivity in N-limited environments such as maquis. However legumes are very sensitive to drought (Serraj et al. 1999) and their abundance in the herbaceous layer is likely to be controlled by the inter-annual variability in rainfall.

The relative proportion of these three annual functional types, legumes, grasses and forbs, influences biomass production in gaps, but its effects have not been addressed yet. The implications for the carbon cycle of shrub replacement by annuals are also little known, despite their importance for carbon sequestration.

This study is based on a 4-year (2004–2007) dataset of plant mass measurements carried out in gaps of a Mediterranean shrub land in Castel Volturno nature reserve. The dataset allowed us to explore how sensitive mass production in gaps is to inter-annual rainfall variability, and to test: 1) how important legumes are as a determinant of biomass production and nitrogen input into the soil, 2) whether litter decomposition and soil organic matter mineralization are higher in gaps than in the understorey, and 3) the effects of shrub replacement by annuals on carbon dynamics in the system.

Material and methods

Study area

This study was carried out in the evergreen Mediterranean shrub land of Castel Volturno nature reserve (40°57'N, 13°33'E; southern Italy). Gaps are dominated by herbs and bryophytes, and cover about 20% of the low Macchia area. The mosaic of plant cover is related mainly to the frequent fires occurring in the reserve especially during summer time. Aboveground shrub biomass, constituted by *Arbutus unedo*, *Cistus* sp. pl., *Myrthus communis*, *Phillyrea* sp. pl., *Pistacia lentiscus*, *Quercus ilex*, and *Rhamnus alaternus*, ranges from 2–4 kg m⁻² (i.e. 20–40 t ha⁻¹) in the low- and high maquis respectively, in the same order of magnitude as in other Mediterranean shrub lands (De Marco et al. 2005).

In Castel Volturno's low Macchia the herbaceous plant cover of gaps is mainly inhabited by *Aetheorizza bulbosa*, *Briza maxima*, *Dactylis hispanica*, *Medicago minima*, *M. litoralis*, *Melilotus neapolitana*, *Petrorragia saxifragae* (most abundant in autumn), *P. velutina* and *Phleum subulatum*. The herbs that occur in gaps are mainly small-sized an-

nuals that germinate in November and conclude their life cycle in late spring. Some, however, re-grow after the first autumn rains (September) and complete their life cycle in October. Herb mass and the fraction of legumes, grasses and forbs vary from year to year.

Soil at the Castel Volturno nature reserve is a calcareous arenosol (FAO 1998) with a sub-alkaline pH. Soil texture (USDA) is sandy (sand 92.7%, loam 5.1% and clay 2.2%) and the amount of organic matter in the surface layer (0–10 cm) in gaps and in the understorey is 3.9 and 4.6 kg m⁻², respectively. The climate is typical Mediterranean.

Sampling and analysis

Aboveground plant mass was harvested from two 20 × 20 cm quadrates in each of nine gaps in the experimental area. In each quadrate two soil cores were taken to a depth of 10 cm. Shoots were separated and sorted into three groups; legumes, grasses and forbs. Roots were recovered by sieving soil cores. Samples of each type of aboveground biomass fraction were analyzed for N- and C-content (CNS gas analyzer) after homogenization in a Fritsch pulverisette. Harvests were carried out a) for the years 2004 and 2005 in March, April, and May, b) for year 2006 in March, April, May, September, October and November, c) for the year 2007 in May and November.

On each sampling date soil water content was determined gravimetrically and soil organic matter by loss by ignition at 550°C (Allen 1989). Soil pH was determined in distilled water (1/2.5, soil/water). Soil nitrogen content was determined by a CNS gas analyzer after homogenization in a mill.

Decomposition of annuals' mass and, for comparison, of *Phillyrea* leaves was measured in laboratory microcosms. The mixture of legumes, grasses and forbs, as collected in the field at the end of June 2004, and senescent leaves of *Phillyrea* picked up from the plant in December 2004, were dried at room temperature and weighed. Cylindrical glass pots (8 cm in Ø 10 cm in height, 500 ml volume) were filled up to 5 cm height with soil taken from gaps and from the understorey of *Phillyrea* individuals. A nylon net (1 mm mesh) was placed on the soil surface and 2 g of plant material were placed on the net. Litter and soil were brought to 55% of water holding capacity. Moisture was maintained at a constant level during the incubation period by evenly distributing a certain amount of distilled water over the sample. Incubation temperature was 25°C. Litter samples (7 replicates per litter type) were collected after 215 d and mass loss was determined. Sub-samples were analyzed for nitrogen content as described above and for lignin content with a modified method by Van Soest and Wine (Fioretto et al. 2005).

Soil microbial biomass and respiration were determined according to Degens (2001), by gas chromatographic measurements of CO₂ evolution from fresh soil

samples. CEM was obtained from respiration and C_{org} and expressed as mg CO₂-C g⁻¹ C_{org} h⁻¹. C_{org} was calculated from the organic matter content divided by 1.72 (the organic matter/organic C ratio).

