Litter share and clay content determine soil restoration effects of rich litter tree species in forests on acidified sandy soils

Ellen Desie [a], Karen Vancampenhout [b], Leon van den Berg [c, d], Bart Nyssen [a, c], Maaike Weijters [e], Jan den Ouden [f], Bart Muys [a]

Affiliations

[a] Division Forest, Nature and Landscape, KU Leuven, Celestijnenlaan 200E, Box 2411, B-3001, Leuven, Belgium
[b] Department of Earth and Environmental Sciences, KU Leuven Campus Geel, Kleinhoefstraat 4, B-2240, Geel, Belgium
[c] Bosgroep Zuid-Nederland, Huisvenseweg 14, 5591 VD Heeze, The Netherlands
[d] Aquatic Ecology & Environmental Biology, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
[e] B-WARE Research Centre/Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands
[f] Forest ecology and management group, Wageningen University, P.O. box 47,Wageningen, The Netherlands

Corresponding author

Ellen Desie – ellen.desie@kuleuven.be , Division Forest, Nature and Landscape, KU Leuven, Celestijnenlaan 200E, Box 2411, B-3001, Leuven, Belgium, +32 16 37 67 42

Bart Muys – bart.muys@kuleuven.be, Division Forest, Nature and Landscape, KU Leuven, Celestijnenlaan 200E, Box 2411, B-3001, Leuven, Belgium, +32 16 32 97 26

Author contributions

ED, KVC, LVDB, BN, JDO, BM designed the study; ED, MW collected the data; ED analyzed the data ; All authors contributed to the interpretation of the results ; ED compiled the manuscript ; All authors contributed critically to the drafts and gave final approval for publication.

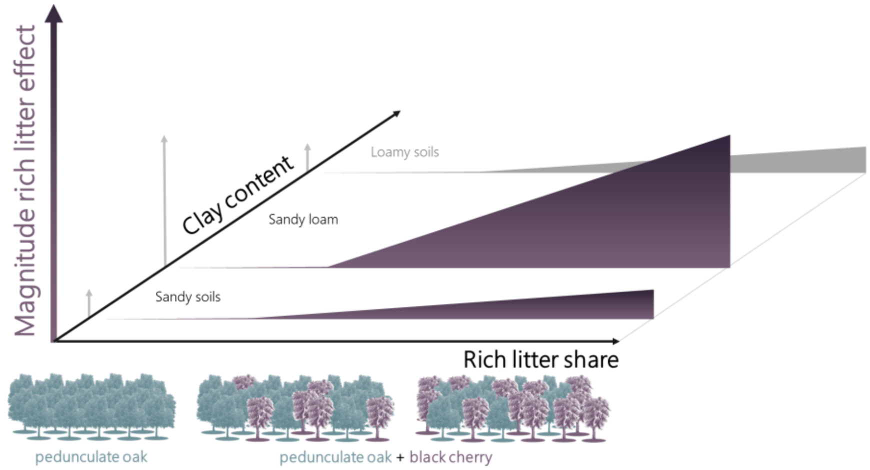
Highlights

1. Rich litter (RL) admixture improves base saturation of oak stands on acidified soils

2. A RL share higher than 30% basal area is needed for a significant effect

3. Clay content amplifies the rich litter effect in these sandy soils

Graphical abstract



Abstract

Many West-European forests are located on degraded and acidified soils. Soil acidification has resulted in hampered ecosystem functioning and lower delivery of ecosystem services. Forest management, particularly the choice of tree species, can accelerate or counteract soil acidification by the quality of litter input. The positive impact of so called 'rich litter' on the soil nutrient status and belowground ecosystem functioning has already been evidenced in common gardens. Here, we evaluate the effect of the rich litter species black cherry (*Prunus serotina* Ehrh) in mixed forest stands dominated by pedunculate oak (*Quercus robur* L.). We study the effects using a replicated set-up of 10 established forest stands (age 40 to 90) in Belgium, the Netherlands and Germany along an edaphic gradient in sandy soils on Pleistocene aeolian deposits. We hypothesize that black cherry has a positive effect on the soil nutrient status and aim to answer the following research questions: (i) does admixture of black cherry increase soil pH and base saturation? (ii) what proportion of rich litter admixture is needed in a poor litter matrix to observe significant improvement of the soil nutrient status? and (iii) does the magnitude of the rich litter effect interact with initial soil properties? The results of this study indicate that admixture of black cherry enhances the forest floor turnover and enriches topsoil chemical conditions significantly. Thickness of the litter layer decreases from a mean of 7cm under oak to a mean of 4.5cm under cherry and correspondingly base saturation increases to a maximum of 25%, NO_3^- concentration to 26mg/mg and organic matter content to 8%. However, large shares of rich litter admixture (>30% basal area) are needed to improve topsoil conditions. Moreover, we find that rich litter effects are more pronounced on sandy soils with higher fine particle (loam + clay) content. This suggests that the actual impact of restoration efforts in acidified forest soils is a product of the trinity "litter quality – litter share – site quality".

Keywords: litter quality ; black cherry ; soil restoration ; clay content ; soil acidification ; nutrient cycling

1. Introduction

Steady nutrient cycling between different compartments of ecosystems is a precondition for the provision of multiple ecosystem services (Lavelle et al., 2003). In that regard, soil acidification jeopardizes the long term functioning of forest ecosystems by altering the availability of critical macro- and micronutrients in the soil (Likens et al., 1996; Schaberg et al., 2001). Although this process occurs naturally in many forest soils, it has increased due to centuries of unsustainable land use, and further accelerated over the last century due to atmospheric acidifying deposition (Galloway, 2001). Soil acidification leads to the loss of the base cations calcium (Ca), magnesium (Mg) and potassium (K), and may increase concentrations of available aluminum (Al) and iron (Fe) to toxic levels (Ulrich and Sumner, 1991; Bowman et al., 2008), which negatively affects the vitality or growth of many plant and soil fauna. Despite coordinated international efforts to reduce atmospheric deposition of sulphur (S) and nitrogen (N) since the 1980s, current nitrogen deposition levels still exceed the critical load, i.e. the level below which no harmful effects can be expected (de Vries et al., 2014; Waldner et al., 2015). Especially in sandy soils, which are more vulnerable to degradation, the ensuing nutrient imbalance (i.e. base cation deprivation along with an overload of N) disturbs ecosystem functioning and reduces the overall vitality of the ecosystem (Schaberg et al., 2001).

As such, forest vitality is far from recovered from the continuous input of acidity over the last century (Schmitz et al., 2019). For example, European oak forests are increasingly affected by acute oak decline, which has been linked to the mentioned changes in soil chemistry and nutrient status (Demchik and Sharpe, 2000; Brown et al., 2018). Oak remains one of the main timber producing species for the West-European wood industry, and simultaneously fulfills an important ecological niche with much associated biodiversity (Peterken, 1996). Increased mortality is not a new phenomenon, but arises when trees are under physiological stress and become more vulnerable to pathogens and tissue damage (Jung et al., 2000; Denman et al., 2010). In order to boost the resilience of West European oak forests, the current cation imbalances in the soil need alleviation and restoration efforts focusing on nutrient status.

To curb soil acidification and its consequences, many restoration strategies have been explored (Kreutzer, 1995; Dumitru et al., 1999; Hüttl and Schneider, 1998; Musil and Pavlicek, 2002). Trials with liming and application of rock dust show promising results, yet only intervene in the abiotic compartment of the forest ecosystem and do not couple belowground nutrient cycles with aboveground biomass, which is important on soils with low cation exchange capacity (CEC) (Formánek and Vranová, 2002). A long-term strategy, aimed at actively incorporating the aboveground compartment into nutrient cycling, is to admix tree species with a favorable litter composition to speed up nutrient cycling, promote more diverse soil communities and improve the soil chemical status (Finzi et al., 1998; Hommel et al., 2007). In acidic edaphic conditions, litter rich in base cations (further: rich litter) promotes earthworm abundance which leads to more incorporation of organic matter in the soil (Muys et al., 1992). In turn, this leads to an improved nutrient binding capacity (higher CEC) and water holding capacity of the topsoil, creating higher resilience against future disturbance (e.g. acid input or drought). Previous studies evaluating tree species litter effects have identified rich-litter species (e.g. *Tilia*, *Acer*, *Fraxinus* and *Prunus* species) and evidenced their soil-enriching capacity on sandy soils (Reich et al., 2005; Mueller et al., 2015; Desie et al., 2020) . However, these studies have evaluated pure tree species effects in common gardens or monoculture stands whereas species can behave differently in mixtures (Hättenschwiler et al., 2005). Tree species currently dominating in areas on sandy soils such as pine, oak, beech, larch and douglas fir all produce litter that is low in base cations (i.e. poor-litter species), therefore a more direct assessment of mixtures with such poor litter is necessary. Moreover, tree species effects differ relative to soil type (Verstraeten et al., 2018; Desie et al., 2019), which may explain why the few studies looking at rich-litter species admixture in poor-litter matrices on the soil nutrient status have reported mixed positive (Carnol and Bazgir, 2013; Aerts et al., 2017), none (Van Nevel et al., 2014) or even negative (Aerts et al., 2017) results. In terms of nutrient cycling, it is therefore important to evaluate whether the rich litter effect will still prevail when rich-litter trees are admixed in stands dominated by poor-litter tree species on a particular soil type, and how the share of that rich litter influences outcomes.

