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THE SOIL ENVIRONMENT FOR *TUBER MAGNATUM* GROWTH IN MOTOVUN FOREST, ISTRIA

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The mixed oak forest located near the town of Motovun is a well-known white truffle (*Tuber magnatum* Pico) producing area of the Istria region. Motovun Forest covers a 900-ha area in the fluvial plain of the Mirna River, which flows into the Adriatic Sea through a hilly landscape originating in a sedimentary sequence of a Triassic-Eocene carbonatic platform and Eocene-Oligocene Flysch turbidites. *T. magnatum* production has been decreasing in the last 10 years and a study was specifically performed in an attempt to explain this. Productive soils of the valley bottom were compared with unproductive soils on the slopes, the latter being drier, thinner and more developed than the former. *T. magnatum* carpophores are not found all over the fluvial plain and Motovun Forest was further subdivided into productive, unproductive and occasionally productive areas. All soils of the valley bottom were thick and continuously rejuvenated by the frequent arrival of fine sediments from slopes, but only unproductive ones were characterized by water saturation in some periods of the year. The soil comparison proved the need of *T. magnatum* for an alkaline, moist, very well drained and aerated soil environment. Moreover, soils suitable for *T. magnatum* should be neither too dry nor too moist. In Motovun Forest, the decrease in production has been taking place in conjunction with public works that have modified the hydraulic equilibrium of the area causing an overall drying of the forest soil.

Key words: *Tuber magnatum*, soil, Motovun forest, Croatia

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Miješana motovunska hrastova šuma jedno je od najznačajnijih područja za sakupljanje bijelog tartufa (*Tuber magnatum* Pico) u Istri. Motovunska šuma pokriva područje od 900 ha u dolini rijeke Mirne, koja utiče u Jadransko more prolazeći kroz brežuljkasti pejzaž stvoren sedimentacijskim procesima na trijas-eocenskoj vapnenačkoj podlozi i eocen-oligocenskim fliš procesima. Bijeli tartuf pronalazi se samo u nizinskom dijelu doline, a pronađene količine u zadnjih nekoliko godina opadaju.

Istraživanje je obavljeno s ciljem da se utvrde karakteristike tla u području Motovuna pogodnog za rast tartufa, i da se pokuša objasniti uzrok pada u njihovoj proizvodnji. Karpofore bijelog tartufa ne pronalaze se u cijelom riječnom području, zato je motovunska šuma podijeljena u produktivna, neproduktivna i povremeno produktivna područja. Produktivna područja u donjem dijelu šume uspoređena su s manje vlažnim, tanjim i bolje razvijenim neproduktivnim područjima na padinama. Sva tla u nizinskom dijelu doline su debela i slabo razvijena zahvaljujući stalnom spuštanju finog sedimenta s padina, ali su samo neproduktivna područja karakterizirana vodenim zasićenjem u nekim periodima u godini. Usporedba tala dokazala je potrebu bijelog tartufa za vlažnim, dobro dreniranim i lužnatim tlom, uz specifične zahtjeve za dobrim prozračivanjem i rahlošću.

Tlo pogodno za rast bijelog tartufa ne smije biti previše suho, ni previše vlažno. Smatramo da je u motovunskoj šumi došlo do pada proizvodnje bijelog tartufa zbog niza javnih radova koji su promijenili vodni režim područja uzrokujući sušenje šumskog tla.

Ključne riječi: *Tuber magnatum*, tlo, motovunska šuma, Hrvatska

INTRODUCTION

The hypogeous ascomycete *Tuber magnatum* Pico lives in ectomycorrhizal symbiosis with oaks, hornbeams, poplars, willows and few other tree species of the Mediterranean regions. Unlike other ectomycorrhizal fungi (HARVEY *et al.*, 1976), the mycelia of *T. magnatum* are not concentrated in or immediately under organic horizons, but grow in the surface mineral layers of soil, where edible carpophores are found from late August to December with the help of specifically trained dogs. *T. magnatum* – the »truffle of Alba« – is best known from Italy, but it also grows in Croatia and Slovenia. The environmental characteristics of Croatian *T. magnatum*-producing habitats remain to be accurately described, although Italian researchers have shown that *T. magnatum* lives in alkaline soils rich in calcium carbonate (MANNOZZI-TORINI, 1965) – a condition common to many heterogeneous Mediterranean soils – characterized by two more restrictive conditions: a very high soil macroporosity – the portion of soil volume where air and water flow – and a microclimate characterized by a short dry season (LULLI *et al.*, 1991; BRAGATO *et al.*, 1992; LULLI & PRIMAVERA, 2001).