Rainfall (P), number of days without rain or with less than 2 mm rain per day (DP), and mean daily temperature (T) were calculated from germination (November) to each of the different sampling dates within the seasonal cycle and for periods between successive sampling dates. When analyzing the late summer production, P, DP and T were calculated for the periods from July to the sampling dates (September, October). Biomass production in the first phase of the growth cycle (November samplings) was assumed to be influenced by the pattern of climatic conditions in September and October; thus P, DP and T were calculated for the period from September to November.

Differences in plant mass and soil characteristics between years were estimated by one way ANOVA, followed by post-hoc Tukey or Dunn tests. Correlations between components of plant mass were analysed using the Spearman's coefficient. Multiple linear regressions of plant mass with P and DP were performed to explain mass variations.

Results

Rainfall and temperature patterns

Rainfall over the growing season (November–May) ranged in the study years between 603 and 804 mm (Table 1). Mean temperature and number of days without rain, or with rain < 2 mm (Table 1) were highest (13.3°C and 155 d, respectively) in 2007. In spite of the relatively low total rainfall, 2004 and 2007 had the wettest late winter and spring months (Table 1). The years 2005 and 2006 had the driest spring (April–May). The year 2005 had the longest recorded dry period in spring time.

Pattern of biomass allocation

Annual herbs germinate and establish in November but their biomass only slightly increases up to March. The highest values of biomass have been recorded in late spring (Fig. 1).

The peak biomass (May) shows a high year-to-year variability (Fig. 1). A significantly higher total mass was produced in gaps in 2004 as compared to 2005 and 2006 (one way ANOVA; Table 1). Statistically significant differences between years was found for aboveground biomass of legumes, grasses and forbs (Table 1). Legumes were most abundant in 2004 and least abundant in 2005, when grasses were most abundant (Fig. 2). Forbs made up most of the aboveground plant mass in May 2006 and May 2007 (Fig. 2).

Table 1. Aboveground, belowground and total plant mass (g m^{-2}) in gaps of the low Macchia at Castel Volturno nature reserve, and main soil and climatic parameters for the periods November–March, November–April, and November–May. Values of biomass and soils parameters are means of 18 measurements at each harvest. Different letters above bars show significant differences among years (Tukey and Dunn tests, $p < 0.05$). P = rainfall in period, dry period = number of days without or with rain < 2 mm, T = mean daily temperature. Figures in parentheses are: 1) for March: P and DP in January, 2) for April: P and DP from March to April, 3) for May: P and DP from March to May.

| | March | | | April | | | May | | | |
|-------------------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|------------------------|-------------------------|------------------------|------------------------|------------------------|
| | 2004 | 2005 | 2006 | 2004 | 2005 | 2006 | 2004 | 2005 | 2006 | 2007 |
| Total biomass (g m^{-2}) | 298 ± 19 ^a | 166 ± 24 ^b | 184 ± 14 ^b | 481 ± 23 ^a | 165 ± 17 ^b | 275 ± 20 ^c | 701 ± 59 ^a | 244 ± 21 ^b | 287 ± 26 ^b | 553 ± 76 ^a |
| Aboveground (g m^{-2}) | 150 ± 10 ^a | 58 ± 8 ^b | 132 ± 12 ^a | 291 ± 21 ^a | 96 ± 11 ^b | 176 ± 14 ^c | 543 ± 55 ^a | 169 ± 22 ^b | 202 ± 25 ^b | 324 ± 55 ^b |
| Legumes (g m^{-2}) | 91 ± 12 ^a | 8 ± 3 ^b | 72 ± 8 ^a | 209 ± 24 ^a | 20 ± 8 ^b | 92 ± 4 ^c | 313 ± 45 ^a | 13 ± 5 ^b | 72 ± 5 ^c | 61 ± 20 ^{bc} |
| Grasses (g m^{-2}) | 38 ± 10 ^{ab} | 36 ± 8 ^a | 15 ± 2 ^b | 56 ± 11 ^a | 47 ± 12 ^{ab} | 17 ± 2 ^b | 148 ± 38 ^a | 106 ± 20 ^a | 27 ± 1 ^b | 97 ± 38 ^{ab} |
| Forbs (g m^{-2}) | 22 ± 4 ^{ab} | 14 ± 3 ^a | 45 ± 5 ^b | 27 ± 5 ^a | 30 ± 6 ^a | 67 ± 9 ^a | 82 ± 27 ^{ab} | 50 ± 15 ^a | 103 ± 22 ^{ab} | 167 ± 40 ^b |
| Belowground (g m^{-2}) | 148 ± 17 ^a | 108 ± 24 ^a | 52 ± 5 ^b | 190 ± 15 ^a | 69 ± 9 ^b | 99 ± 9 ^{ab} | 158 ± 22 ^a | 75 ± 8 ^b | 85 ± 8 ^b | 241 ± 47 ^a |
| Below/aboveground | 1.0 ± 0.2 | 1.9 ± 0.4 | 0.5 ± 0.05 | 0.7 ± 0.08 | 0.8 ± 0.1 | 0.6 ± 0.06 | 0.3 ± 0.02 | 0.5 ± 0.1 | 0.5 ± 0.06 | 0.9 ± 0.3 |
| Soil pH | 7.4 ± 0.1 ^a | 7.5 ± 0.1 ^a | 7.8 ± 0.1 ^b | 7.3 ± 0.1 ^a | 7.6 ± 0.1 ^a | 7.9 ± 0.1 ^b | 7.1 ± 0.1 ^a | 7.1 ± 0.1 ^a | 8.0 ± 0.1 ^b | 7.8 ± 0.1 ^b |
| SOM (%) | 9.3 ± 0.7 ^a | 7.4 ± 0.2 ^b | 6.0 ± 0.3 ^c | 9.8 ± 0.4 ^a | 7.5 ± 0.3 ^a | 5.7 ± 0.2 ^b | 8.3 ± 0.2 ^a | 6.8 ± 0.2 ^b | 5.8 ± 0.3 ^b | 6.9 ± 0.4 ^b |
| SWC (%) | 21.6 ± 0.7 ^a | 16.4 ± 0.8 ^b | 14.1 ± 0.7 ^c | 20.3 ± 0.7 ^a | 18.4 ± 0.6 ^a | 5.0 ± 0.2 ^b | 14.8 ± 0.6 ^a | 2.5 ± 0.1 ^b | 2.5 ± 0.1 ^b | 2.6 ± 0.2 ^b |
| P (mm) | 488.4 (144) | 682.4 (87.8) | 626.4 (58.4) | 586.2 (97.8) | 729.0 (46.6) | 638.6 (12.2) | 659.2 (289.8) | 804 (225.2) | 695.4 (191.8) | 603 (231.4) |
| T (°C) | 10.0 | 8.3 | 9.3 | 10.7 | 9.5 | 9.9 | 11.46 | 11.38 | 11.13 | 13.3 |
| Dry period | 100 (19) | 89 (24) | 102 (26) | 116 (16) | 113 (24) | 120 (18) | 140 (59) | 150 (74) | 149 (68) | 155 (69) |