This study aims to evaluate whether admixture of a rich-litter species in pedunculate oak (*Quercus robur* L.) stands enhances the soil nutrient status of poorly buffered acidified sandy soils. We chose to study the admixture of black cherry (*Prunus serotina* Ehrh) as we know from national forest inventories and our own observations that it is the only rich-litter species occurring in sufficient frequency (and as mature and dominant overstory tree) in admixtures of oak stands on relatively poor sandy soils in our study region. We wanted to make abstraction of the invasive species debate with regard to black cherry, and use it as a model species for the evaluation of the impact of rich litter on nutrient cycles in forests on acidified sandy soils. We hypothesize that admixture black cherry has a positive effect on the soil nutrient status and is functional as a management measure for soil restoration. Particularly, we address the following research questions: (i) Does admixture of black cherry increase soil base saturation, pH and available N? (ii) How much admixture of rich litter is needed in a poor litter matrix to observe significant improvement of the soil nutrient status? And (iii) Does the magnitude of the rich litter effect depend on initial soil properties? These questions were answered using a replicated set-up established in 10 established (age 40 to 90), mixed forest sites in Belgium, the Netherlands and Germany along an edaphic gradient of sandy soils (texture ranging from 56% to 95% sand).

2. Materials and Methods

2.1. Study region and sampling design

This study focused on mixed forest stands located in Northern Belgium, Southern Netherlands and the adjacent area in Germany (center 51° 17′ N, 5° 31′ E, altitude 30-80masl). The region is characterized by Pleistocene sandy aeolian deposits of variable thickness, locally admixed with sediments from marine or riverine origin (Kasse et al., 2007). Hence, soil textures vary from almost pure sand, over loamy or clayey sands to sandy loams (Van Ranst and Sys, 2000). The fraction of particles < 50 µm can vary from ca. 50% to almost zero. The climate is temperate with a mean annual precipitation (MAP) of circa 800mm and a mean annual temperature (MAT) of 10.5°C (data provided by the Royal Meteorological Institute of Belgium). Ten sites were selected, based on the presence of a mixture of pedunculate oak (*Quercus robur* L.) and black cherry (*Prunus serotine* Ehrh.) in the upper canopy (Table 1) and along a gradient in soil texture.

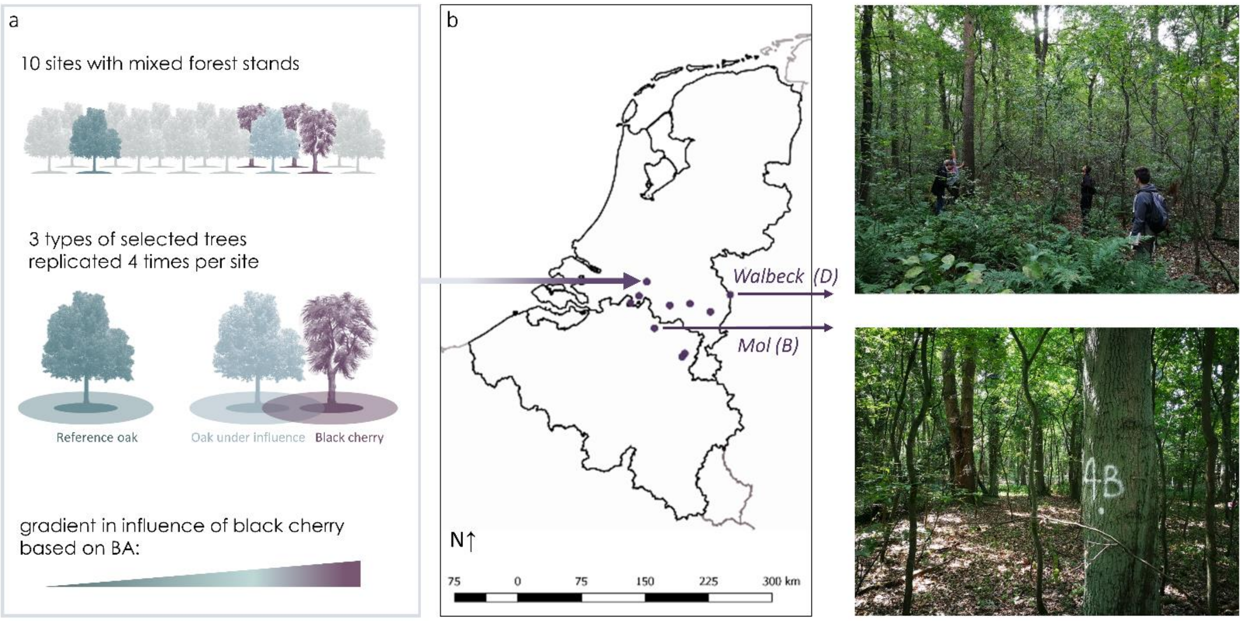


Figure 1: (a) Study design and (b) study region located over Belgium, the Netherlands and Germany. The sampling design exists of 3 types of target trees: a dominant black cherry tree, an oak under influence of black cherry and a reference oak without direct influence of mature black cherry trees. Per site four trees of each type are selected (N=12 per site). The 10 mixed forest sites are indicated by purple dots. Photos of site in Walbeck (top right) and Mol (bottom right).

In each mixed forest site, 4 replicates of 3 types of trees were selected: a dominant black cherry tree, a neighbouring oak tree under influence of black cherry (at a maximum of one tree height distance from the black cherry) and a reference oak tree without direct influence of dominant black cherry trees (Figure 1). By selecting the reference trees in the same forest stand on the same site (maximum 230 m distance from oak under influence) and by evaluating historical maps, we assured that all selected trees grew under the same environmental conditions (climate and topography) and had the same land-use legacy. By sampling both cherry and oak in the same forest stand confounding factors were limited as to assure that the actual differences reported can be appointed to tree species effects and not initial differences in site conditions. We may even underestimate black cherry influence as, because of the design, some reference oak trees were under minor influence of black cherry. In four sites (Genk, Mol, Walbeck, t'Zand) we could not find four dominant black cherry trees present that met our selection criteria, therefore we sampled two oak trees under influence of the same dominant cherry present. In total we selected and sampled 115 trees.

2.2. Sampling and laboratory analysis

Sampling

Under each selected tree, soil samples were taken and humus descriptions were made in July 2017. We sampled around each selected tree in all wind directions at a distance of 1/3 crown radius from the stem. For each selected tree the humus layer was described three times following the European humus reference base (Zanella et al. 2014). We measured the thickness of the OL, OF and OH layer separately and determined the humus type using the humus index (HI) (Ponge et al., 2002). Further analysis of these data was based on the mean of the 3 replications (for humus index the median). Around each selected tree, five bulk mineral soil samples were taken from two depths (0-10cm and 20-30cm mineral soil depth for topsoil and subsoil samples respectively, where 0 cm depth starts directly under the forest floor layer at the top of the mineral soil), and merged in one composite sample per depth for chemical analysis. The forest floor layer itself was not sampled. At each site an augering was performed and the soil type was described according to the FAO guidelines for soil description (FAO, 2006). Soil classifications were executed on each site according to WRB guidelines (IUSS Working Group WRB, 2015). An additional soil sample of the subsoil (C-horizon) was sampled on each site for texture analysis.

