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Compaction by a forest machine affects soil quality and *Quercus robur* L. seedling performance in an experimental field

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ABSTRACT

In recent decades, the use of heavy machinery in forest management has significantly increased, causing the compaction of forest soils and potentially affecting seedling survival and establishment. We thus investigated the effects of soil compaction on soil physical parameters, microarthropod biodiversity, soil respiration, as well as growth and physiology of Pedunculated Oak (*Quercus robur*) seedlings in an experimental field in central Italy (coarse loamy soil). Two levels of soil compaction were simulated, i.e. 10 tractor passes vs. 25 tractor passes. The larger number of tractor passes increased soil bulk density (+27%) and penetration resistance (+46%), while porosity declined (−11%). Compaction decreased the qualitative biodiversity of soil microarthropods (−13%), the number of growth flushes (−22%) and of leaves (−22%), shoot biomass (−26%), the shoot/root ratio (−10%), the main root length (−24%) and the longest first-order later root length in the top 10 cm of soil (−31%). The decreased growth of seedlings in the soil compaction treatment was accompanied by lower photosynthetic rate (−34%) and leaf nitrogen content (−27%). We concluded that limited access and acquisition of nutrients and water due to the shorter length of main root likely played a key role for growth and physiological responses to soil compaction in *Q. robur* seedlings.

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1. Introduction

Compacted soil layers due to forest machine traffic are the most common problem affecting seedling regeneration after forest operations (Marshall, 2000; Bekele et al., 2007). Soil compaction can cause significant changes in the soil structure, and it is a priority research area for soil protection in Europe (Bolat et al., 2015). The extent of compaction is usually evaluated in terms of bulk density, soil resistance to penetration, and porosity (Cambi et al., 2015). The degree of soil compaction depends on soil texture, soil moisture, pH, organic matter content (Assouline et al., 1995) but also from vehicle mass, axle/wheel/track load, contact area of the vehicle with the soil, slope of the terrain, tire pressure (Jansson and Johansson, 1998; Alakukku et al., 2003; Bygdén et al., 2004). The compaction typically alters soil structure and hydrology, breaking down soil aggregates, decreasing porosity, aeration and water infiltration capacity and increasing strength and bulk density (Kozłowski, 1999). Resistance to root growth typically

increases (Foil and Ralston, 1966; Kozłowski, 1999). Post-logging compaction has been shown to have a long-term negative impact on tree growth particularly on the primary snig tracks, log landings and general logging areas (Froehlich et al., 1985; Rab, 1996; Croke et al., 2001). Severe compaction affects the growth of plants by a combination of physical soil changes and plant physiological dysfunctions (Wronski and Murphy, 1994; Nadezhdina et al., 2006). McMahon (1995) supposed a direct relation between the rate of damage to both soils and tree roots, and the frequency of passes of machines along tracks.

Soil compaction also affects soil biota. Soil fauna is usually affected by changes in the relative proportions of water and air volume in the soil (Brussaard and van Faassen, 1994). Light displacement of soil due to forest operations may result in a short-term increase in the abundance of microarthropod (Venanzi et al., 2016). The QBS-ar is a good index to detecting soil impacts (Blasi et al., 2013), and is based on the concept that the higher the soil quality, the higher the number of microarthropod groups (Parisi et al., 2005).

In general, soil compaction favors the occurrence of anoxic conditions, thus depressing soil respiration (Conlin and van den

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Driessche, 2000; Goutal et al., 2012). The efflux of CO₂, i.e. soil respiration, can indicate soil condition (Goutal et al., 2012) and is an indicator of soil degradation following compaction (Ampoorter et al., 2010). However, different responses of soil respiration to soil compaction have been recorded: Goutal et al. (2012) reported a decrease while Ponder (2005) and Busse et al. (2006) reported no change of the respiration rate of forest soils by soil compaction. Soil compaction also can reduce the rate of photosynthesis (Wieniarska et al., 1987) because an increase in the mechanical resistance of the soil is often followed by stomatal closure (Masle and Passioura, 1987) which decreases photosynthesis by inhibiting the diffusion of CO₂ to the mesophyll.

Taken together, all these effects may represent a barrier to seedling establishment and growth (Bassett et al., 2005), even because the radicle penetration may be impaired or delayed (Smith et al., 2001). However, a lack of quantitative information does not allow to assess the extent to which compaction may be affecting regeneration (Bassett et al., 2005). According to the literature (Brais, 2001; Gomez et al., 2002; Parker et al., 2007; Smith, 2003), a negative influence on plant development and soil environment generally occurs when penetration resistance values are higher than 2.5 MPa (Mancilla-Leyton et al., 2016). The effects of a moderate increase in penetration resistance are unclear.

We hypothesized that a moderate increase in soil compaction following forest operations is able to: (i) affect the physical traits of a forest soil and thus impair the early growth of tree regeneration, (ii) alter soil fauna (microarthropods) and emission of the greenhouse gas carbon dioxide (soil respiration), (iii) impair root growth and nitrogen uptake from the soil, thus affecting photosynthetic and leaf traits. Our work thus aimed to investigate the effects of forest-machinery compaction on both soil environment and regeneration of *Quercus robur*, which is a widespread tree species in Europe including the Mediterranean region. In parallel, we also investigated whether the effects of soil compaction are transient or last for an entire growing season. Two levels of soil compaction, that were within moderate soil compaction (<0.5 MPa) according to Alameda and Villar (2009), were compared to assess their influence on soil conditions (soil physical characteristics - i.e. bulk density, penetration resistance and soil porosity -, microarthropod diversity, soil respiration) and seedling physiology (photosynthetic and leaf traits) and growth (shoot and root morphology and biomass) during the first growing season (since germination). We expect that these results will improve our understanding of seedling performance in moderately-compacted soils and help forest managers in planning sustainable forest operations.