In Croatia, an important production area for *T. magnatum* is the forest located near the Istrian town of Motovun (Fig. 1), where truffle production has been known since the 1930s. Motovun Forest is what remains of ancient common oak (*Quercus robur* L.) and narrow-leaved ash (*Fraxinus angustifolia* L.) forests that covered the fluvial plains of the northern Adriatic Sea area for thousands of years. From the 15^{th} to the 19^{th} century the area produced valuable ship timber. In the second half of the 15^{th} century, the Republic of Venice specifically entrusted a high officer – the »Capitano della Valle« – with the forest and water management of the area. In the 19^{th} century the wood cover decreased from the original 1800 ha to 900 ha and the forest composition changed after the introduction of iron hulls into the shipbuilding industry. Motovun Forest has remained a state property and is now managed by the Hrvatske Šume. Two other important changes affected the forest in the last forty years. Between 1967 and 1980 a new Mirna riverbed was excavated to bypass the low lying areas of the valley bottom and a road was built on its right bank (Fig. 1). Afterwards, a water reservoir was built along the Butoniga River – the main tributary of the Mirna River – to supply the water system of Southern Istria. Both public works modified the hydrographic network and the quantity of water flowing in the valley bottom, causing an overall drying of the soil under Motovun Forest.

The present study derived from observations by the Istrian truffle-searchers associations of a net decrease in truffle production in Motovun Forest similar to the decline that occurred in Italy in the last thirty years. The investigation was aimed at: i) characterizing the soil environment of the Motovun area suitable for truffle production; ii) comparing its features with those of the productive areas of the Italian valley bottoms; and iii) explaining why a decrease in production is now taking place.

MATERIALS AND METHODS

The study area

Motovun Forest is located at 10–13 m a.s.l. and covers a 25-km long and 1–1.5-km wide area in the fluvial plain of the Mirna River – which flows into the Adriatic Sea to the south of Novigrad – and the Butoniga River. The Motovun area is characterized by hills 300 to 400-m-high with slope gradients ranging from 5 % to 65 %. The hilly landscape was created by the outcrop of the sedimentary sequence of a Triassic-Eocene carbonatic platform and Eocene-Oligocene Flysch turbidites. The erodibility of Flysch sediments and the slope gradient are responsible for the large production of fine sediments that floods concentrate in the valley bottom, thus creating very thick, scarcely differentiated alluvial deposits. Because of the continuous erosion of mineral particles from the slopes and their deposition in the valley bottoms, the soils of the Motovun area are scarcely developed. According to the soil map of Croatia – Pazin 1 sheet (VIDAČEK *et al.*, 1978) – the most widespread soil units of the Motovun area are the AG-HG unit in the valley bottom, and

Fig. 1. Photo of investigated area (fluvial plain of River Mirna).

the RI-PS and S-R units on the slopes. Their features, obtained from the map legend, are reported in Tab. 1.