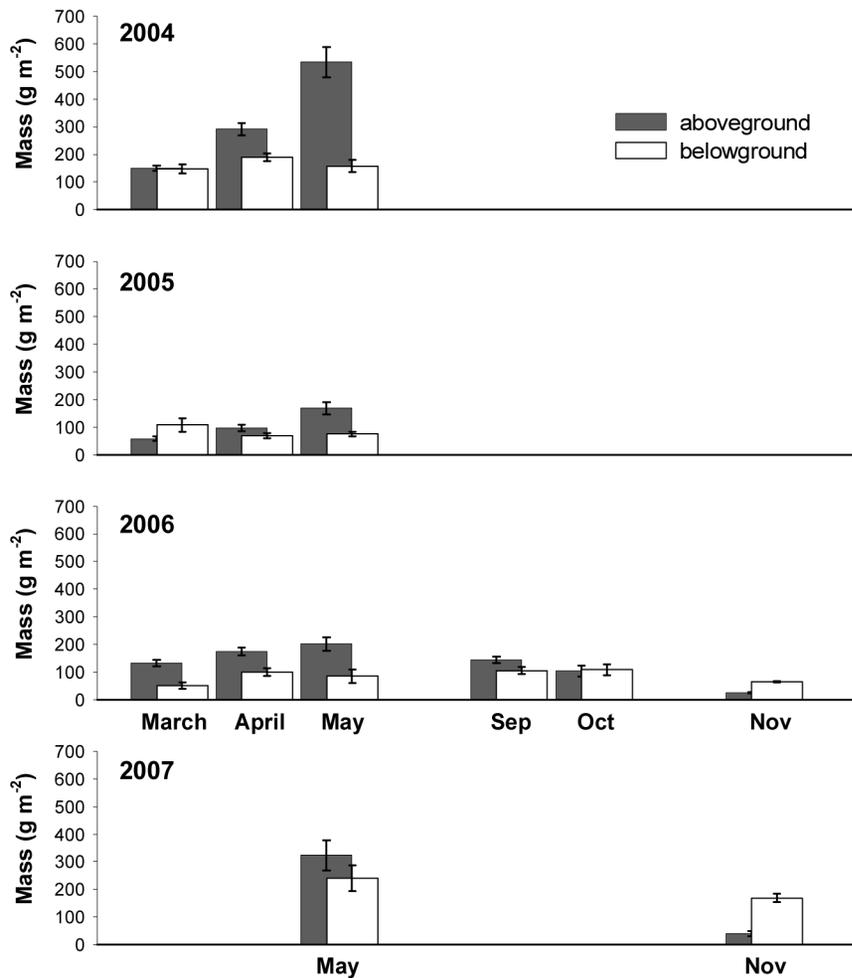


Fig. 1. Aboveground and belowground mass (g m^{-2}) measured in gaps of the low Macchia at Castel Volturno nature reserve during the study years. Values are means of 18 measurements at each harvest.

In 2004 legumes grew up to May (Fig. 3) while in the drier years 2005 and 2006 they showed a shorter life cycle and reached the peak biomass in April. For grasses and forbs the maximum biomass increased from April to May (Fig. 3).