In autumn 2018 we placed one litter trap (1m high, 0.2 m^2 circular surface area) under each selected tree at a distance of 1/3 crown radius from the stem. Per site we placed all traps at the same orientation (dominant wind direction) from the tree. Litter traps were emptied 3 times between October and December. The collected material was oven dried at 60°C and weighed per litter category (leaf litter of oak, cherry, conifers and other broadleaved, and non-foliar litter) and per collection date (Figure S2). Data for selected trees with damaged litter traps (n=26) were omitted.

In the winter of 2018-2019 we mapped the forest structure of all sites using the FieldMap instrument (FieldMap, IFER, Czech Republic). All trees with a diameter at breast height (DBH) higher than 15cm (Vannoppen et al., 2020) and within a radius of 15m around the selected tree were spatially mapped and species, DBH and height of the tree were included in the map.

Laboratory analysis

Soil pH, NO_3^- and NH_4^+ concentration were determined in salt extracts (after mixing fresh soil (17.5 g) with 50 mL 0.2 M NaCl solution). The $pH_{(NaCl)}$ was measured immediately after extraction using a combined pH electrode (radiometer and a TIM840 pH meter). NO_3^- and NH_4^+ concentrations were determined colorimetrically with a Seal auto-analyser III, using salicylate, hydrazin sulphate and ammoniummolybdate/ascorbic acid reagent, respectively (Grasshoff and Johannsen, 1977; Technicon, 1969). Acid extractable element concentrations (Al, Ca, Fe, K, Mg, Mn, S, Si, P, Zn) of soil and litter samples were determined by digesting 200 mg of dried (24 h, 70 °C) and homogenized (by mortar) sample in 4 ml concentrated HNO3 and 1 ml 30% H2O2 (Milestone microwave MLS 1200 Mega) (Kingston and Haswell, 1997). Cation Exchange Capacity (CEC) and base saturation were determined by mixing an amount of dry soil equivalent of 5 g fresh soil in 200 ml 0.2 M $SrCl_2$ (Liu et al., 2001). All the soil extracts were measured with ICP, as mentioned above. Base saturation was calculated as the sum of exchangeable Ca^{2+}, Mg^{2+} and K^+ (in terms of charge equivalents) divided by the CEC and expressed as %. Soil and leaf litter total nitrogen (N) and carbon (C) concentrations were measured with a CNS analyzer (Model NA 1500; Carlo Erba Instruments, Milan, Italy). Soil organic matter content was determined by weighed loss-on-ignition after burning samples at 550°C for a minimum of 6 hours (Schulte and Hopkins, 1996). Soil texture was analyzed by laser diffractometry using a laser diffraction particle size analyzer - LS 13 320) (Buurman et al., 2001). The fine particle content is based on the sum of the clay content and loam content.

2.3. Data analysis

Stand characteristics

Based on the collected stand structure data, following variables were calculated for each selected tree. The basal area (BA) of all neighbors was calculated as follows: $\sum_{i=1}^{n} 0.25\,\pi\,(d_i)^2$ in a 15m radius with d_i the DBH of the i^{th} tree. Competition was calculated using $\sum_{i=1}^{n} di/(d \times dist_i)$ according to Contreras et al. (2011) with $dist_i$ representing the distance between the selected tree with diameter d and the competing tree i with diameter d_i. The influence of black cherry (further called Prunus influence) on each selected tree was calculated using the BA of black cherry in a 15m radius around the selected tree (including the selected tree itself) where the BA area was weighted based on the relative distance to the selected tree ($dist_j$) and relative to the total amount of neighbors (of any species) in a 15m radius:

$$\text{Prunus influence} = \frac{\sum_1^i \left(\left(1-\frac{dist_i}{15m}\right) BA\,cherry_{\,i}\right)}{\sum_1^j \left(\left(1-\frac{dist_j}{15m}\right) BA\,neighbor_j\right)}$$

Statistical analysis

Descriptive statistics were executed for most tree-species independent soil properties per site (Table 1). The effect of Prunus influence on different soil properties was tested by means of mixed models with site as a random effect using the package nlme in R. The normality of the residuals and their relation to the fitted values was evaluated graphically. When Prunus influence was a significant predictor in the mixed model, it is portrayed by a solid line in the figures 4, 5 and 6, other non-significant relations are portrayed by dotted lines. Additionally, clay content (or fine particles content respectively) was included in the mixed models twice: as a main effect and in interaction with Prunus influence. Because clay content is a group-level variable, i.e. only measured per site, and the response soil properties are population-level variables, i.e. measured under each selected tree (12 times per site), we are dealing with multilevel data. This implies that caution is necessary when interpreting the P-values of the interaction effect with clay content (Qian et al., 2010). Significance of the predictors was tested by a type II analysis of variance (anova) using the package car in R. All predictors were standardized (to a of mean of 0 and sd of 1) so that the standardized coefficients (Table 2) can be interpreted easily. All analyses were performed in R version 3.4.4 (R Core Team, 2019).

3. Results

3.1 Research design

Texture of the study sites ranges from sandy loam to sand (56% - 95% sand) (Table 1). Soils belong to three different WRB Soil Reference Groups, i.e. Anthrosols, Arenosols and Podsols, which is representative for the typical gradient in soil properties in sandy sites in Belgium and the Netherlands. In terms of land-use history, some sites were afforested 170 years ago whereas others only recently (30 years ago after a period of agricultural use or heathland cover). Subsoil P and N show considerable variation among sites ranging from 28.77 to 263.24 mg/kg DW for total P and 2.82 to 9.05 mg/kg DW for the sum of ammonium and nitrate. The overstory tree species composition varied over the 10 sites, with the respective proportion of pedunculate oak ranging from 27% to 60% and that of black cherry from 12 to 38% (based on basal area). Evaluation of the design showed that the weighted influence of black cherry, based on basal area share in a 15m radius around the selected tree, increased from the reference tree (mean 2%±3%) to the oak under influence (mean 30%±14%) to the soil under the black cherry tree itself (mean 42%±16%) (Figure S1).

Table 1: Characteristics per site located in Belgium (B), the Netherlands (NL) or Germany (D). Texture and soil type were determined per site (group-level variables). The mean of subsoil CEC, OM, N, P, BA and species composition was calculated based on all selected trees per site (population-level variables). The earliest indication of forest on available maps is indicated as 'forested since' (note this is not the stand age). Sites are ranked based on increasing sand content.