As far as the climate is concerned, the 1961–1990 meteorological data recordings of the nearby Pazin station report a mean annual temperature of 11.1 °C. The months with the mean minimum and maximum values are January and July with 2.5 °C and 20.4 °C, respectively. The rainfall is minimum in July – 72 mm – and maximum in November – 134 mm – with a mean annual value of 1168 mm. According to the classification of KÖPPEN & GEIGER (1936), the Motovun area has a subcontinental temperate climate of type *Cf w'w«b*. This kind of climate is typical of the North Adriatic coast, and the Mirna valley bottom is a corridor along which the Adriatic Sea affects the climate of the internal part of Istria. Thanks to their climatic conditions, the Central and Western areas of the Istrian peninsula belong to the Central Europe biogeographic region (EUROPEAN ENVIRONMENT AGENCY, 2003). In the Motovun area, the most relevant phytocenosis is a mixed oak wood belonging to the *Querco roboris – Carpinetum betuli submediterraneum* Bert. The most widespread tree species of Motovun Forest are those of many European fluvial plain landscapes: common oak, narrow-leaved ash, oriental hornbeam (*Carpinus orientalis* Mill.), common maple (*Acer campestris* L.), elm (*Ulmus minor* Mill.), grey alder (*Alnus incana* Moench.), poplars (*Populus* spp.) and willows (*Salix* spp.). The composition of the wood cover has been strongly influenced by man. Until the first half of the 19th century, common oak formed more than 90 % of the wood cover of Motovun Forest. Nowadays, it has decreased to 45 % of the wood cover, the remaining part being mainly represented by narrow-leaved ash and the Euro-American poplar, which was introduced in the Mirna valley in single-species stands in the sixties.

Tab. 1. Main features of the investigated soil units (VIDAČEK *et al.*, 1978).

Characteristics	Soil units AG-HG	RI-PS	S-R
Bedrock and parent material	present alluvial sediments	Eocene-Oligocene Flysh, silty marl and silty sandstone sequences	Eocene-Oligocene Flysh, densely stratified silty marl and silty sandstone sequences
Slope gradient	0–3 %	0–8%	16–65%
Surface stoniness	absent	0–2%	10–25%
Textural classes	Loamy clay to Clay	Loamy to Clay	Loamy clay to Clay loam
Main soil types	– Hydroameliorated Amphigleic and Hypogleic Eugley (80%); – Hydroameliorated Alluvial Semigley (20%)	– Rigosols (40%); – Eutric and Dystric Pseudogley (20%); – Rendzina (20%); – Regosols (20%).	– Regosols (80%); – Rendzina (20%).

Stratification and selection of sampling locations

The study area was subdivided into 7 strata (Fig. 2) on the basis of the soil map and of the experiences of truffle searchers. Even if *T. magnatum* carpophores are found only in the AG-HG soil unit, the unproductive RI-PS and S-R soil units on slopes were respectively included in Strata no. 6 and 7 (St 6 and St 7) so that their soils could be compared with those of the fluvial plain. The Mirna and Butoniga valleys were subdivided into 5 strata following the indications of truffle searchers. The subdivision of the productive area into St 1, St 2 and St 4 is based on the stream that originated their sediments. According to local truffle searchers, the largest and best-shaped carpophores are found in St 4. In the other two strata of the valley bottom, on the other hand, carpophore production is absent (St 3) or limited to the driest years, with low-quality carpophores (St 5).

Sampling locations were selected following a stratified random sampling scheme. The Universal Transverse Mercator (UTM) metric coordinates of sampling locations were selected with the aid of a random number generator: once a pair of UTM coordinates was chosen, the area was located in the map and selected or discarded according to whether the location was inside or outside the stratum of interest. The procedure was iterated until all sampling locations were selected. All strata