Belowground plant mass (Fig. 1) was lowest in 2005 and 2006 (Table 1). Between March and May there was only a weak increase, if any, in belowground mass; the opposite to aboveground biomass (Fig. 1, Table 1).

Belowground/aboveground biomass ratio (B/A) at the peak mass (Table 1) was lowest in the wet spring of 2004, the time with the highest proportion of legumes in gaps (Fig. 2). B/A was highest in 2007, which was characterized by the greatest proportion of forbs. B/A showed the highest values, 3.0 and 5.7, in the early phase of the vegetative cycle, in November 2006 and 2007, respectively (Table 2).

Measurements of plant mass made in late summer and early autumn 2006 revealed that forbs resumed growth with

the first rain after summer drought, reaching mass values similar to those measured in May (Table 1, 2) and then senesced. It has to be emphasized that in September and October forbs contributed most to the total aboveground plant mass while the contribution of legumes and grasses was very small (Fig. 2). In September and October, *Petrorragia saxifragae* (a biennial forb) made up most of the forb mass. In the early phase of the herbs' life cycle (November) forbs were the most important component of plant mass in gaps (Table 2, Fig. 2).

Relationships between climatic factors and amount of biomass

To assess if the observed differences in plant mass among years were related to rainfall (P) and to the length of the dry period (DP), we performed multiple linear regressions including climate parameters.

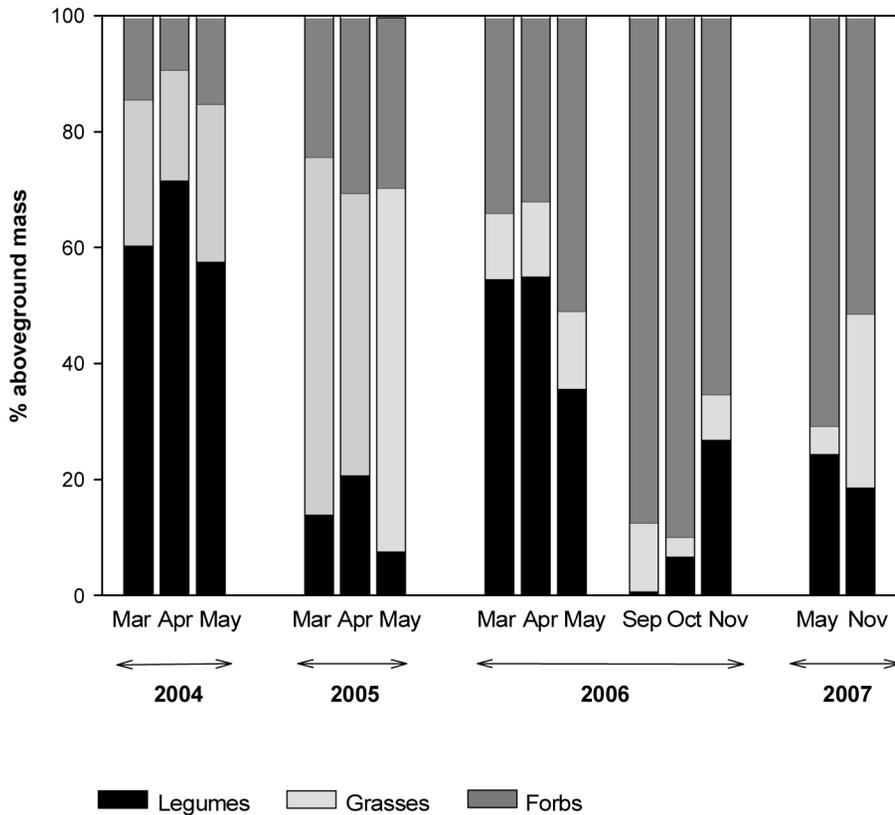


Fig. 2. Inter-annual changes in the proportion of legumes, grasses and forbs over the total aboveground plant mass.

In the early phase of the life cycle (November) belowground mass was negatively correlated to rainfall over the period September–November and positively correlated to the number of dry days in the same period (Table 3). At the end of the life cycle (May) belowground mass was significantly and negatively related to rainfall total over the whole growing season (November–May, Table 3).

The belowground/aboveground biomass ratio (B/A) in November was negatively correlated to total rainfall over the period September–November and positively correlated to the number of days without rain in the period (Table 3). Consequently, at the end of the life cycle (May) B/A was significantly and positively correlated to the number of days without rain over the whole growing season (November–May, Table 3).

Legumes mass in early spring (March) was positively correlated to January rainfall (P) and negatively correlated to January DP (Table 3). The increase in legume mass from March to April was positively correlated to P and negatively correlated to DP in the period (Table 3).

Relationships between biomass components

Legume, grass and forb mass were all significantly and positively correlated to aboveground mass in May (Table

4). In March only legume and forb mass were correlated to aboveground mass (Table 4). In November forb mass was correlated to aboveground mass (Table 4). The increments in aboveground mass and in legume mass in the period March–April were positively correlated (Table 4). Legume mass was negatively correlated to forb mass in November, whereas forb and grass mass were negatively correlated in May (Table 4).