2. Materials and methods

2.1. Study site, soil compaction simulation and plant material

The trial was carried out in a flat terrain within an experimental field of the Department of Agricultural, Food and Forestry System of University of Florence (Italy, 43°48'30.53"N; 11°12'01.46"E; 50 m a.s.l.) during the growing season 2015. The climate is between hot-summer Mediterranean and humid temperate (Köppen, 1936). The mean precipitation during the growing season (March–October) was 687 mm. The mean annual temperature was 14.6 °C, with a minimum in February (monthly mean 6.4 °C) and a maximum in July (monthly mean 26.6 °C).

Tractor passes were carried out after manual logging of the pre-existing forest and without loads. A wheeled tractor Carraro Supertigre Tritrac 7700 (47 kW engine power - empty mass of 2540 kg) equipped with isodiametric tires - power drive forestry Pirelli TM 200 12.4R20 (320/85 R20) 116A8 - was used in our study. Two levels of compaction were simulated: a “moderately compacted”

(C1), obtained with 10 tractor passes and a “highly compacted” (C2) obtained with 25 tractor passes. Previous trials were performed to test the passes needed to reach the minimum threshold of desired compaction. C1 and C2 were replicated three times in form of 5.5-m long track, for a total of six track (2 compaction levels × 3 replicated tracks). Tracks were 30 cm far from each other.

The seeds were collected in an autochthonous stand (according to 1999/105/CE) in Northern Italy officially approved for seed production (provenance: Bosco Fontana; 10°44'20"E; 45°12'05"N). At the beginning of March, pre-germinated seeds with similar radicle length were sowed at a distance of 25 cm from each other, 66 seeds per soil compaction level were used, for a total of 132 seedlings.

The 25 year-old Norway spruce (*Picea abies*) forest was harvested manually in February i.e. one month before the experiment.

2.2. Soil environment

2.2.1. Soil properties

The soil developed below the forest was classified as Fluventic Dystrudepts based on the Soil Taxonomy (USDA – NRCS, 1999). Soil particle size distribution was as follows (% on weight): coarse sand 3%, medium sand 7%, fine sand 15%, silt 61%, clay 14%, by the hydrometer method (Gee and Bauder, 1986) on five samples of the top 30 cm of mineral soil, randomly distributed throughout the study area. In order to assess bulk density (BD), 30 soil samples (5 per replicated row) were collected by means of a metal cylinder (8.5 cm high and 5.0 cm inner diameter), after litter removal. BD cores were dried for 24 h at 105 °C before weighing. Soil strength was assessed as penetration resistance (PR) with a penetrometer (TONS/FT2) by 30 triplicated measures at a depth of about 4 cm. Soil porosity (POR) was determined by the following equation (Blake, 1965): $POR = ((D_p - BD)/D_p) * 100$, where D_p is the particle density measured by a pycnometer (Multipycnometer, Quantachrome, Boynton Beach, FL, USA) on the same soil samples used to determine BD. The sampling and the analysis for BD and PR were performed three times: April, i.e. at the beginning of the experiment; July, i.e. at half of the experimental period; and October, i.e. at the end of the experiment.

Soil respiration was measured by a closed system using an infrared gas analyzer (CIRAS-2, PP Systems, Herts, UK) with a dark soil respiration chamber (volume 1.1 L) and a soil temperature probe (EGM-4 with SRC-1, PP-Systems, Herts, UK). Soil collars made by PVC, 10 cm diameter and 12 cm long, were inserted 10 cm into the soil in the experimental field (3–5 collars per each soil-compaction treatment, 1–2 per replicated row), which was deep enough to seal the soil respiration chamber. Each measurement was completed in approximately 120 s. Soil temperature near the chamber was measured at a depth of 0–15 cm. At the same time, volumetric soil water content at the same depth was measured using a soil moisture probe (EC-5, Decagon, Pullman, WA). The measurements were made on 25–26 June, 30 July, 25 September and 2 November 2015 (9:00–12:00 h).

2.2.2. QBS-ar index and microarthropods community

The QBS-ar index was assessed after the end of the experiment (November 2015). Three soil cores with an area of 100 cm² and 10 cm depth were sampled in each soil-compaction treatment, one per each replicated row. Microarthropods were extracted using a Berlese-Tullgren funnel, collected in a preserving solution (75% ethyl alcohol and 25% glycerol by volume) and identified to different taxonomic levels (class for Myriapoda and order for Insecta, Chelicerata and Crustacea) using a stereo microscope (Wild Heerbrugg M420, Makroskop Lab 1.25X Microscope, 6.3–32X). They were separated into biological forms and associated with a score of adaptation (EMI, eco-morphological index), which ranges from

1 to 20. The QBS-ar index was finally calculated as the sum of the EMI values of all groups (Parisi et al., 2005; Gardi et al., 2008; Tabaglio et al., 2009; Menta et al., 2010).

2.3. Seedling performance

2.3.1. Seedling growth

Seedling height (H) was measured on a subsample of 54 seedlings per soil compaction level (18 seedlings per replicated row) by means of a yardstick from collar to top. Starting about 1 month and half after sowing, data were collected periodically (about every two weeks) during the first part of the growing season until the end of July (May 28th, June 11th, June 25th, July 8th, July 17th, July 30th). Then, the measures were repeated at the beginning of September (11th) and at the end of the growing season (October 25th, H Final). In November, the plants were accurately excavated and washed in order to preserve fine roots. Root system width and depth were immediately measured to prevent deformation caused by storage. The root system was divided into main roots and first order lateral roots (FOLR) as well as into two depth layers (from collar to 10 cm and >10 cm). Main root length, length of the longest FOLR with junction on the main root (total and per depth layer), main root biomass (total and per depth layer), FOLR biomass (total and per depth layer), leaf biomass, stem biomass (including branches, when present), total above and below ground biomass, the shoot (no leaves)/root and leaves/root ratios were assessed. Dry weights were obtained placing the samples in paper bags in a forced-air oven 70 °C until constant weight.