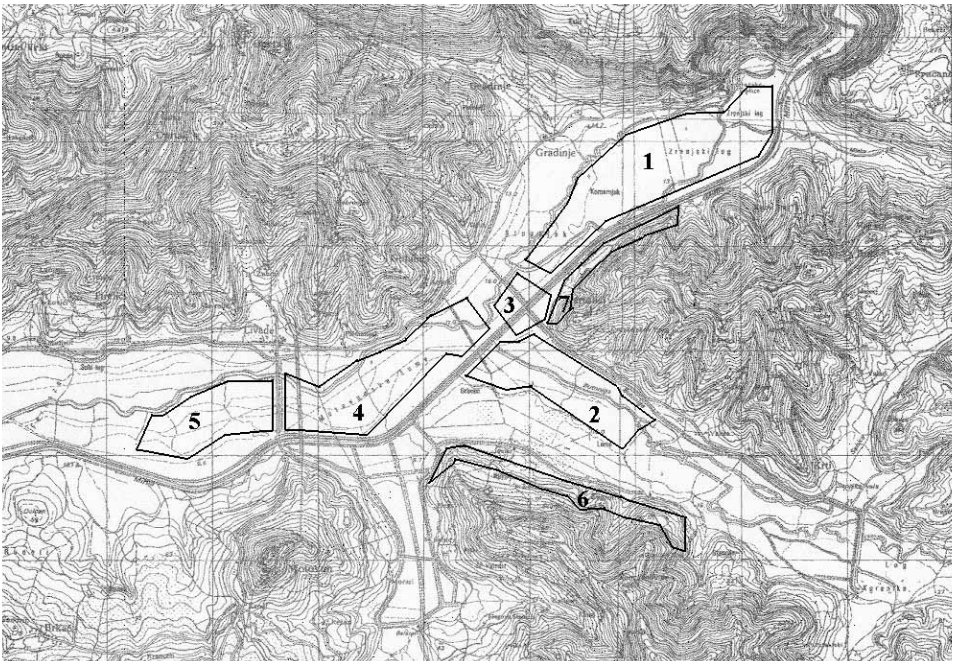

Fig. 2. The Motovun area and the investigated strata. In the valley bottom, strata No 1, 2 and 4 are productive; No 3 is unproductive and No 5 occasionally unproductive. The unproductive strata No 6 e 7 are located on slopes.

but St 3 and St 7 were sampled in 8 locations on the basis of an approximate sample density of 1 observation every 10 ha. *St 3* and *St 7* covered much smaller areas. They were respectively sampled in 4 and 5 locations.

Field observations and laboratory analyses

During the summer of 2002, sampling points were located on the ground with a Garmin 12 GPS instrument. An area of about 100 m^2 was delimited around each point and the following features were recorded inside it: wood and undergrowth cover and composition, geomorphology, slope aspect, lithology. The soil morphological features of the locations were observed in samples augered to a depth of 100 cm – or less in the presence of a rocky layer. Augered samples were subdivided into genetic horizons and characterized in terms of: horizon thickness; Munsell colour of the matrix; colour, size and area percentage of gleys and mottles; structural organization of mineral particles; effervescence to 1 *N* HCl. Carpophores are usually found within a few centimetres of the soil surface. In each location, an undisturbed sample was then collected driving a steel cylinder into the 0–10 cm soil layer. The sample was removed from the cylinder, transported to the laboratory, air-dried and analysed for water content, bulk density, grain size distribution (pipette method), pH in water, organic carbon content (Walkley-Black method) and calcium carbonate content (calcimetry) (Ministero per le Politiche Agricole, 1997; 2000).

RESULTS AND DISCUSSION

The soil types

Tab. 2 summarizes the soil morphological features observed in the investigated strata. Some of them are also illustrated in Fig. 3, which shows the first 25 cm of four undisturbed samples of St 1, St 3, St 5 and St 6 strata, respectively. Augered samples were formed by two or more of the horizons that are reported in the first column of Tab. 2. Soil horizons are the soil layers that environmental processes differentiate while acting on the underlying soil parent material. The organic OF horizon (St 3) is constituted by partially decomposed organic materials. The mineral A and AC horizons originate from the accumulation of organic matter in mineral layers located near the surface. The mineral B horizon (St 6 and St 7) is produced by long-lasting soil processes that, in the Motovun area, are represented by the downward migration of calcium carbonates and the increasing structural organization of mineral particles.

Soils of the slopes look quite different from those of the valley bottom in terms of colour, structural organization and horizon sequence. Even if soil erosion has made them thinner, the St 6 and St 7 soils are more developed than those of the fluvial plain because they show a redder, 10YR hue (Fig. 3); a well-organized structure; and a more or less developed B horizon in depth. The difference between St 6 and St 7 in terms of soil thickness is instead related to the Flysch facies from which

Tab. 2. Morphological soil properties of the investigated locations.