Input of nitrogen from legumes, grasses and forbs to the soil

The amount of legume, grass and forb mass at the end of the life cycle and their relative nitrogen concentration were used to calculate the input of nitrogen to the soil in 2004 and 2005. As compared with 2005 tissue, N-concentration of legumes, grasses and forbs was higher in the year 2004. The abundance of legumes was responsible for marked differences between years in nitrogen input to the soil (Fig. 4). Consequently, soil N-concentration was higher in 2004 than in 2005 when herb mass was lower in legumes. It is worth noting that soil N-concentration increased from March to May in parallel to the increase in legume mass.

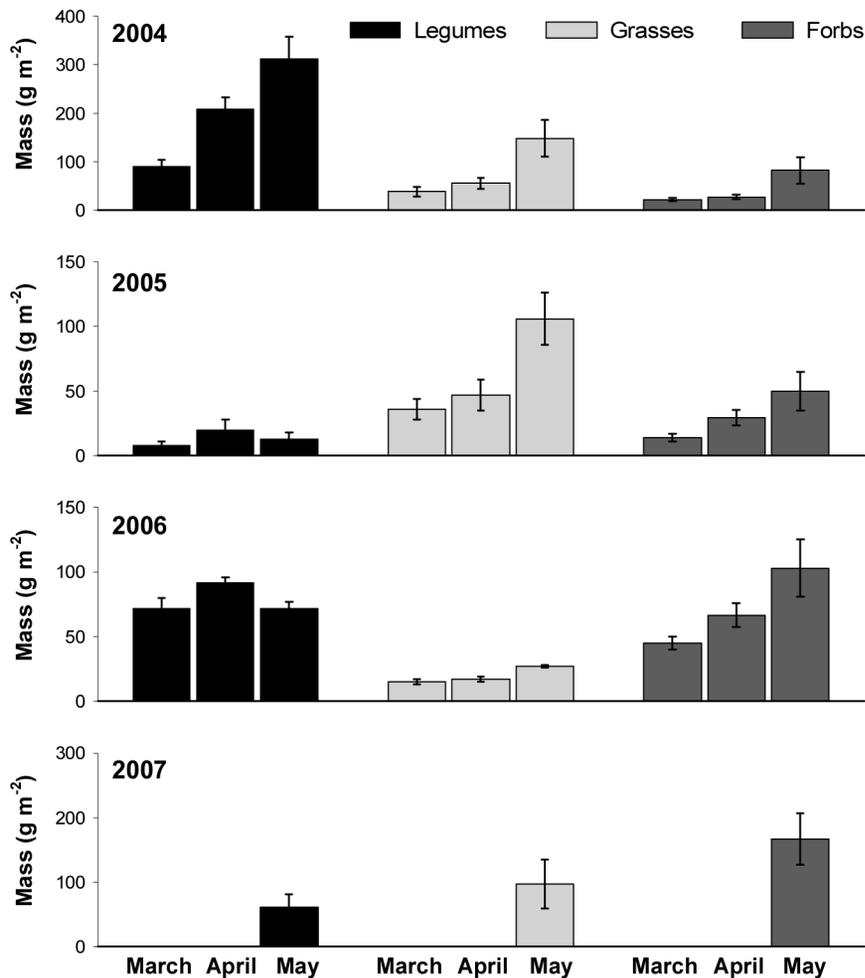


Fig. 3. Mass of legumes, grasses and forbs (g m^{-2}), determined in gaps of the low Macchia at Castel Volturno nature reserve in spring. Values are means of 18 measurements at each harvest. Note the different scale used for 2005 and 2006.

Decomposition of litter and soil organic matter

The decomposition of senesced herbs collected from gaps at the end of June 2004 was compared to the decomposition of leaf litter of *Phillyrea*, the most abundant shrub species at the study site. Herbs were richer than leaves of *Phillyrea* in lignin (20.6% versus 15.2%), had a higher water holding capacity (311% versus 91%) and a slightly lower nitrogen content (1.07% versus 1.37%). Sampling of senesced herbs was performed at the end of June when several leaves were already fallen (especially for legumes). Therefore, the material was relatively poor in nitrogen when compared to plants collected at the peak biomass in May (Fig. 4). The results of the microcosm experiment, performed under not limiting temperature and humidity conditions, showed that mass loss and lignin decomposition were significantly higher for herbs than for *Phillyrea* leaves. Nitrogen was

immobilized during decomposition in the decaying herbs while in *Phillyrea* only slightly decreased compared to the initial level (Fig. 5).

Laboratory measurements made on soil samples collected in December 2004 in gaps and of *Phillyrea* specimens showed that soil organic carbon and microbial biomass were somewhat higher in *Phillyrea* soil than in gap soil. By contrast, respiration per unit microbial biomass and the fraction of mineralized soil organic matter (coefficient of endogenous mineralization) were significantly higher in gap soils than in *Phillyrea* soils (Fig. 5).