2.3.2. Leaf gas exchange and chlorophyll fluorescence

Target leaves (3–5th from the tip of the seedling, one leaf per plant, 5–6 plants per each soil-compaction treatment, 1–3 per replicated row) which had a healthy appearance were measured. Steady-state leaf gas exchange was measured using a portable infra-red gas analyzer (CIRAS-2, PP Systems, Herts, UK) at controlled values of leaf temperature (25 °C), leaf-to-air vapour pressure deficit (1.0–1.8 kPa), saturating light (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD, photosynthetic photon flux density) and ambient CO_2 concentration (380 $\mu\text{mol mol}^{-1}$). We determined light-saturated net photosynthetic rate (A_{sat}) and stomatal conductance (g_s). The measurements were made on 25–30 June, 30 July–4 August, 22–28 September and 2–4 November 2015 (9:00–12:00 h). Concurrent with gas exchange measurements, chlorophyll *a* fluorescence of photosystem II (PSII) was measured on the adaxial surface of interveinal leaf parts with a fluorometer (Handy PEA, Hansatech Instruments., Norfolk, UK). Before the measurement, leaflets were dark-adapted for 40 min with leaf clips. In the dark-adapted state, initial fluorescence (F_0 , when all PSII reaction centers were open) was measured. Then the rising transient was induced with a saturating actinic light pulse (3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, duration 1 s) to determine maximum fluorescence (F_m , when all PSII reaction centers were closed). Maximum quantum yield for primary photochemistry (F_v/F_m) was calculated as $(F_m - F_0)/F_m$ (Maxwell and Johnson, 2000).

To assess leaf photosynthetic capacity, the response curve of net photosynthetic rate (A) to intercellular CO_2 concentration (C_i), i.e., the A/C_i curve, was measured over 22–25 September. Six seedlings in each treatment were selected for this measurement. The measurements were carried out at controlled PPFD (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$), leaf temperature (25 °C) and leaf-to-air vapour pressure deficit (VPD, 1.0–1.8 kPa). The A/C_i curve was obtained by measurement over eight CO_2 steps (C_a , 380, 200, 100, 50, 380, 900, 1400, 1800 $\mu\text{mol mol}^{-1}$). The stomatal limitation of photosynthesis at ambient CO_2 concentration ($=1 - [\text{actual } A]/[A_{(C_i=C_a, 380 \mu\text{mol mol}^{-1})}]$), the maximum rate of carboxylation (V_{cmax}), the maximum rate of electron transport (J_{max}) and the CO_2 saturated net photosynthetic

rate (A_{max}) were calculated from the A/C_i curve (Farquhar et al., 1980; Ethier and Livingston, 2004). Values of the Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) Michaelis constants for CO_2 (K_c) and O_2 (K_o), and the CO_2 compensation point in the absence of dark respiration (Γ^*), were derived according to the methodology of Ethier and Livingston (2004). All gas exchange measurements relevant to the A/C_i curve were carried out on clear sky days (9:00–12:00 h).

2.3.3. Leaf traits

After measurements of gas exchange in September, the leaves were collected to determine their mass per area (LMA) and nitrogen content (5 plants per each soil-compaction treatment, 1–2 per replicated row). Leaf area was measured by scanning and calculating the area using an AM300 area meter (ADC, BioScientific Ltd, Herts UK). Leaves were dried in an oven at 70 °C until constant weight. LMA was calculated as the ratio of the dry mass to the area of the leaves. The nitrogen content of the leaves per unit mass (N_{mass}) was determined by using thermal conductivity with a LECO TruSpec C/N analyzer (Cools and De Vos, 2010; ISO 13878, LECO Corporation, 2006). We calculated the area-based nitrogen content (N_{area}) as the product of N_{mass} and LMA, and the PNUE (Photosynthetic Nitrogen Use Efficiency) as A_{sat} divided by N_{area} .

2.4. Statistical analysis

Statistical analyses were carried out with the Statistica 7.1 (2007) Software. As a first step, data distribution was plotted and checked for normality (Lilliefors) and homogeneity of variance (Levene test). For normally distributed data, Student *t*-test was applied for comparing the parameters between the two soil compaction levels, and repeated-measures ANOVA was applied for comparing seedling height, leaf gas exchange and chlorophyll fluorescence. ANCOVA was applied to test the differences between regression lines of soil respiration in the two compaction levels. When data were not normally distributed and with insufficient homogeneity of variance, non-parametric ANOVA and Kruskal–Wallis test were applied.

3. Results

3.1. Soil environment

All physical parameters were significantly higher in C2 than in C1 (Table 1). There was no seasonal trend in any of the parameters. The larger number of tractor passes (C2) increased bulk density by 27% and penetration resistance by 46%, while porosity declined by 11% (Table 1).

The microarthropod density was significantly higher in C2 than in C1 (Table 1). This higher density was due to an increment of Acari and Collembola, while the other biological forms found in C1 disappeared in C2 (Fig. 1). QBS-ar index was lower where compaction was higher; –13% in C2 in comparison with C1. QBS values showed a relation with soil compaction and consequently with the changes in soil physical characteristics.

Soil respiration rate exhibited positive exponential relationships with soil temperature (Fig. 2), with no difference due to the compaction level. These exponential relationships were statistically significant. Soil compaction did not significantly affect soil respiration rate, although slightly lower soil respiration rate was observed in C2 than in C1 (–5% at 25 °C of soil temperature). Volumetric soil water content at a depth of 0–15 cm did not show any difference between treatments during the measurements (data not shown). The mean values were 0.16, 0.11, 0.14 $\text{m}^3 \text{m}^{-3}$ in July, September and November, respectively.

Table 1

Soil bulk density (BD), penetration resistances (PR), porosity (POR) and microarthropod density (mean $\pm$ standard deviation) for two soil compaction levels (C1, 10 tractor passes; C2, 25 tractor passes) over the season. Bold *p* values show significant differences between the compaction levels (*t*-test, *N* = 5 for BD, POR and PR; χ^2 test, *N* = 3 for microarthropod density).