Horizon	Stratum						
	St 1	St 2	St 3	St 4	St 5	St 6	St 7
	valley bottom, productive	valley bottom, productive	valley bottom, unproductive	valley bottom, productive	valley bottom, occasionally productive	slope, unproductive	slope, unproductive
No. of locations	8	8	4	8	8	8	5
OF							
Depth, cm			1,5–0				
Munsell colour			2.5YR 2/1				
A							
Depth, cm	0–10	0–8	0–15	0–8	0–15	0–8	0–5
Munsell colour	2.5YR 4/2	2.5YR 4/2	2.5YR 4/1	2.5YR 4/2	2.5YR 4/2	10YR 3/3	10YR 3/2
Mottles			2 mm, 10 %				
Structure grade	weak	weak	weak	weak	weak	moderate	moderate
AC							
Depth, cm	10–33	8–30		8–33			
Munsell colour	2.5YR 4/3	2.5YR 4/3		2.5YR 4/3			
Structure grade	weak	weak		weak			
BC/Bw							
Depth, cm						8–39	5–15
Munsell colour						10YR 4/4	10YR 4/4
Structure grade						strong	strong
C							
Depth, cm	33–100+	30–100+	15–100+	33–100+	15–100+	39–65	15–31
Munsell colour	2.5YR 5/4	2.5YR 5/4	2.5YR 5/5	2.5YR 5/4	2.5YR 5/4	10YR 4/6	10YR 4/6
Mottles			4 mm, 30 %		3 mm, 15 %		

the two groups of soils developed. The gentler slope of St 6, in particular, made its soils more stable, thicker and more easily cultivable than those of St 7.

Unlike those of the slopes, the soils of the valley bottom are very deep, their mineral particles are weakly organized and their A horizon is slightly different from the original alluvial sediments. Even if the St 1 – St 5 soils were originated by

Fig. 3. Undisturbed 25 cm long samples of four locations belonging, from left to right, to St 1, St 5, St 3 and St 6 soils.

the same alluvial depositions associated with the periodical flooding of the investigated fluvial plain, the soils are not homogeneous all over the area. The truffle-producing St 1, St 2 and St 4 strata have an intermediate AC horizon that is not present in St 3 and St 5 strata. The unproductive or occasionally productive strata, on the contrary, show mottles – a symptom of periodical water saturation of soil – near the soil surface. The distance of mottles from the surface and the area percentage they occupy in the vertical section of a soil core indicate the intensity of soil watering processes: the shorter the distance and the larger the area percentage, the stronger the effect of water saturation on a soil location. From this point of view, St 3 is affected by stagnation of flooded water for longer periods than St 5. Two other features are useful to define the soil environment of Motovun Forest. In all strata but St 3, earthworm casts were commonly observed on the surface, whereas in St 3 the surface was dominated by poorly decomposed wood litter materials.

In the very young alluvial soils of Motovun Forest the differentiation between A, AC and C horizons is due to the way the litter is decomposed, mixed with mineral particles and transported into the soil. The features of the St 1 – St 5 soils reported in Tab. 2 suggest which are the processes involved in the organic matter cycle in Motovun Forest soils, and indicate the eco-functional properties of a soil environment suitable for *T. magnatum* growth. The wood litter released in winter usually disappears by the end of June due to the activity of earthworms (Fig. 3). According to the morphogenetic classification of humus forms of JABIOL *et al.* (1995), the soil environment of Motovun Forest belongs to the Eumull class because organic materials are rapidly transformed and incorporated into the soil thanks to the vertical-moving activity of anecic earthworms that release them in depth. The sensitivity of anecic earthworms to anaerobiosis explains also the lack of an AC horizon in St 3 and St 5 because both strata are influenced by a shallow water table and the seasonal inundation of their surface. In St 3, water stagnation in autumn and winter is prolonged enough to drive earthworms away, whereas in St 5 a periodical rise of the water table up to 15 cm from the surface limits the movement of earthworms to the 0–15 cm soil layer. In St 3, the functions of earthworms are probably performed by arthropods, which move easily on the soil surface but are less efficient in the transformation of organic materials, releasing the slightly transformed organic materials only on the surface of soil aggregates (JABIOL *et al.*, 1995). The overall effect, illustrated in Fig. 3, is the creation of an OF horizon, the development of a scarcely mixed A horizon, and the abrupt horizon change from a yellowish grey A to a yellowish brown C horizon, properties that are all diagnostic to assign the St 3 humus form to the Dysmull class.