Site	Texture			Soil type	Topsoil (0-10cm)						Subsoil (20-30cm)					Species composition (%)							Forested since
	clay	Silt	Sand	reference group	pH	BS	Al	$NO_3^- + NH_4^+$	CEC	OM	$NO_3^- + NH_4^+$	CEC	OM	Total P	Basal area	*Quercus robur*	*Prunus serotina*	*Pinus sylvestris*	*Betula pendula*	*Fagus sylvatica*	*Quercus rubra*	other	(according to historical maps)
	(%)	*(%)*	*(%)*			*(%)*	*mg/kg*	*mg/kg*	*(meq/100g)*	*(%)*	*(mg/kg)*	*(meq/100g)*	*(%)*	*(mg/kg)*		*(%)*	*(%)*	*(%)*	*(%)*	*(%)*	*(%)*	*(%)*	
Genk (B)	12.7	30.5	56.8	Arenosol	3.11 ±0.10	33.77 ±13.95	19.53 ±6.86	41.56 ±21.67	4.07 ±1.35	7.09 ±2.92	5.26 ±2.48	1.65 ±0.40	2.06 ±0.68	263.24 ±39.22	2.42 ±0.40	38	12	46	1				1971
Veldhoven (NL)	3.6	29.0	67.4	Anthrosol	3.20 ±0.11	23.86 ±13.50	42.80 ±6.60	30.72 ±22.46	3.60 ±0.88	5.58 ±1.84	4.43 ±2.20	1.47 ±0.32	1.91 ±0.25	262.9 ±30.15	1.71 ±0.77	46	19	3	9			9	1850
Walbeck (D)	6.7	24.5	68.8	Arenosol	2.86 ±0.06	22.75 ±9.30	70.42 ±19.37	67.16 ±26.44	7.39 ±2.23	16.44 ±4.79	8.35 ±3.92	2.87 ±0.64	3.98 ±1.28	184.01 ±0.54	2.05±0.33	60	24	6	1				1850
As (B)	5.5	23.6	70.9	Anthrosol	3.23 ±0.09	35.20 ±6.79	18.57 ±4.61	36.40 ±14.51	3.53 ±0.63	6.26 ±0.93	5.00 ±2.54	1.61 ±0.12	2.5 ±0.37	183.23 ±23.90	2.23 ±0.61	52	28	10	8				1971
Loon op zand (NL)	2.0	19.8	80.4	Podzol	3.05 ±0.12	12.56 ±6.11	38.18 ±9.10	12.78 ±5.02	4.08 ±1.28	5.82 ±2.10	4.50 ±4.32	1.96 ±0.48	2.08 ±0.92	39.54 ±7.32	1,82 ±0.35	54	13		8	8			1988
Someren (NL)	2.0	13.2	86.6	Arenosol	3.22 ±0.14	13.56 ±3.86	36.84 ±5.78	17.28 ±5.48	3.56 ±0.78	4.55 ±1.01	6.07 ±4.17	2.19 ±1.17	2.23 ±0.79	184.99 ±71.75	1.71 ±0.24	56	23	3	13			3	1983
Grashoek (NL)	1.7	9.1	89.2	Podzol	2.99 ±0.06	16.51 ±11.95	33.60 ±12.36	17.43 ±6.14	3.82 ±0.79	5.01 ±1.68	7.00 ±3.69	3.85 ±1.25	4.11 ±1.37	71.75 ±37.49	1.95 ±0.47	27	19	19	32				1926
Mol (B)	1.1	5.3	93.9	Arenosol	3.33 ±0.30	32.19 ±12.52	28.71 ±10.74	46.50 ±17.10	5.87 ±1.17	9.97 ±1.26	9.05 ±4.34	2.64 ±1.23	3.48 ±0.82	135.36 ±61.63	2.03 ±0.39	57	15	15	8		2		1971
t'Zand (NL)	1.3	3.9	94.8	Arenosol	3.15 ±0.10	21.50 ±10.80	30.43 ±4.23	7.42 ±3.67	2.55 ±0.65	3.02 ±1.72	2.82 ±1.89	1.36 ±0.144	2.96 ±4.64	28.77 ±7.83	2.39 ±0.42	50	15	27					1899
Hoogstraten (B)	1.0	4.5	95.1	Podzol	2.83 ±0.14	8.70 ±3.14	39.60 ±13.00	16.01 ±7.29	4.77 ±0.78	5.93 ±1.20	9.02 ±12.69	3.49 ±1.08	3.79 ±1.06	69.04 ±17.96	1.09 ±0.29	51	34		5	1	1		1846

3.2 Prunus influence

3.2.1. Litter layer and humus classification

Accumulation in the OF and OH layer decreased with increasing Prunus influence (P<0.001) (Figure 2a and Figure S4). Moreover, we found significant differences between each type of selected tree: the thickness of the OF-OH layer was larger under the reference oak trees compared to the oaks under influence (Figure S5). The humus type did not significantly change with increasing Prunus influence (P= 0.44) (Figure 2b).

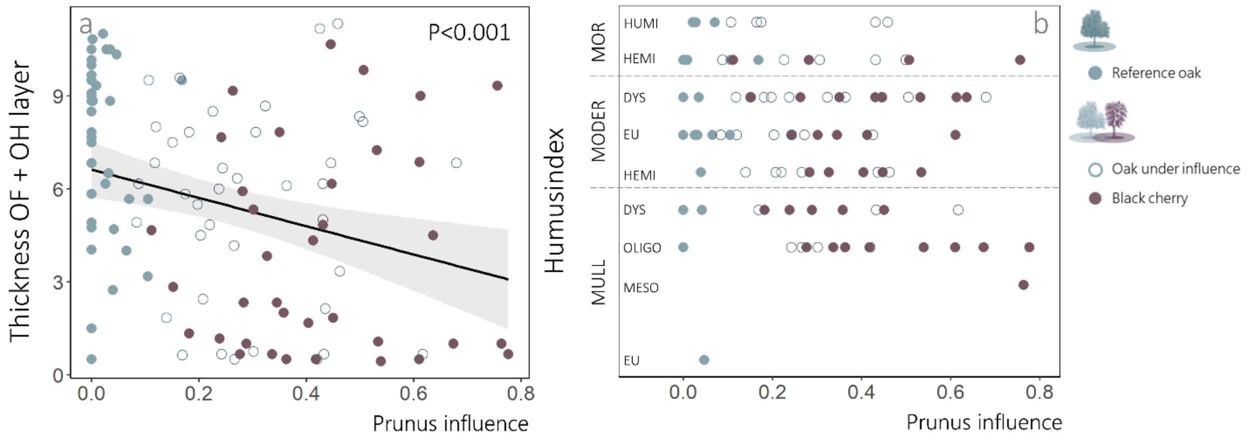


Figure 2: a) thickness of the OF+OH layer and b) humus type as a function of Prunus influence. The type of tree is indicated by the color and shape of the circles: reference oak (light green – fill), oak under influence (light green – no fill), black cherry (dark pink - fill). P-values for the variable ‘Prunus influence’ determined in a mixed model (Table 2) accounting for site effects are indicated in the top right corner.

3.2.2. Topsoil chemistry

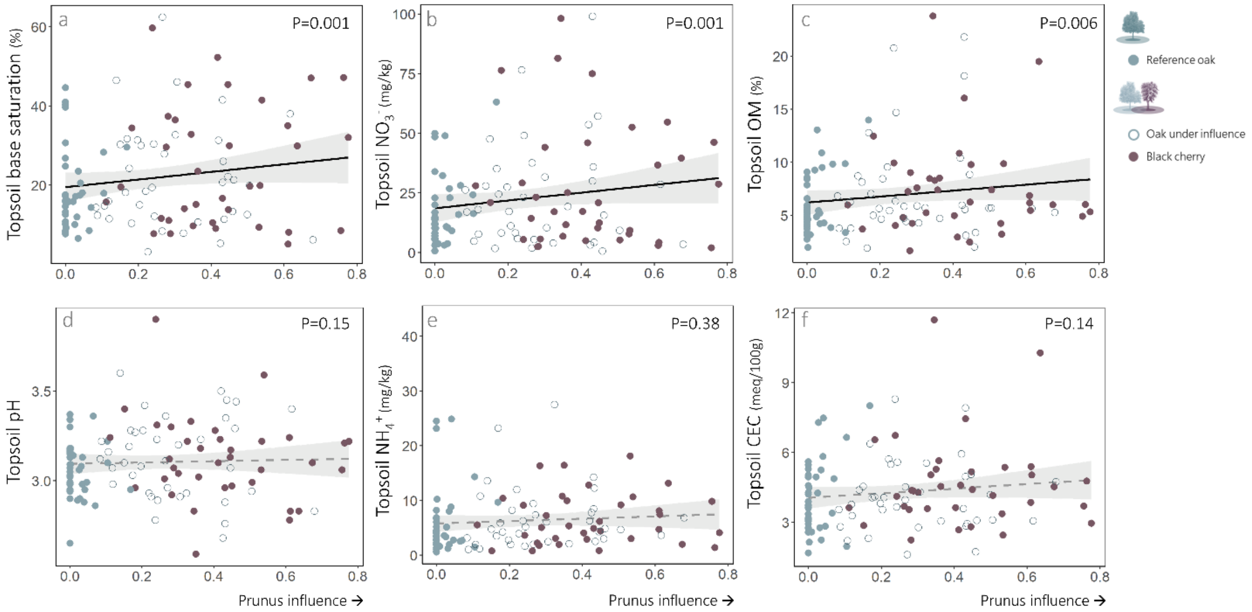


Figure 3: Topsoil variables as a function of Prunus influence: a) base saturation (%), b) NO_3^- concentration (mg/kg DW), c) organic matter content (%), d) $pH_{(NaCl)}$, e) NH_4^+ concentration (mg/kg DW) and f) CEC (meq/100g). The type of tree is indicated by the color and shape of the circles: reference oak (light green – fill), oak under influence (light green – no fill), black cherry (dark pink - fill). Significant relations are represented by full lines whereas relations that are not significant are indicated by dotted lines. P-values for the variable 'Prunus influence' determined in a mixed model (Table 2) accounting for site effects are indicated in the top right corner.