Parameters	Date	C1	C2	<i>p</i>
BD (g/cm ³)	April	0.73 $\pm$ 0.01	0.93 $\pm$ 0.01	0.0010
	July	0.73 $\pm$ 0.01	0.93 $\pm$ 0.01	0.0012
	October	0.74 $\pm$ 0.01	0.94 $\pm$ 0.01	0.0011
PR (MPa)	April	0.23 $\pm$ 0.22	0.34 $\pm$ 0.32	0.0011
	July	0.24 $\pm$ 0.23	0.35 $\pm$ 0.32	0.0014
	October	0.25 $\pm$ 0.23	0.35 $\pm$ 0.32	0.0015
POR (%)	April	73 $\pm$ 0.01	65 $\pm$ 0.01	0.0010
	July	73 $\pm$ 0.01	65 $\pm$ 0.01	0.0012
	October	73 $\pm$ 0.01	65 $\pm$ 0.01	0.0012
Microarthropod density (ind/dm ²)	November	208.3 $\pm$ 17.2	282.6 $\pm$ 22.8	0.005

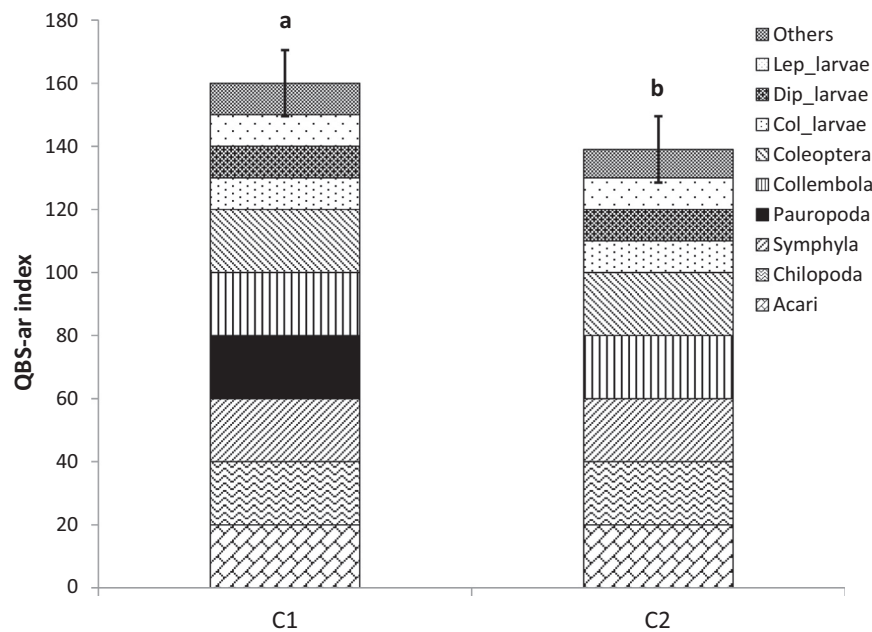


Fig. 1. Diversity of soil microarthropod community expressed as QBS-ar index (median $\pm$ standard deviation) and biological forms, for two soil compaction levels (C1, 10 tractor passes; C2, 25 tractor passes) at the end of the growing season. Lep_larvae: Lepidoptera (larvae), Dip_larvae: Diptera (Larvae), Col_larvae: Coleoptera (larvae). Different letters show significant differences between the compaction levels (Kruskal Wallis test, *N* = 3, *p* < 0.05).

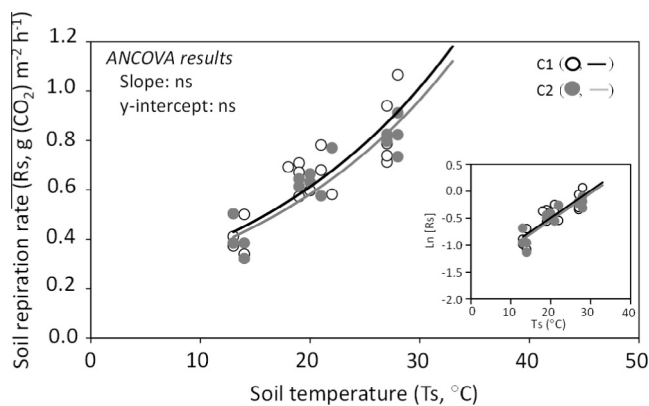


Fig. 2. Relationships between soil respiration (*R_s*) and soil temperature (*T_s*) at a depth of 0–15 cm in 2015. C1: 10 tractor passes, C2: 25 tractor passes. Exponential regression lines were as follows: $y = 0.22e^{(0.051x)}$ ($R^2 = 0.74$), $y = 0.21e^{(0.050x)}$ ($R^2 = 0.84$) at C1 and C2, respectively. All lines were statistically significant (*p* < 0.05). ANCOVA was applied against log-transformed data. ns denotes not significant.

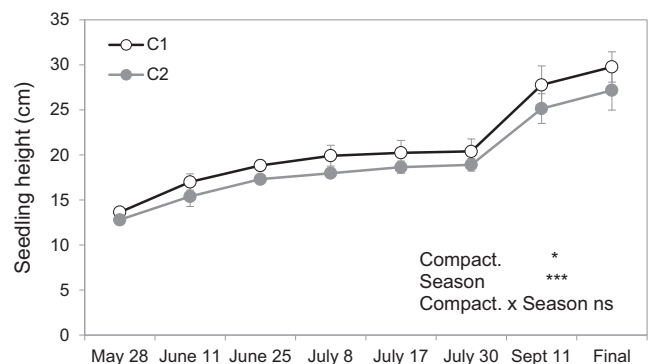


Fig. 3. Seedling height (mean $\pm$ standard deviation) in the two soil compaction treatments (C1 and C2) during and at the end of the growing season. Differences between treatments were significant according to repeated-measures ANOVA.

3.2. Seedlings performance

Seedlings in C2 showed a lower height than seedlings in C1 across the growing season (Fig. 3), and at the final harvest were 9% shorter.