The characteristics of the St 3 soil environment suggest that the lack of *T. magnatum* carpophores may be due to water stagnation in the soil and its related chemical and biochemical processes. The simultaneous presence of an organic OF horizon and a mottled A horizon can be used to delineate fluvial plain areas under mixed oak wood that are unsuitable for *T. magnatum* production. The St 5 limited production also suggests that all portions of a fluvial plain that are periodically saturated by water under the A horizon are to be considered unsuitable for the white truffle.

The vegetation cover

While soils and humus forms of the Motovun area were only partially affected by man, its vegetation cover and composition have been strongly influenced by forestry and agriculture. Tab. 3 reports the percentages of wood and undergrowth cover in the investigated area. Overall means are of 45 % and 15 % for wood and undergrowth cover, respectively, but are higher in St 3 due to periodical floods that limit the timber exploitation in this area. The wood cover is large also in St 2, an area less involved in wood cutting in the near past, whereas large undergrowth cover values were recorded in the sloping St 6 and St 7 strata, where a widespread re-naturalization is taking place in slope terraces that were cultivated in the past.

Tab. 3. Mean and standard error (in brackets) of the wood and undergrowth cover[†]. Values with the same letter are not significantly different at *P*< 0.05 when compared with the Student's *t* test.

Settore	Cover, %			
	wood		undergrowth	
St 1 valley bottom, productive (*n=8*)	41 (3)	a	10 (2)	a
St 2 valley bottom, productive (*n=8*)	51 (5)	ab	14 (2)	ab
St 3 valley bottom, unproductive (*n=4*)	59 (8)	b	23 (1)	c
St 4 valley bottom, productive (*n=8*)	39 (2)	a	8 (2)	a
St 5 valley bottom, occasionally productive (*n=8*)	44 (4)	a	16 (2)	ab
St 6 slope, unproductive (*n=8*)	39 (2)	a	18 (1)	bc
St 7 slope, unproductive (*n=5*)	45 (3)	a	15 (3)	ab

[†] The number of locations is the same reported in Table 2.

The composition of the wood and undergrowth cover is recorded in Tab. 4, which reports the percentage of wood cover interested by the main tree species of the Motovun area (common oak, narrow-leaved ash, grey alder) and the frequency of secondary wood and undergrowth species. Also in this case slopes are different from the valley bottom. Narrow-leaved ash and oriental hornbeam gradually thin out – and hawthorn (*Crataegus monogyna* Jacq.) is almost absent – as the height of the slope increases, and are replaced by grey alder, common maple and cornelian cherry (*Cornus mas* L.). The different wood composition is probably due to the different quantity of water the thick soils of the fluvial plain and the thin soils on slopes make available to plants, the latter also losing part of the rainwater by surface runoff. Some differences concern valley bottom strata too. Common oak and narrow-leaved ash are usually present in similar percentages and represent more than 90 % of Motovun Forest cover. Their presence, however, shows a complex distribution because common oak prevails over narrow-leaved ash in all strata but St 3, where narrow-leaved ash is more tolerant of water stagnation, and St 5, where the wood has been recently harvested under a shelter wood silvicultural system. Finally, it must be stressed that the wood composition directly affects truffle production because only common oak and oriental hornbeam are *T. magnatum* symbionts.

The truffle-producing soil layer

T. magnatum carpophores are usually found in the 0–10 cm soil layer and the physico-chemical properties of such layer can have a fundamental role for

Tab. 4. Mean and standard error (in brackets) of the percent of wood cover occupied by the main forestry tree species and frequency of secondary wood and undergrowth species[†]. Values with the same letter are not significantly different at $P< 0.05$ when compared with the Student's *t* test.

Stratum	Percentage of wood cover occupied by			Percentage of locations with			
	Common oak (*Qercus robur*)	Narrowleaf ash (*Fraxinus oxycarpa*)	Grey alder (*Alnus incana*)	Oriental hornbeam (*Carpinus orientalis*)	Common maple (*Acer campestre*)	Hawthorn (*Crataegus monogyna*)	Cornelian cherry (*Cornus mas*)
St 1 valley bottom, productive	54 (10) b	21 (3) a	–	63	38	88	25
St 2 valley bottom, productive	59 (10) b	22 (3) a	–	75	50	38	50
St 3 valley bottom, unproductive	26 (9) a	66 (19) b	–	50	–	75	25
St 4 valley bottom, productive	53 (9) b	43 (10) b	–	75	25	75	38
St 5 valley bottom, occasionally productive	23 (5) a	69 (6) b	–	43	14	100	57
St 6 slope, unproductive	50 (9) b	15 (5) a	24 (10)	25	50	25	63
St 7 slope, unproductive	56 (7) b	20 (6) a	16 (8)	20	40	–	40

[†] The number of locations is the same reported in Table 2.

carpophore growth. Such properties are summarized in Tab. 5, where data are compared with Student's *t* test.