Discussion

Plant productivity in gaps varied up to threefold (244–701 g m^{-2}) between years, and was lowest in years with the driest spring (2005 and 2006). Even higher (up to twentyfold)

Table 2. Total, aboveground and belowground phytomass (g m^{-2}) in gaps of the low Macchia at Castel Volturno nature reserve and main soil parameters measured in September and October 2006 (late summer production), in November 2006 and 2007 (early phase production of the vegetative cycle). Climatic parameters refer to the periods July–September, July–October for late summer production, and September–November for the early phase production. Values of biomass and soils parameters are means of 18 measurements at each harvest.

| | 2006 | | | 2007 |
|--|-----------|------------|-----------|-----------|
| | September | October | November | November |
| Total mass (g m^{-2}) | 250 ± 31 | 212 ± 21 | 90.6 ± 9 | 210 ± 22 |
| Aboveground mass (g m^{-2}) | 144 ± 12 | 104 ± 20 | 26 ± 3 | 41 ± 9 |
| Legumes (g m^{-2}) | 1 ± 0.2 | 7 ± 2 | 7 ± 2 | 10 ± 5 |
| Grasses (g m^{-2}) | 17 ± 2 | 3.5 ± 1 | 2 ± 0.6 | 2 ± 0.4 |
| Forbs (g m^{-2}) | 126 ± 38 | 94 ± 22 | 17 ± 3 | 29 ± 10 |
| Belowground mass (g m^{-2}) | 106 ± 5 | 108 ± 8 | 65 ± 6 | 169 ± 16 |
| Below/aboveground | 0.9 ± 0.2 | 1.6 ± 0.4 | 3.0 ± 0.4 | 5.7 ± 1.2 |
| Soil pH | 8.0 ± 0.1 | 8.0 ± 0.1 | 7.9 ± 0.1 | 7.8 ± 0.2 |
| SOM (%) | 5.2 ± 0.3 | 7.5 ± 0.9 | 5.5 ± 0.3 | 6.1 ± 0.4 |
| SWC (%) | 8.5 ± 0.6 | 10.1 ± 0.6 | 13 ± 0.7 | 13 ± 1.4 |
| P (mm) | 227 | 239 | 280.4 | 134 |
| T (°C) | 23.2 | 22.1 | 17.7 | 16.6 |
| Dry period | 78 | 107 | 76 | 77 |

were the changes in amount of legume mass. The highest mass production and the highest amount of legumes were measured in the year 2004. This suggests a dominant effect of legumes on productivity of gaps. Legumes are known to improve nutritional status and growth of other plants by improving soil nutrient composition due to nitrogen fixation (Callaway 1995). The positive effect of legumes on other species and the consequent increase of productivity has been reported for many natural and agricultural systems (Spehn et al. 2002). The pattern of mass production in gaps throughout the study years is

consistent with such reports. Production in gaps declined dramatically when the legume fraction dropped (from about 60% of aboveground plant mass in 2004 to less than 10% in 2005), and increased again in the year 2006 when legumes increased to about 35%.

The relative proportion of legumes, grasses and forbs may be determined by their tolerance to aridity. Legumes, because the symbiotic N_2 -fixation, are most sensitive to drought (Serraj et al. 1999). Our work demonstrates that legume productivity is dependent on rainfall. Also nitrogen concentration in legumes was lower in the dry 2005

Table 3. Multiple linear regressions with the climate variables rainfall (P) and dry period (DP) explaining variations of biomass. Regression coefficients for P and DP are reported. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns: not significant.

| | | P | DP |
|------------------------------------|--------------------------|------------|-------------|
| Belowground mass (B) | November B vs Sept–Nov | –0.866*** | +0.866*** |
| | May B vs Nov–May | –0.586*** | +0.586 (ns) |
| Belowground/aboveground mass (B/A) | November B/A vs Sept–Nov | –0.520* | +0.512* |
| | March B/A vs Jan | –0.650*** | +0.650*** |
| | May B vs Nov–May | –0.451(ns) | +0.451* |
| Legume mass (L) | March L vs Jan | +0.740*** | –0.740*** |
| | L increment vs Mar–Apr | +0.743*** | –0.743* |

Table 4. Linear regression between components of the biomass. Spearman's coefficients are reported. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Parameters | Date | r |
|---------------------------------|-------------------|-----------|
| Legume mass vs aboveground mass | March | +0.614** |
| | Increment Mar–Apr | +0.586** |
| | May | +0.732*** |
| Legume mass vs forb mass | November | −0.520* |
| Grass mass vs aboveground mass | May | +0.450* |
| Forb mass vs aboveground mass | November | +0.590** |
| | March | +0.527** |
| | May | +0.409* |
| Forb mass vs grass mass | May | −0.338* |

than in the wet year 2004, likely due to nitrogen fixation constraints. Finally, the sensitivity to drought is responsible for a shorter life cycle of legumes in years with drier springs.

Forbs seem to be better adapted to drought in the gap community. They were the most abundant fraction of aboveground plant mass in 2006 and 2007, the years with the longer drought periods. Moreover, forbs exhibited the largest mass increments late in the growth season when rainfall decreased. Forbs are the main fraction (about 90%) of gap plant cover in September and October (late summer production), whereas their importance during spring is much lower.

Grasses, like forbs, exhibited the largest biomass increments late in spring, when legumes stopped growing and soil nitrogen was more abundant.