A second growth flush started in August (Fig. 3). At the end of the season the number of growth flushes (−21.7%) and of leaves (−22.2%) were significantly lower in the seedlings grown in the more compacted C2 soil (Table 2). Seedlings in C2 showed a narrower root system (−26.8%). The roots in C2 were also shorter, in the case of both the main root (−24.3%) and the longest first-order later root in the top 10 cm of soil (−31%). Seedlings in C2 had a lower shoot biomass (−26.5%) and shoot/root ratio (−9.7%). All the other morphological variables did not show significant differences between soil compaction levels, even though seedlings in C1 had always higher values, with the only exception of FOLR DW >10.

No difference in LMA was recorded between soil compaction treatments in September (Table 3). Higher compaction decreased both N_{mass} and N_{area} of *Q. robur* seedlings. Fig. 4A shows the relationship between N_{mass} and the main-root length. We found a significant positive correlation in the relationship. N_{mass} did not change in the range of 10–40 cm of the main-root length. We did not find a significant relationship between N_{area} and the main-root length (data not shown).

A_{sat} reached its maximum in September regardless of treatments, and decreased in November due to senescence of leaves (Fig. 5). Soil compaction significantly decreased A_{sat} , g_s and F_v/F_m . No significant interactive effects of soil compaction and season were shown.

In addition to a significant decrease of A_{sat} by heavy soil compaction (−12 to −34%, Fig. 5), lower net photosynthetic rate at CO_2 -saturated condition (A_{max}) was found (−34%, Table 3). Both V_{cmax} and J_{max} declined in C2 relative to C1 (−39% and −33% in V_{cmax} and J_{max} , respectively). Those photosynthetic parameters (i.e., A_{sat} , V_{cmax} and J_{max}) decreased with decreasing N_{mass} (Fig. 4B–D). Soil compaction did not induce a significant decrease of PNUE (Table 3). While soil compaction significantly decreased g_s (−29 to −43% during June–September, Fig. 5), no significant dif-

Table 3

Leaf and photosynthetic traits (mean $\pm$ standard deviation) of *Quercus robur* seedlings subject to two soil compaction levels (C1, 10 tractor passes; C2, 25 tractor passes) and measured in September. Significant differences are highlighted in bold (t -test, $p \leq 0.05$, $N = 3$). LMA, leaf mass per area; N_{mass} and N_{area} , mass-based and area-based leaf nitrogen content, respectively; V_{cmax} , maximum rate of carboxylation; J_{max} , maximum rate of electron transport; A_{max} , CO_2 -saturated net photosynthetic rate; Stomatal limitation, stomatal limitation of photosynthesis; PNUE, photosynthetic nitrogen use efficiency.

	C1	C2	<i>p</i>
<i>Leaf traits</i>			
LMA (g m^{-2})	48.8 $\pm$ 8.1	51.9 $\pm$ 5.2	0.990
N_{mass} (g g^{-1})	0.026 $\pm$ 0.001	0.019 $\pm$ 0.001	0.001
N_{area} (g m^{-2})	1.3 $\pm$ 0.1	1.0 $\pm$ 0.1	0.024
<i>Photosynthetic traits</i>			
V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	74.6 $\pm$ 4.8	45.5 $\pm$ 8.4	0.007
J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	129.7 $\pm$ 8.9	86.3 $\pm$ 16.2	0.015
A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	29.0 $\pm$ 1.9	19.0 $\pm$ 4.0	0.017
Stomatal limitation	0.30 $\pm$ 0.03	0.32 $\pm$ 0.04	0.550
PNUE ($\mu\text{mol g}^{-1} \text{N s}^{-1}$)	10.0 $\pm$ 0.5	8.8 $\pm$ 1.8	0.150

ference of stomatal limitation of photosynthesis was observed between the treatments (Table 3).

4. Discussion

4.1. Effects on soil environment

Soil compaction is one of the disturbance factors that can affect the development of plant (Kozłowski, 1999) but few papers have studied it from an ecological point of view (Alameda and Villar, 2009). Our study assessed soil compaction due to forest operations, artificially simulated by applying a different number of tractor passes (C1, 10 passes; C2, 25 passes) on a forest soil developed in a young Norway spruce stand. This simulation produced two well distinct soil compaction levels, that were stable over the experimental period. In contrast, experiments on soil compaction following logging in natural forests suffer of inhomogeneous distribution of tractor passes (Froehlich et al., 1985). The soil physical properties analyzed in this study (bulk density, penetration resistances and soil porosity) are generally assumed as the most representative for the assessment of soil compaction (Hillel, 1998; Williamson and Neilsen, 2000; Powers et al., 2005; Ampoorter et al., 2010; Cambi et al., 2015), and are useful predictors of root system performance (Unger and Kaspar, 1994; Whalley et al., 1995; Kozłowski, 1999; Gaertig et al., 2002; Viswanathana et al., 2011). The increase of passes led to significant differences in all soil physical parameters, as found in other studies (Cambi et al., 2016a, 2016b) and affected other parameters.

The diversity of the microarthropod community decreased with increasing soil compaction due to the disappearance of specialized groups such as Pauropoda, Protura, Diplura and Diplopoda, Chilopoda (Fig. 1). Such over-simplification of the faunistic assemblages suggests a loss of taxonomic and functional groups. The QBS-ar index determined for both our soil compaction levels was below 200 (value given by Blasi et al. (2013) for undisturbed soil). In the high compacted soil (C2), the QBS-ar index was below the critical threshold of 150, suggesting important impacts, i.e. unsustainable resource use according to Blasi et al., 2013.

We did not find any seasonal changes in the soil physical parameters after compaction, suggesting that the impacts lasted for the entire growing season. Nevertheless, recent studies (Venanzi et al., 2016; Marchi et al., 2016) highlighted that such a level of compaction on forest soils may be completely recovered in 2–16 years.

Table 2

Growth and biomass (mean $\pm$ standard deviation) of above- and below-ground systems of *Quercus robur* seedlings grown at different soil compaction levels (C1, 10 tractor passes; C2, 25 tractor passes) at the end of the growing season. Significant differences are highlighted in bold (ANOVA, $p \leq 0.05$, $N = 54$) (RcD = root collar diameter; H = height; FOLR = first order lateral roots; DW = dry weight).