The grain size distribution on the slopes is coarser than in the valley bottom. The sand fraction, in particular, decreases from 15–22 % on the slopes to 5–11 % in the fluvial plain. The sand content is also related to the Flysch facies of the slopes; the sediments are coarser in steep St 7 soils. The grain size distribution in the valley bottom is instead influenced by the fluvial dynamics. From this point of view, the clay fraction is quite meaningful because its sedimentation is strongly influenced

Tab. 5. Mean and standard error (in brackets) of some quantitative attributes recorded in the 0–10 cm soil layer†. Values with the same letter are not significantly different at $P<$ 0.05 when compared with the Student's t test.

Stratum	Sand, %	Silt, %	Clay, %	Bulk density, kg L^{-1}	Organic C, g kg^{-1}	pH	Ca carbonates, %
St 1 valley bottom, productive	10.5 (1.3) ab	70.6 (1.4) c	18.9 (1.7) a	1.10 (0.05) a	37.5 (4.1) a	7.83 (0.05) b	33.4 (0.7) b
St 2 valley bottom, productive	9.8 (2.3) ab	64.6 (2.0) bc	25.6 (3.0) ab	1.14 (0.03) a	35.9 (2.2) a	7.73 (0.02) b	33.2 (1.3) b
St 3 valley bottom, unproductive	5.4 (0.8) a	53.8 (2.4) a	40.8 (2.9) c	1.10 (0.02) a	33.0 (2.1) a	7.29 (0.03) a	27.8 (1.4) b
St 4 valley bottom, productive	10.2 (1.4) ab	66.7 (2.3) bc	23.2 (2.5) ab	1.10 (0.04) a	45.5 (3.8) a	7.69 (0.07) b	29.2 (0.7) b
St 5 valley bottom, occasionally productive	8.0 (1.0) a	61.8 (1.7) b	30.2 (2.6) b	1.05 (0.08) a	44.1 (2.6) a	7.78 (0.05) b	30.1 (1.2) b
St 6 slope, unproductive	15.3 (1.0) b	52.6 (1.4) a	32.1 (2.2) b	1.37 (0.07) b	30.8 (3.1) a	7.23 (0.16) a	1.4 (0.6) a
St 7 slope, unproductive	22.4 (2.4) c	51.2 (1.7) a	26.4 (1.8) ab	1.40 (0.07) b	44.0 (8.1) a	7.65 (0.09) b	6.1 (1.4) a

† The number of locations is the same reported in Table 2.

by the energy of floods and clay particles accumulating in the lower areas of the fluvial plain, where water tends to stop longer. In the Mirna and Butoniga valleys, the clay fraction increases from 20 % in productive strata, to about 30 % in the occasionally productive St 5, and to more than 40 % in the unproductive St 3 area. The clay content is not an indicator in itself of soil suitability for truffle production. The clay content in the unproductive soils of St 3 is, for instance, comparable to the values recorded in the Acqualagna territory (LULLI *et al.*, 1993), one of the most suitable areas for *T. magnatum* in Italy. This notwithstanding, grain size distribution is useful when examined in the environmental context of interest: in Motovun Forest it is another characteristic proving that productive and unproductive strata differ in the hydraulic behaviour of their soils.