Competitive interactions between functional herb groups are suggested by the negative relationships occurring between forbs and grasses in May and between forbs and legumes in November.

Belowground biomass was produced mostly in the early phase of the vegetative cycle (November–March) and did not increase during later phases. Biomass allocation to roots varied from year to year depending on rainfall, as suggested by the significant negative relationships of both belowground mass and belowground/aboveground ratio with rainfall, and by the positive relationship with the number of days without rain. Biomass allocation to roots allows herbs to cope with low soil water availability. Increased root-to-shoot ratios in response to lengthened dry intervals between rain events have been reported by Fay et al. (2003) for a tall grass prairie ecosystem in northeastern Kansas. We could speculate that the high belowground/aboveground ratio in the year 2005 and 2007 was, at least in part, dependent on the low fraction of legumes in the gap community and likely advantageous for nutrient exploitation.

Although annual species in gaps are strictly drought avoiders, they are able to somehow cope with seasonal and inter-annual variability in precipitation. The occurrence of different functional groups (legumes, grasses and forbs) with different growth patterns extends the suitable time period for biomass production. The fractions of the three different functional groups vary from year to year with the species most sensitive to drought reducing their abundance in favour of the most resistant species in the drier years. Changes in species composition and abundance in Mediterranean grass lands in response to inter-annual variability in total precipitation have been reported by Figueroa and Davy (1991). Furthermore, broad-scale surveys (Ehrman and Cocks 1990) have shown that legume populations usually are much smaller in drier than in wetter Mediterranean grass lands in Syria.

Because legumes are the most sensitive group, water shortage entails the reduction of nitrogen fixation and thus shortage of a limiting nutrient with the consequent reduction of biomass production. In conclusion, inter-annual variation in rainfall affects plant community composition in gaps and thereby ecosystem function. The sandy soil, characterized by poor water retention, further enhances aridity and limits plant growth and microbial activity (De Marco et al. 2005). Biomass production is likely constrained by an interaction between climatic and biogeochemical conditions. The year-to-year variation in biomass production and in the fraction of legumes is responsible of a variable flux of carbon and nitrogen into the soil. The main observed effect of legume abundance is the increase of nitrogen concentration in soil during the growth period. The high concentration of nitrogen in grass and forb tissue during the year with the highest legume production is likely a consequence of N-fixation by legumes. In agreement with these results, Rodriguez et al. (2007) found that in a heath land in northwest Spain the main effect of legume presence was an increase in nitrification rate and of

N-uptake by plants in the understorey. They found a lower level of microbial biomass-N under legumes, i.e. a lower level of N immobilized by soil microbes, that may result in enhanced N-losses from the ecosystem. After the season with the highest legume production (2004), no increase in the soil N-pool was observed in gaps, suggesting that the system loses nitrogen probably through leaching and

denitrification (Castaldi and Aragosa 2002), particularly under wet conditions in late autumn and winter when annual herbs are just establishing and have low growth rates. By contrast, the evergreen shrub cover that is able to

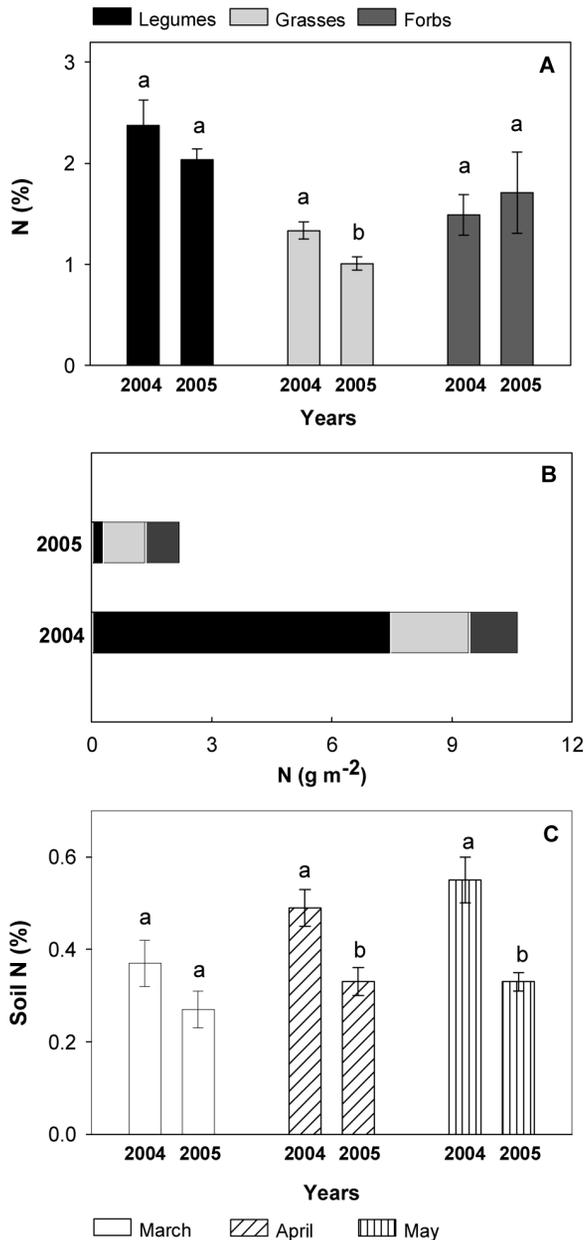


Fig. 4. N-concentration in legumes, grasses and forbs at the peak standing biomass in May 2004 and in May 2005 (A), amount of N reaching the soil with the peak mass of legumes, grasses and forbs (B), changes in N-concentration in soil gaps during the spring growth season (C).