	C1	C2	<i>p</i>
RcD (mm)	6.2 $\pm$ 1.3	5.8 $\pm$ 1.0	0.057
H/RcD	5.0 $\pm$ 1.3	4.7 $\pm$ 1.3	0.341
Flushes (no.)	2.3 $\pm$ 0.8	1.8 $\pm$ 0.8	0.002
Leaves (no.)	20.7 $\pm$ 8.9	16.1 $\pm$ 6.4	0.003
Roots depth (cm)	36.6 $\pm$ 17.3	31.1 $\pm$ 12.7	0.070
Roots width (cm)	16.8 $\pm$ 10.9	12.3 $\pm$ 6.0	0.012
Main root length (cm)	38.2 $\pm$ 21.2	28.9 $\pm$ 13.9	0.011
FOLR max length (cm) (<10)	19.0 $\pm$ 15.8	13.1 $\pm$ 7.9	0.019
FOLR max length (cm) (>10)	6.4 $\pm$ 5.3	5.6 $\pm$ 4.2	0.432
Main root DW (g) (<10)	3.02 $\pm$ 1.6	2.84 $\pm$ 1.4	0.560
Main root DW (g) (>10)	1.95 $\pm$ 2.0	1.44 $\pm$ 1.3	0.153
Main root DW (g)	4.88 $\pm$ 3.3	4.14 $\pm$ 2.4	0.200
FOLR DW (g) (<10)	1.00 $\pm$ 1.1	0.80 $\pm$ 1.3	0.420
FOLR DW (g) (>10)	0.12 $\pm$ 0.3	0.21 $\pm$ 0.5	0.349
FOLR DW (g)	1.07 $\pm$ 1.1	0.93 $\pm$ 1.4	0.601
Leaves DW (g)	1.65 $\pm$ 1.3	1.47 $\pm$ 1.0	0.424
Stem and branches DW (g)	2.22 $\pm$ 1.4	1.63 $\pm$ 0.9	0.013
Root system DW (g)	5.95 $\pm$ 3.8	5.07 $\pm$ 3.2	0.219
Shoot system DW (g)	3.88 $\pm$ 2.5	3.04 $\pm$ 1.7	0.054
Shoot (no leaves)/root ratio	0.40 $\pm$ 0.2	0.34 $\pm$ 0.1	0.050
Leaves/root ratio	0.28 $\pm$ 0.1	0.31 $\pm$ 0.2	0.335

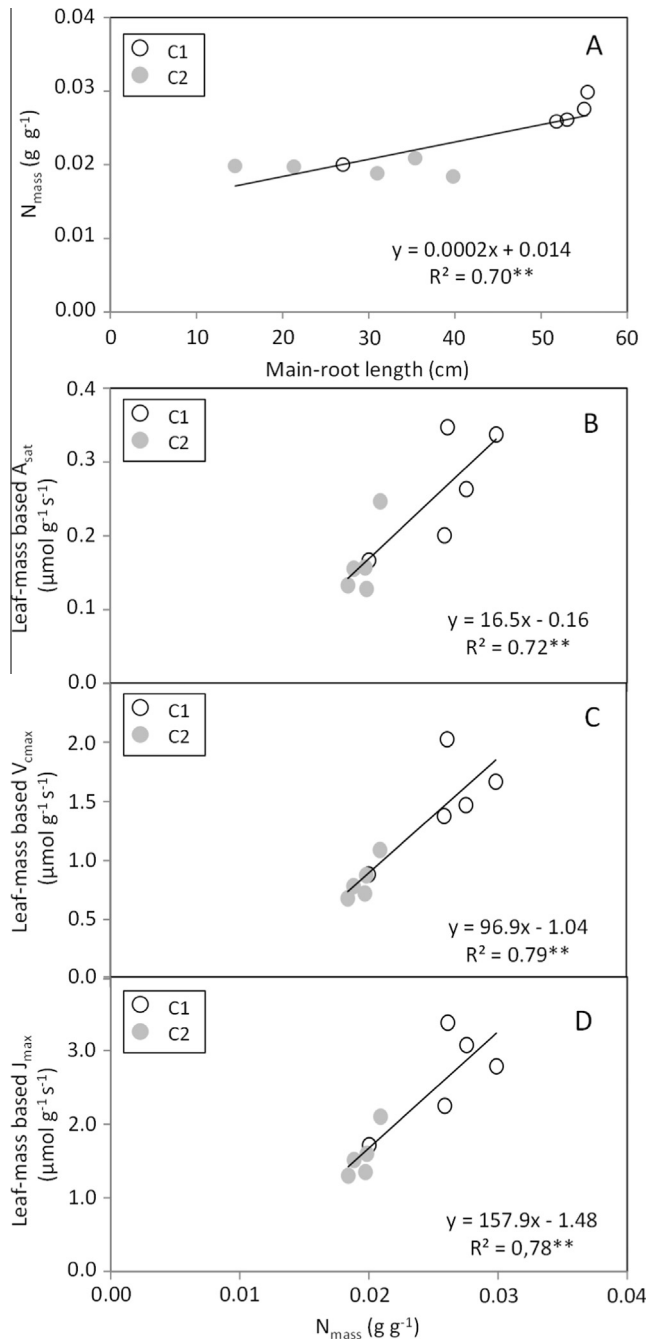


Fig. 4. Relationship between mass based N content (N_{mass}) and main-root length (A) and relationships between N_{mass} and leaf-mass based light-saturated net photosynthetic rate (A_{sat} , B), maximum rate of carboxylation (V_{cmax} , C), and maximum rate of electron transport (J_{max} , D) for *Quercus robur* seedlings measured in September (C1: 10 tractor passes, C2: 25 tractor passes). $^{**}p < 0.01$.