Topsoil base saturation increased significantly with increasing Prunus influence (P=0.001) (Figure 3a). This was mirrored in the differences between all types of selected trees: mean base saturation increased from 19±10% under the reference oak to 21±13% under the oak under influence and 25±15% under the black cherry tree. Only base saturation under the cherry tree differed significantly from under the reference oak (Figure S6). An increase in basal area of black cherry in a 15m radius from 0% to 80% black cherry (corrected for distance) corresponds with an increase in topsoil base saturation from 22% to 25% (Figure 3 and Table 2). This trend was not significant for topsoil $pH_{(NaCl)}$ (P=0.15) and topsoil aluminum (P=0.09) (Figure 3d). Topsoil NO_3^- increased significantly with increasing Prunus influence (P=0.001) (Figure 3b, Table 2). No trend was found for topsoil NH_4^+ (P=0.38) (Figure 3e). Topsoil CEC showed no relation with Prunus influence (P=0.14), however a positive linear relation was found with topsoil organic matter (OM) concentration

(P=0.006) (Figure 3 f and c). For subsoil chemistry we only found a marginally significant relation between NO_3^- concentration and Prunus influence (P=0.05) (Figure S7).

3.3 Mediation by clay content

Clay content has, additionally, a significant positive effect on topsoil base saturation, topsoil OM and topsoil NO_3^-. Finally, we found significant positive interactions between Prunus influence and clay content for thickness of the OF-OH layer, topsoil base saturation, topsoil OM and topsoil NO_3^- indicating the greater impact of prunus on sites with a higher clay content. We found the same significant interaction effects with the totpl fine fraction (silt + clay content, reported in Table S3).

Table 2: Standardized coefficients, standard deviations and P-values of fixed effects (intercept, Prunus influence, clay and prunus*clay interaction) of mixed models accounting for site as a random effect explaining different topsoil response variables.

Response	Intercept	Prunus influence	Clay	Interaction
OF+OH layer	**5.47 (±0.82) $^{P<0.001}$**	**-1.09 (±0.21) $^{P<0.001}$**	-0.97 (±0.75) $^{P=0.19}$	**-0.59 (±0.27) $^{P=0.03}$**
Topsoil base saturation	**22.28 (±2.49) $^{P<0.001}$**	**3.11 (±0.93) $^{P=0.001}$**	**5.40 (±2.38) $^{P=0.02}$**	**2.55 (±1.22) $^{P=0.03}$**
Topsoil $pH_{(NaCl)}$	**3.10 (±0.05) $^{P<0.001}$**	0.02 (±0.01) $^{P=0.15}$	-0.009 (±0.05) $^{P=0.85}$	-0.01 (±0.01) $^{P=0.53}$
Topsoil Al	**35.62 (±4.90) $^{P<0.001}$**	1.70 (±1.01) $^{P=0.09}$	0.71 (±4.26) $^{P=0.86}$	-1.06 (±1.33) $^{P=0.42}$
Topsoil OM	**6.99 (±1.20) $^{P<0.001}$**	**0.58 (±0.20) $^{P=0.006}$**	**1.89 (±0.99) $^{P=0.06}$**	**0.68 (±0.27) $^{P=0.015}$**
Topsoil CEC	**4.32 (±0.45) $^{P<0.001}$**	0.16 (±0.11) $^{P=0.14}$	-0.02 (±0.40) $^{P=0.94}$	0.25 (±0.14) $^{P=0.08}$
Topsoil NO_3^-	**22.83 (±4.82) $^{P<0.001}$**	**4.22 (±1.22) $^{P<0.001}$**	**15.99 (±4.36) $^{P<0.001}$**	**4.32 (±1.60) $^{P=0.008}$**
Topsoil NH_4^+	**6.41 (±1.04) $^{P<0.001}$**	0.28 (±0.48) $^{P=0.66}$	-0.86 (±1.01) $^{P=0.39}$	0.53 (±0.63) $^{P=0.39}$

We evaluated the slopes of the topsoil – Prunus influence relation per site (Figure S8) and plotted them as function of clay (Figure 6 left) and fine particles content (clay + silt) (Figure 6 right) to graphically assess the interaction effect, i.e. how texture magnifies the cherry effect (Figure 6, Figure S8).

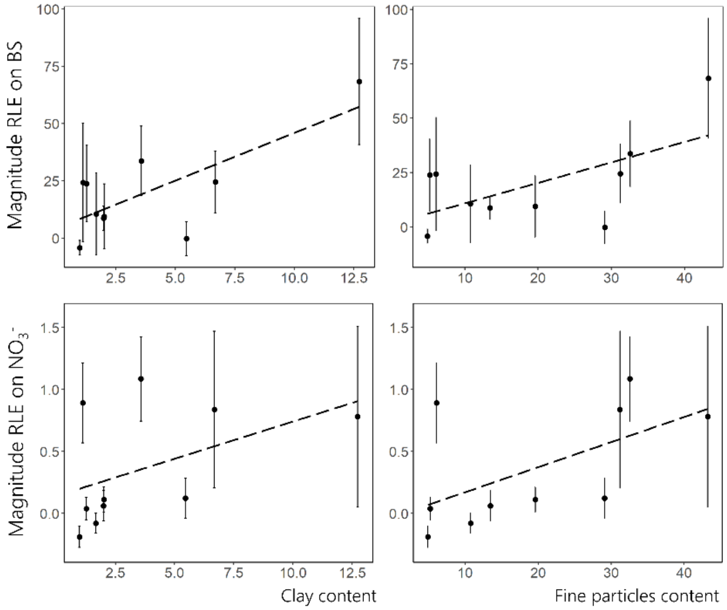


Figure 4: Magnitude of the rich litter effect (mean and se), i.e. the slope of the relation with Prunus influence, as a function of clay content (left) and fine particles content (clay + silt) (right). The magnitude is expressed as the slope of the topsoil base saturation or NO_3^- concentration – Prunus influence relation per site.

To evaluate the correlation between texture and Prunus influence we investigated the potential link with base cation concentration of the cherry litter. Yet, base cation content of the leaf litter of all selected black cherries per site is not significantly related to clay content or fine particle content, even when accounting for the outlying site Mol (Figure 7). When evaluating litter quality of the cherry trees we found significant relations between litter base cations and topsoil base saturation (P=0.005) and topsoil pH (P<0.001) (Figure S9).

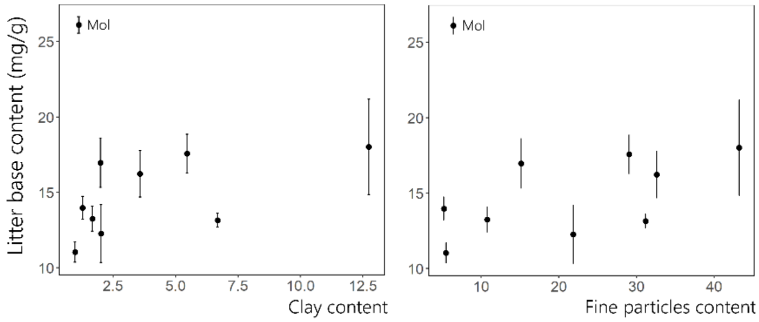


Figure 5: Base cation content of the black cherry litter (mean and se) per site as a function of clay content (left) and fine particles content (clay + silt) (right). Mol is (graphically) identified as an extreme value.

4. Discussion

4.1. Rich litter effect of *Prunus serotina* ?

4.1.1. Litter quality

Previous studies illustrated the difference in forest floor thickness and humus form between different tree species in monoculture stands on the same site, including the large difference in litter quality between black cherry and pedunculate oak (von Wendorff, 1952; Vanderhoeven et al., 2005; Dassonville et al., 2008; Desie et al., 2020) . Although the effect of tree species, for example litter quality, can be different in mixtures compared to pure stands (Hättenschwiler et al., 2005), we found that the effect of black cherry reported for monocultures, is maintained in mixed oak stands on acidic sandy soils. Increasing Prunus influence is significantly and negatively related to litter accumulation in the forest floor. This effect, also reported by Lorenz et al. (2004), can be attributed to the promotion of microbial and faunal activity through the provision of base cation rich litter and subsequent improved decomposition (Reich et al., 2005; Hobbie et al., 2006). In this study we make the assumption that the positive effects are linked to the high litter quality of cherry, as we did not measure oak litter quality and cannot directly evidence the higher quality of litter of cherry compared to oak, which was also the main reason for its massive introduction in West-Europe (Klaus Lorenz et al., 2004).