Contrary to grain size distribution, bulk density does not change in the valley bottom strata, where its general mean value is 1.10 g L^{-1}. In fact, it depends on the degree of soil structural organization, increasing to a mean value of 1.40 g L^{-1} in the moderately to strongly structured St 6 and St 7 soils. Bulk density is inversely related to the portion of soil volume occupied by pores. In the Motovun area, bulk densities of 1.10 g L^{-1} and 1.40 g L^{-1} indicate that total porosity occupies about 58 % of the soil volume in the valley bottom and decreases to 47 % on slopes. Investigations on soil thin sections of truffle-producing areas showed that *T. magnatum* carpophores grow in soil layers where porosity is larger than 50 % of total soil volume (BRAGATO *et al.*, 1992; LULLI *et al.*, 1993). Moreover, they noticed that the decrease of porosity recorded on developed, unproductive soils almost only concerns pores having a diameter larger than 50 µm – the macropores – along which water flows and air exchange between soil and atmosphere occurs. Soil bulk density therefore represents a meaningful property for an aerobic species like *T. magnatum* because a decrease of soil macroporosity reduces air flow and the oxygen tension in the soil.

Other important properties a soil should have to be suitable for the production of *T. magnatum* are calcium carbonate content and pH. These properties are chemically related and a huge number of Italian data allowed LULLI & PRIMAVERA (2001) to propose the continuous presence of carbonates and a pH higher than 7.50 as suitability parameters for *T. magnatum* growth. Because of different environmental processes, only St 3 and St 6 soils have pH values lower than 7.50. The lower pH of soils on slopes is determined by the leaching of carbonates from A horizon to the subsurface horizons, and a calcium carbonate content of 1.4 % is unable to keep the pH at a value higher than 7.50 in the most »ancient« soils of St 6. In St 3 the presence of carbonates is quite high, however. Its soils are as »young« as those of the other strata of the valley bottom and the low pH values seem related to the same environmental processes responsible for the genesis of a Dysmull: the low-grade metabolization of wood litter produces enough organic acids to modify the reaction equilibrium of the CO_2-$Ca(HCO_3)_2$-$CaCO_3$ system and to lower pH below 7.50.

CONCLUSIONS

The results of the comparison between the productive fluvial plain of Motovun Forest and the nearby unproductive slopes are in line with the observations made in Italian white truffle-producing areas. *T. magnatum* grows and produces carpophores in moist and drained environments of tectonically active areas where soils are continuously rejuvenated. In the Motovun area, rejuvenation is guaranteed by the continuous arrival of alkaline particles eroded from slopes and redeposited in the fluvial plain. The scattered and chaotic redeposition of particles creates very porous, highly aerated, soft soils, with an interconnected macroporosity that allows this hypogeous fungus to breathe and its carpophores to grow in size without physical constraints. *T. magnatum* also needs a specific soil water regime that must be neither too dry, as it is on the slopes of the Motovun area, nor too moist, as in the low-lying soils of the fluvial plain periodically saturated by water. Motovun Forest represents the first *T.*

magnatum study case of the latter situation, where water stagnation appears to affect hypogeous aerobic organisms like earthworms and *T. magnatum*.

Our results suggest that the environment suitable for *T. magnatum* ranges between the soil climate limits of the Motovun area. The variation between dry and moist boundaries may explain the fluctuations of white truffle production usually observed over the years. In a mid-term view, however, the most critical situation for *T. magnatum* in Motovun Forest seems to be the increasing dryness of its soils. In the highly drained soils that are suitable for white truffle, the surrounding environment must supply the soil system with adequate water in the summer. It is notable that a strong decrease of *T. magnatum* production has coincided with the recent modification of the hydraulic equilibrium of the Mirna and Butoniga valley bottom. According to SHAW *et al.* (1996), the production decline could be alternatively attributed to the nitrogen fertilizer pollution that in Northern Europe seems to affect ectomycorrhizal fungi. We are however doubtful about the effect of nitrogen pollution on *T. magnatum* in an area where agricultural activities are negligible, while we think that a partial restoration of the previous hydrological situation – for instance, a partial diversion of stream waters inside the forest – may stop the decrease of white truffle production in the Mirna valley.

Finally, the climatic sequence of Motovun Forest – i.e. from the wet soil environment of low-lying areas to the relatively dry soils of high ground areas – is typical of fluvial plains and our data suggest that a fluvial plain with carbonated soils and mixed oak wood could be one of the best environments for *T. magnatum*, if not the most suitable altogether.

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