The seasonality of soil respiration was affected by the change of soil temperature independently on the level of compaction. The observed range of soil respiration in this study was comparable to the measured values in forest soils in southern Europe (Rey et al., 2002; Certini et al., 2003). The increase of numbers of tractor passes did not significantly affect soil respiration rate, although a slight decline was observed in C2 relative to C1 (−5% at 25 °C of soil temperature). In general, soil compaction may reduce soil respiration (e.g., Conlin and van den Driessche, 2000). This is primarily due to restricted gas diffusion (Xu et al., 1992; Goutal et al., 2012), causing an accumulation of CO_2 concentration inside the

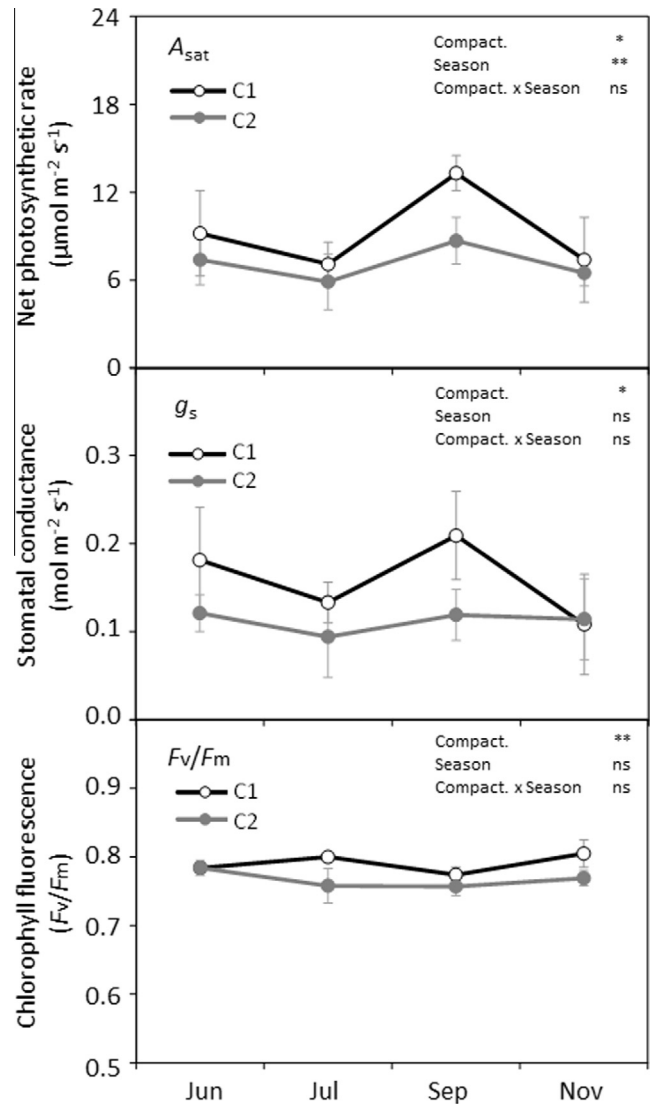


Fig. 5. Effects of soil compaction on seasonal change of net photosynthetic rate (A_{sat}), stomatal conductance (g_s) and chlorophyll fluorescence (F_v/F_m) for *Quercus robur* seedlings (C1: 10 tractor passes, C2: 25 tractor passes). Each value denotes the mean ($\pm$ standard deviation) of 3 replicated tracks. Repeated-measures ANOVA, $^{*}p < 0.01$, ns: not significant.

soil (Conlin and van den Driessche, 2000; Goutal et al., 2012), reduced microbial activity and reduced root respiration by increasing anaerobic spaces (Torbert and Wood, 1992). However, several studies reported no significant effect of soil compaction on the respiration rate of forest soils (Ponder, 2005; Busse et al., 2006). The susceptibility of compaction-related change of soil respiration may depend on soil types (Shestak and Busse, 2005) and soil moisture levels (Linn and Doran, 1984; Ruser et al., 2006). Ruser et al. (2006) did not find a compaction-related decrease of soil respiration under relatively dry soils in potato fields (water filled air spaces $\leq 70\%$) because anaerobic spaces, which relate to root respiration and microbial activity, also depend on the water status of the soil. In fact, our field site had a hot and dry summer, i.e., typical Mediterranean climate, with a mean soil water content of 0.11–0.16 $\text{m}^3 \text{m}^{-3}$ at the measurement days, i.e. well below the field capacity of this kind of soil (coarse-loamy soil: $\sim 0.25 \text{m}^3 \text{m}^{-3}$, Lee and Pielke, 1991; Mintz and Walker, 1993). Mordhorst et al. (2014) reported that the compaction-related decrease of soil respiration was not persistent after re-equilibration of hydraulic and cli-

mate conditions. In the case of unaffected respiration rate by soil compaction with restricted gas diffusion, Weisskopf et al. (2010) also suggested the possibility of the compensation of CO₂ production by anoxic decomposition processes.

4.2. Effects on seedling performance

Plant growth is usually negatively affected by soil compaction (Alameda and Villar, 2009) due to the resistance of the soil to be penetrated by the radicle (Day and Bassuk, 1994; Kozłowski, 1999; Bassett et al., 2005). According to our results, a higher soil compaction reduced the seedling performance in terms of height and root growth. Similar root responses were reported by Thomson et al. (1986), Kozłowski (1999) and Bengough et al. (2011). Mancilla-Leyton et al. (2016) reported that root-system biomass of *Quercus ilex* seedlings was significantly affected by soil compaction with values of penetration resistance of 2.5 MPa. Negative effects of compaction on main root growth were observed by Misra and Gibbons (1996) and Bejarano et al. (2010) in hardwood species. Concerning FOLR development in the top soil layer, similar results were reported for *Quercus petraea* (Gaertig et al., 2002), *Liquidambar styraciflua* (Viswanathana et al., 2011), *Populus tremuloides* (Berger et al., 2004; Puettmann et al., 2008), and conifers (McNabb et al., 2001). Analogous results for root system lateral expansion were described by Misra and Gibbons (1996) in *Eucalyptus regnans*.