Our study clearly indicates that the effect of admixture of black cherry on topsoil chemistry is multiple. Admixture of cherry in acidified oak stands enhanced the nutrient status of the soils (both NO_3^- concentration as well as base saturation increase in the topsoil). The positive relation with topsoil base saturation can be explained by the higher base cation concentrations of fresh black cherry litter and the related accelerated turnover and incorporation of organic matter (Lavelle et al., 2004; Reich et al., 2005) . Higher NO_3^- concentrations in proximity of black cherry are probably a consequence of the promoted nitrification explained by improved edaphic conditions for nitrifying microbes. Indeed an earlier study has found increased nitrification rates with increased soil pH and buffering (Ste-Marie and Paré, 1999). Despite the significant enrichment under black cherry, base saturation does not increase above the 30% threshold that is linked to a shift in soil buffering domain from a state dominated by Al to a state dominated by base cations (Vitousek and Chadwick, 2013; Desie et al., 2019). Soil pH changes when one buffering mechanism (for example Al buffering) is replaced by another (for example base cation buffering). In acid soils with pH below 4.5, the exchange complex is saturated with H^+ , Fe and Al ions, and soil pH will only respond markedly if base saturation can be raised above 30%. The soils in our study remain in the Al buffering range. As a result, the pH of the topsoil did not increase significantly with black cherry admixture.

Although organic matter turnover and incorporation increased under black cherry, illustrated by the relation with topsoil OM, a significant relation with topsoil CEC was not found. We expected the CEC to increase as OM significantly contributes to the number of exchange places, especially in sandy soils with low CEC_{clay} (Gruba and Mulder, 2015). The lack of effect on CEC can potentially be explained by the pH-dependent charge of the OM, i.e. OM will only contribute significantly to the CEC if the pH increases.

4.1.2. Litter share

Although we found significant effects of rich litter admixture, the effects are small in absolute terms. This corresponds with a previous study by Van Nevel et al. (2014) who found that dense understory shrub layers (with up to 90% cover) of rich litter species, among which black cherry, had no impact on topsoil chemistry of acidified sandy soils as the contribution to total litterfall was insufficient. They suggest that an improved overstory tree species selection would have more potential to improve topsoil conditions as compared to dense shrub layers of rich litter species. Indeed, our study corroborates these propositions, because we find significant positive effects of mature cherry trees on the soil conditions, which can be explained by the longer time period that rich litter effect has been active and the larger volume of litter produced by a mature tree. Moreover, the relative amount of rich-litter tree species needed in the overstory will depend on species-specific concentrations of base cations in the leaves. For example admixture of mature *Betula pubescens* trees (up to 63% of BA) proved insufficient to improve mineral soil conditions in *Picea abies* stands (Brandtberg et al., 2000). This can be explained by the relatively lower litter quality of birch, i.e. lower litter base cation concentrations, in comparison to other rich litter tree species (Desie et al., 2020), emphasizing that the community weighted mean of the litter composition remains the essence of soil nutrient status restoration.

We took both litter quality and the share of rich litter admixture into account by using mixed stands with mature, dominant black cherry trees, a tree species that has high concentrations of base cations in its litter (Desie et al., 2020). In our stands, an increase in basal area of black cherry from 0% to 80% black cherry (corrected for distance) translated in an actual increase of share in litterfall from 10% to 40% of black cherry, and corresponds with a small increase in topsoil base saturation from 22% to 25%. The 10% black cherry admixture in the litterfall of plots with 0% black cherry basal area shows that our basal area calculations cause an underestimation of black cherry litter share, because the basal area only included trees with a diameter higher than 15cm, while the smaller diameter classes (<15cm) were almost all black cherry. Despite the fact that the actual leaf litter share in stands with high basal area remains limited, base saturation increased significantly. It is however clear that on poorly buffered sandy soils large amounts of admixture of black cherry (i.e. large concentrations of base cations) are needed to significantly impact the forest floor thickness and the soil base saturation and nutrient status. It remains to be seen if a longer period of rich litter influence will be able to increase base saturation further.

4.1.3. Limitations of the study

We found that cherry admixture has a positive effect on the forest floor and topsoil chemistry in mixed forest stands. Since we did not sample and measure litter quality of the oaks, we cannot directly evidence that the improved topsoil chemistry is a consequence of the richer litter of cherry. However, there is an extensive literature base that reports the high quality litter of black cherry (von Wendorff, 1952; Vanderhoeven et al., 2005; Desie et al., 2020) and explores the potential of this species for soil restoration (Carnol and Bazgir, 2013; Van Nevel et al., 2014). Therefore it is the most probable explanation.

Furthermore, the base cation concentrations of cherry litter reported in this study may be an underestimation due to the long period between collection dates and potential leaching of mobile compounds from the litter in the traps. Secondly, we extended our litter trap mass data, which had multiple missing values, with more precise and quantitative basal area measurements of the overstory composition, which can be used as a proxy for litter contributions (Jonard et al., 2006; Nickmans et al., 2019). The correlation of both measures is illustrated in Figure S3 and Table S2. We have made the assumption that the contribution of cherry in basal area corresponds with the contribution of litter to the forest floor. However, it should be addressed as a limitation of our study that we do not directly use litter share based on litter mass measurements.

4.2. Impact on the aboveground ecosystem compartment

Current forest management strategies are increasingly focused on boosting tree diversity in order to have higher insurance in a future shaped by increased frequency of disturbances (Paquette et al., 2018). Admixture of rich litter tree species offers an additional incentive through its ability to restore acidified, nutrient-imbalanced forest soils and is hypothesized to improve the overall vitality of the forest. The accelerating effect on nutrient cycling by rich litter species, such as black cherry, has been reported before (Lorenz et al., 2004; Vanderhoeven et al., 2005; Dassonville et al., 2008). Yet, whether this increased availability translates in higher uptake of nitrogen by the neighboring oak trees or, contrary, is short-circuited to the black cherry tree via its dense and superficial root system, remains an important question to be answered. The competitive behavior of black cherry could be appointed to the rooting system. Hence, subsequent research should evaluate the relative importance of litter and root dynamics of black cherry and whether this is also context dependent. In this study we merely focused on the litter-soil pathway. In terms of nutrient cycling, studies report diverse and even contradicting results: from increasing nutrient concentrations and pH (Lorenz et al., 2004; Vanderhoeven et al., 2005; Dassonville et al., 2008) to negatively affecting the belowground nutrient status (pH and N) (Starfinger et al., 2003) or having negative effects on neighboring native species and their foliage nutrient uptake (Aerts et al., 2017). Aerts et al. (2017) reported lower foliar nutrient concentrations of beech and oak in the close presence of black cherry, whereas higher foliar P concentration in pines were found in a different edaphic setting.

Finally, we want to point out that in this study on the management intervention “*admixing rich litter tree species*” black cherry served merely as a model species, that in the implementation of restoration can be replaced by other, native rich litter tree species better adapted to the management goals. In our previous study (Desie et al., 2020) we highlighted the potential of *Tilia*, *Acer* and *Alnus* as potential rich litter species for soil restoration. Moreover, further research should tackle the feedback of increased nutrient availability to the aboveground ecosystem and elucidate which species, in what conditions, have beneficial effects on the vitality of other trees.

4.3. Interaction with edaphic factors

We found significant relations between soil texture and topsoil base saturation and topsoil nitrate concentration. More intriguing, however, is the significant interaction between texture and rich litter effects: the higher the fraction of clay or fine particles (clay and silt combined) the greater the positive impact of admixing black cherry on topsoil conditions. This positive interaction cannot be explained by the higher litter quality of black cherry on sites with finer textures as we found no significant relation between litter base cation content and texture, implying that there is no feedback via base cations in the litter. We did find correlations between litter base cation content and topsoil base saturation and topsoil pH. Moreover, the high base cation content of litter from the site Mol can be explained by the input of base cations via Ca rich groundwater (neighboring a canal with Ca-rich water), which also explains the high subsoil base saturation in this site.