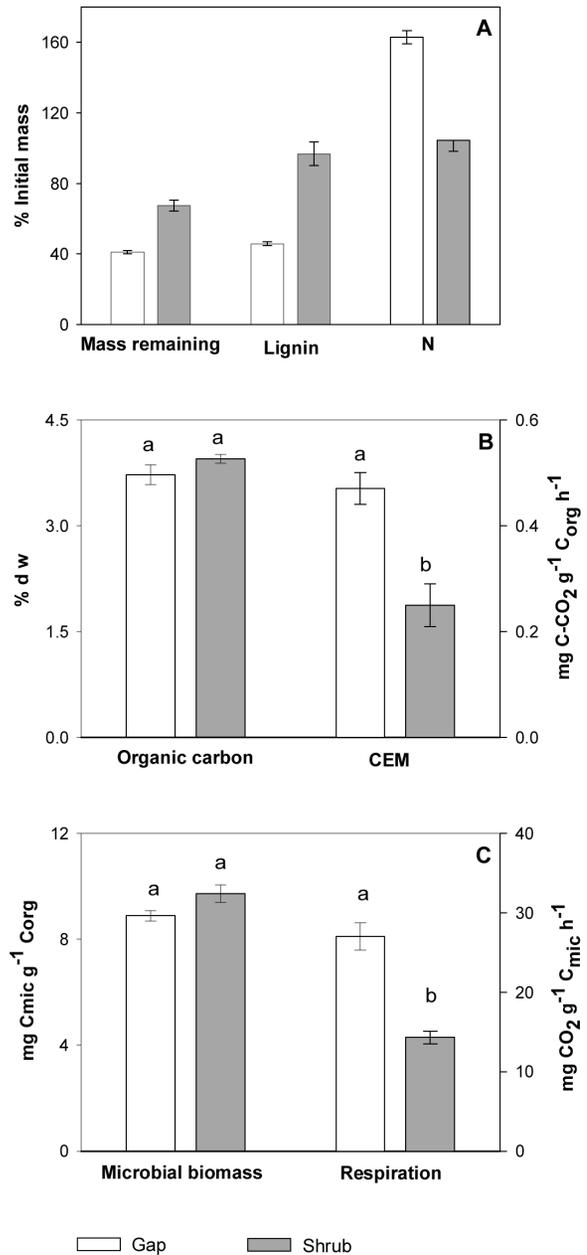


Fig. 5. Mass remaining (% initial mass), and lignin and nitrogen amount (over % initial mass) after 215 days of incubation in laboratory microcosms; values are means of 7 measurements for mass remaining and mean of 3 measurements for lignin and nitrogen amount (A), Organic carbon (%) and coefficient of endogenous mineralization (CEM) (B), microbial biomass and respiration (C), measured on fresh soil samples collected on December 2004 in gaps and in the understorey of *Phillyrea* shrubs; values are mean of 5 measurements.

fix carbon at any favourable time period during the year is more prone to retain and recycle nutrients.

Even in the most favourable year, herb aboveground mass in gaps was not more than about 25% of the aboveground shrub mass in the low Macchia at the Castel Volturno nature reserve. Thus shrub replacement by annual grass lands dramatically reduces carbon storage. Moreover, annuals' mass result in the input of more easily degradable organic matter to the soil. Our work demonstrates that herbs are more decomposable than shrub leaves. In addition, organic matter of gap soil is less stable and exhibits a higher mineralization coefficient (CEM). This result is consistent with that of a study comparing the stability of organic carbon pools in several Mediterranean soils, including the low Macchia and the gaps of Castel Volturno (Rutigliano et al. 2001). Microbial activity is dependent on resources and climatic factors alike and therefore varies seasonally both in shrub soil (De Marco et al. 2005) and in gap soil. CEM values reported here refer to December. In gaps, CEM values were similar in December and May, at the peak biomass production, and somewhat higher compared to CEM measured in early spring (data not shown); microbial activity during summer drought is strongly inhibited, resulting in very low CEM value (data not shown). Based on the simultaneously measured December CEM (0.25 and 0.47 mg CO₂-C g⁻¹ C_{org} h⁻¹, respectively in shrub and gap soils) and on the quantity of organic matter occurring in the 0–10 cm soil layer (4.65 and 3.95 under shrubs and in gaps, respectively), the potential loss of carbon from gaps might be 1.6 times higher than the loss of carbon from shrub soil. We may conclude that the change of plant cover from shrubs to annual plants can strongly influence ecosystem functions in terms of biomass production, decomposition and soil organic matter stability.

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