Concerning above-ground growth, the higher soil compaction significantly reduced height values, although they were still in the range observed by other studies on one-year *Q. robur* seedlings in the field (Mariotti et al., 2015). In addition, the higher compaction reduced the number of growth flushes. Environmental conditions are known to affect the number of flushes in *Quercus* species (Collet and Frochot, 1996; Lof, 2000; Schmal et al., 2011). In *Q. robur*, a higher flush number is generally related to better environmental conditions (Collet and Frochot, 1996). However, in both treatments the flushing values were around two, i.e. lower than the number observed in favorable conditions, which can be up to six (Lavarenne-Allary, 1965; Mariotti et al., 2015); thus, both compaction levels may have affected above-ground growth.

The negative effects of soil compaction on morphological attributes can be explained by the physiological status of the seedlings. Several studies have shown that soil compaction impacts plant metabolism such as by decreasing photosynthesis, reducing foliage area and plant growth (Arvidsson and Jokela, 1995; Bassett et al., 2005; Ampoorter et al., 2010; Soto et al., 2015). The results of our study confirm these aspects. In fact, soil compaction reduced the photosynthetic traits of our leaves. This result is in agreement with previous studies (Masle and Passioura, 1987; Masle and Farquhar, 1988; Wieniarska et al., 1987; Conlin and van den Driessche, 1996; Kamaluddin et al., 2005), although some studies reported no significant reduction of photosynthesis after soil compaction (e.g., Andrade et al., 1993). The reduction of A_{sat} of seedlings grown under compacted soils may be attributed to both stomatal and non-stomatal inhibition (Kozłowski, 1999). Masle and Passioura (1987) and Masle and Farquhar (1988) suggested that stomatal closure may be a major factor to decrease photosynthesis by inhibiting the diffusion of CO₂ to the mesophyll. However, our results indicate no increase of stomatal limitation to photosynthesis under the higher soil-compaction level, suggesting that the reduction of A_{sat} was not mainly caused by stomatal closure but by the reduction of photosynthetic activity in the chloroplasts (biochemical assimilation capacity, i.e., V_{cmax} and J_{max}). The significant decline of g_s was likely an effect of reduced A_{sat} , because g_s generally correlates with photosynthesis (Lambers et al., 2008). A similar non-stomatal inhibition of photosynthesis by soil compaction was found in maize (*Zea mays* L.) (Bethenod and Tardieu, 1990).

Leaf N is strongly correlated with photosynthesis, and N is considered one of the important regulatory factors to photosynthetic activity (Lambers et al., 2008). Soil compaction significantly decreased leaf N content in *Q. robur*. In addition, we found joint decreases in photosynthetic parameters (A_{sat} , V_{cmax} and J_{max}) and N_{mass} under the higher soil-compaction treatment. The decrease of photosynthetic activities by soil compaction was therefore mainly due to a reduction of leaf N content. Kamaluddin et al. (2005) similarly reported a reduction of leaf N content by soil compaction in *Pinus contorta*, in association with lower photosynthetic capacity. The reduced leaf N content of our seedlings may be explained by the restricted lengthening of the main root (i.e., tap-root). The development of tap-root plays an important role for absorbing water and nutrients in the stage of oak seedlings (Chirino et al., 2008; Johnson et al., 2009). Chirino et al. (2008) suggested that the limitation of tap-root growth finally reduced the total biomass of oak seedlings. Net photosynthetic rate differed greatly between the compaction treatments in late summer (Fig. 5, in September), although no seasonal response of the photosynthetic traits to soil compaction was observed. Especially in Mediterranean forests, the shorter main roots developed due to soil compaction may limit the availability of water and nutrients to seedlings for more favorable climatic conditions after the summer drought.

Measurements of chlorophyll fluorescence revealed a decrease of Fv/Fm in leaves of *Q. robur* grown under compacted soils. This result suggests depression in photosynthetic efficiency by excess light energy, which is known as photoinhibition, mainly due to oxidative damage to the photosystem II (PSII) (Powles, 1984). Previous studies also found a decline of Fv/Fm induced by soil compaction for crops (maize: *Zea mays* L., and triticale: *Triticosecale* Wittm.) (Grzesiak, 2009) and ornamental trees (*Lagerstroemia speciosa*) (Philip and Azlin, 2005). The extent of photoinhibition can be considered as a consequence of photodamage to PSII and repair of the damage (Ohad et al., 1984). Takahashi and Murata (2005) suggested that the interruption of the Calvin cycle inhibited the repair of photodamaged PSII. Soil compaction may decrease the activity of the Calvin cycle through a lower V_{cmax} and J_{max} , implying the decrease of tolerance against photoinhibition. Also, low transpiration due to stomatal closure observed in compacted-soil condition inhibits evaporative cooling and increases leaf temperature, which could exacerbate photoinhibition of photosynthesis (Kitao et al., 2000).

5. Conclusions

This study allowed an assessment of the impact on forest soil generated by tractor compaction due to different number of passes. Physical, chemical and biological soil properties are often significantly impacted by compaction. In this study a simulation of a ground based extraction system was carried out to evaluate soil compaction and consequent restrictions to seedling growth and natural regeneration. Our findings demonstrated that physical and biological soil features were strongly impacted by the moderate level of soil compaction (0.24 vs. 0.35 MPa as soil resistance) following tractor trafficking. Interestingly, soil respiration was more affected by changes of soil temperature rather than by soil compaction. Effects of soil compaction on soil physical traits, seedling height and photosynthetic traits were constant over the growing season, i.e. they were persistent over time. The main negative effects on seedling growth were on the roots, in particular the main root length, on height and on the number of shoot flushes and thus of leaves. Limited access to water and nutrient, in particular nitrogen, due to shorter main roots was likely an important determi-

nant of the physiological and growth impairment following soil compaction.

We expect that these results will improve our understanding of seedling performance in moderately-compacted soils and help forest managers in planning sustainable forest operations.

On the basis of both literature and our findings, the main general suggestions for mitigating soil disturbance during forest operation are; (i) to reduce as much as possible the number of machine passes, (ii) to carefully plan a skid trails network in order to limit the area affected by machine trafficking; (iii) to use a brush mat on the skid trail in order to reduce the pressure exerted on soil.

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