In our observations, clay content (or fine particle content) amplifies the positive effect of higher litter quality. Seemingly in contrast, Verstraeten et al. (2018) and Desie et al. (2019) concluded from their results that restoration may be more difficult in soils with a high clay content due to Al saturation of the exchange complex with aluminum and thus restoration on sandy soils is more feasible. These opposing trends in the relation between clay content and tree species litter effects can be explained by the context:

In soils with high CEC, Al saturation is typically difficult (or even impossible) to overcome since the total amount of aluminum sorbed on exchange sites is too high to be replaced by base cations through litter input. For agricultural settings a maximum value of CEC 24 meq/100g clay is set (Driessen et al., 2001). Below this threshold restoration via litter input has more potential.

On the other hand, in soils with very low CEC values, such as our current study (subsoil CEC ranging between 1.36 and 3.85 meq/100g soil DW with an average of 2.30 meq/100g soil DW), the added benefit of a larger fine fraction in terms of soil fertility, SOM stabilization, aggregation, weatherable reserve and water holding capacity most likely is more determining than Al saturation on the exchange complex, explaining the positive relation with clay content.

Hence, the direction of the interaction with clay is context dependent, as biogeochemical equilibria in soils display considerable pedogenic inertia (so-called soil process domains; Ulrich and Sumner, 1991; Vitousek and Chadwick, 2013), interchanged by steep thresholds when one mechanism is exhausted and replaced by another (Chadwick and Chorover, 2001). Depending on the acid buffering capacity (which is arguably proxied by CEC) and the distance to a pedogenic threshold (proxied by base saturation), tree species can therefore have extensive, limited or no effect on soil acidification. Acidified soils that consist of almost pure sand or, contrary, acidified soils with a high clay content are opposite extremes (in CEC) that are trapped in so called pedogenic inertia and therefore very hard to affect by aboveground litter quality input.

Concluding, there is a window of opportunity for restoration in terms of site quality. In sandy soils (with low CEC), yet with considerable contribution of fine fractions (clay and silt), the admixture of rich litter trees can have maximum impact, i.e. around a pedogenic threshold in acid buffering small changes can have large impact. Hommel et al. (2007) indicated a requirement of >15% loam for admixture of rich litter to be successful. Van Nevel et al. (2014) also attribute the absence of rich litter effects to the high sand percentage of their study site. Nonetheless, under pure rich litter stands on poorly buffered sandy soils, we found significant positive effects (Desie et al 2020). This suggests that the ultimate result of restoration efforts is a product of the trinity litter quality – litter share – clay content. Hence, our study is emphasizing once more the importance of taking into account the boundary conditions determined by soil type when making forest management decisions.

5. Conclusion

Our study provides evidence that admixture of rich litter trees, in this case black cherry, in pedunculate oak stands leads to less accumulation of organic material in the forest floor and improves topsoil chemical conditions (base saturation, NO_3^- and organic matter content) significantly. Hence, we accept our hypothesis that rich litter admixture can be used as a management measure for soil restoration. However, although the conditions improved, they did change not to such an extent that it does induce a regime shift to a more favorable soil process domain. We found that large shares of rich litter admixture (>30% basal area) are needed to improve soil conditions and that such rich litter effects are more pronounced on sandy soils with higher clay content. Optimization of tree species selection as a management tool should focus on the regeneration of tree species with rich litter (i.e. elevated base cation concentrations), augmenting the relative share of such tree species in the forest overstory composition and targeting efforts to sites where pedogenic inertia does not limit the potential, i.e. soils with either very low or very high clay contents and corresponding CECs. Admixing rich litter holds great promise and may ultimately restore nutrient cycling in forests of acidified sandy soils.

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8. Supporting information

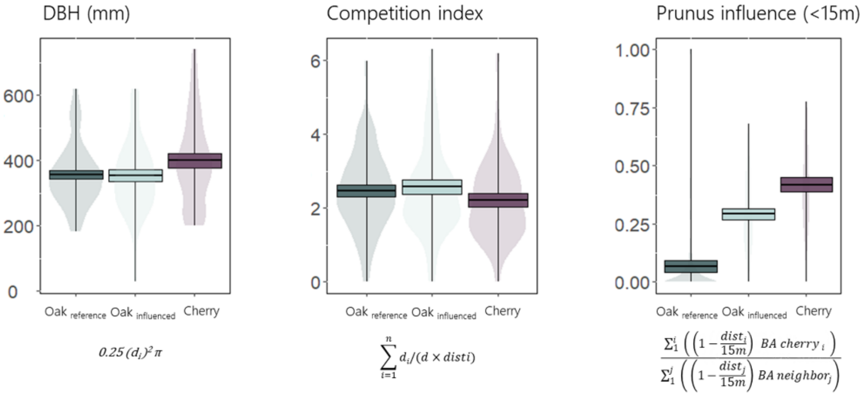

Figure S1: Evaluation of sampling design. The comparison of different types of selected trees (mean, sd and range) for dimensions and social position based on the FieldMap collected data in circular plots around every selected tree (radius 15m).

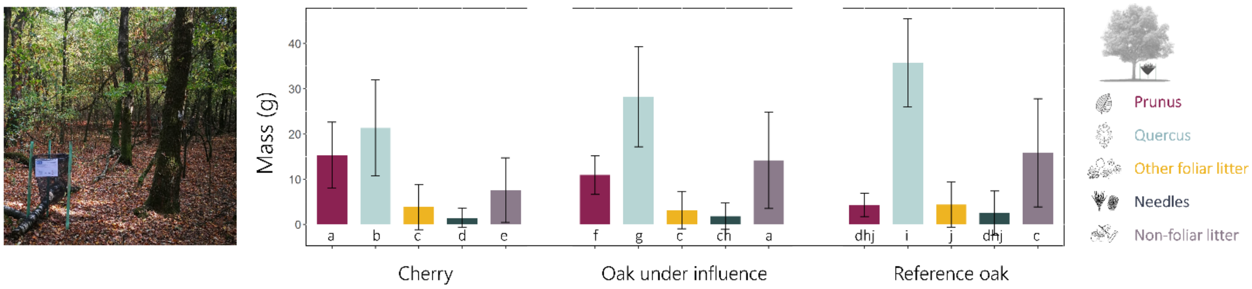

Figure S2: Left: photo of litter trap in the field. Right: mean mass and se per type of selected tree per litter type collected in the litter traps. A distinction is made between prunus litter (pink), quercus litter (light blue), other foliar litter (yellow), needles (dark green) and non-foliar litter (purple). Results of a multiple comparison test are indicated below the bars: different letters indicate significant differences.

Table S1: Litter trap data per site. The number of reliable observations are indicated by obs (ideally 12 per site). Values (mean and sd) of litter mass (total, cherry and oak) collected from October till December in a 0,2m2 litter trap and the relative contribution of cherry and oak. Values are extrapolated to ton/ha.

Site	Obs	Total (ton/ha)		Cherry (ton/ha)		Cherry (%)		Oak (ton/ha)		Oak (%)	
As	11	4.835	±1.54	0.635	±0.555	14.6	±11.7	2.125	±0.555	46.4	±13.3
Genk	8	3.38	±0.625	0.333	±0.2435	10.5	±8.38	1.66	±0.535	48.9	±11.2
Grashoek	8	2.13	±0.655	0.387	±0.086	19.8	±7.49	0.655	±0.312	29.9	±9.9
Hoogstraten	10	1.99	±0.3805	0.565	±0.308	29.9	±18.3	0.99	±0.341	49.5	±14.6
Loz	12	2.565	±0.63	0.405	±0.2765	17.7	±14.5	1.175	±0.383	45.7	±9.9
Mol	11	3.265	±0.565	0.5	±0.2435	15.4	±7.45	1.95	±0.273	60.4	±7
Someren	3	2.57	±0.655	0.3585	±0.114	14.5	±6.11	1.53	±0.408	59.4	±1.3
Veldhoven	10	3.195	±0.64	0.775	±0.625	27	±23.6	1.52	±0.74	46.2	±18.4
Walbeck	8	3.28	±1.015	0.665	±0.2715	22.7	±13.1	1.55	±0.62	47.9	±19.7
Zand	10	2.935	±0.7	0.535	±0.3865	19	±15.7	1.665	±0.545	57.1	±16.8

Table S2: Correlation of different radius of FieldMap data with data from the litter traps. Correlation is highest for a radius of 15m using a distance weighted formula. All correlations reported are significant ($P<0.001$).

Prunus influence fieldmap in radius of:	Correlation factor (with prunus litter collected in trap)
5m	0.57
7m	0.53
8m	0.54
9m	0.57
10m	0.53
11m	0.53
12m	0.54
13m	0.57
14m	0.54
15m	0.54
5m weighted for distance	0.56
7m weighted for distance	0.59
8m weighted for distance	0.59
9m weighted for distance	0.6
10m weighted for distance	0.6
11m weighted for distance	0.6
12m weighted for distance	0.59
13m weighted for distance	0.6
14m weighted for distance	0.6
15m weighted for distance	**0.6**

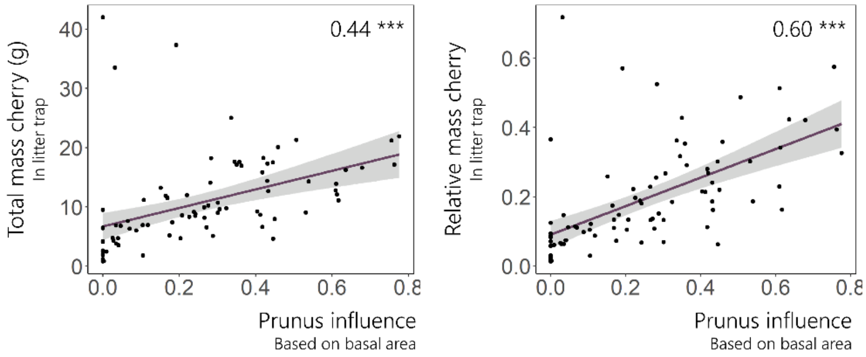

Figure S3: Relation between litter trap data and fieldmap data. Prunus influence is the calculated using the weighted basal area contribution of cherry in a 15m radius (see M&M for formula). Total mass cherry (g DW) is based on the collected litter material of the litter traps. Relative mass cherry is the ratio of total mass cherry over the total litter mass independent of litter type. The correlation coefficient and significance level are reported in the top right corner. *** $P<0.001$.

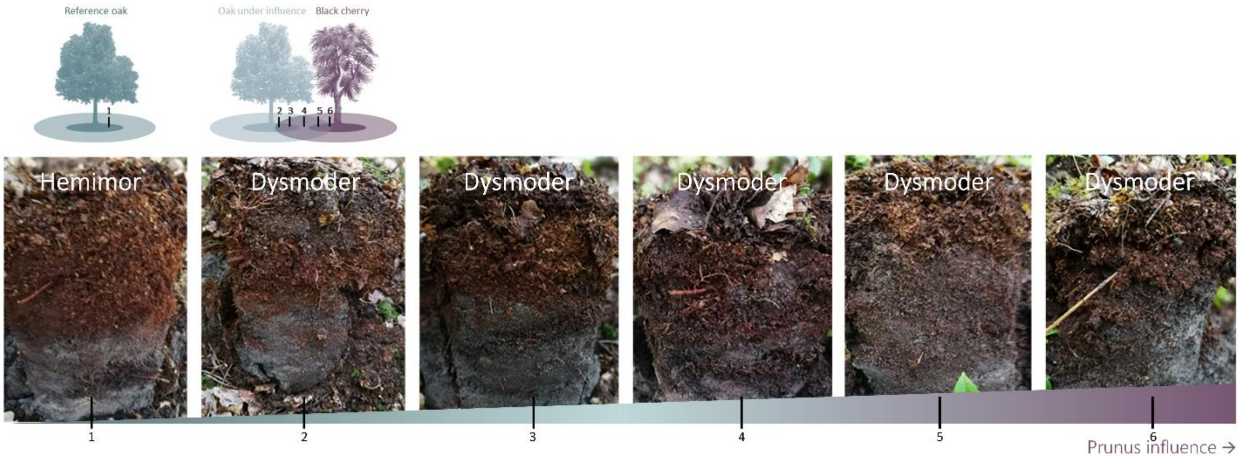

Figure S4: Gradient in humus profiles from reference oak tree to black cherry *at the* Grashoek *site* (NL). The sampling positions are indicated by the black stripes and numbers in the set-up. The ectorganic layer (OL+OF+OH) decreases with increasing Prunus influence. The transition between the OH layer and the mineral soil is sharpest in 1 and the transition zone increases with increasing Prunus influence.

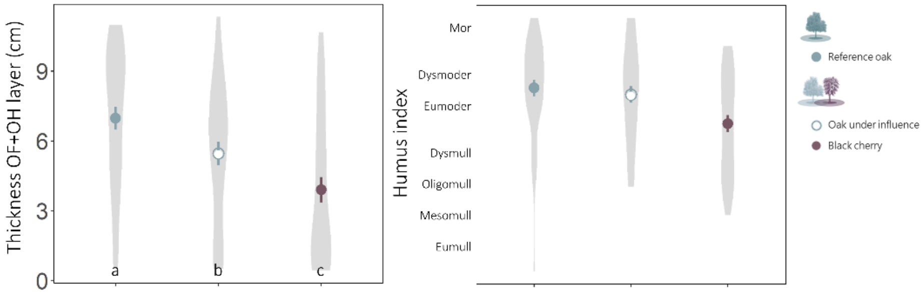

Figure S5: Left: mean thickness of the OF+OH layer per selected tree: the reference oak (full dark green circle), the oak under influence (full light green circle) and the black cherry (pink circle). Results of a multiple comparison test are indicated in the bottom of each graph, different letters indicate significant differences.

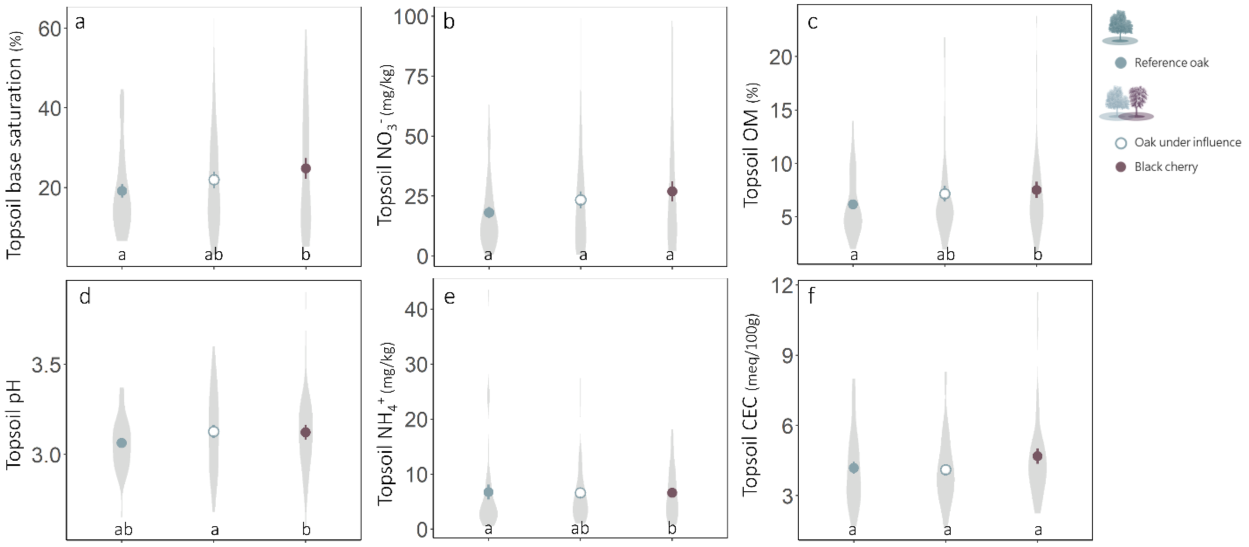

Figure S6: Base saturation, topsoil NO$_3^-$ concentration, topsoil organic matter (OM) content, topsoil pH$_{(NaCl)}$, topsoil NH$_4^+$ concentration and topsoil cation exchange capacity (CEC) per selected tree: the reference oak (full light green circle), the oak under influence (light green circle) and the black cherry (full dark pink circle). Results of a multiple comparison test are indicated in the bottom of each graph, different letters indicate significant differences.

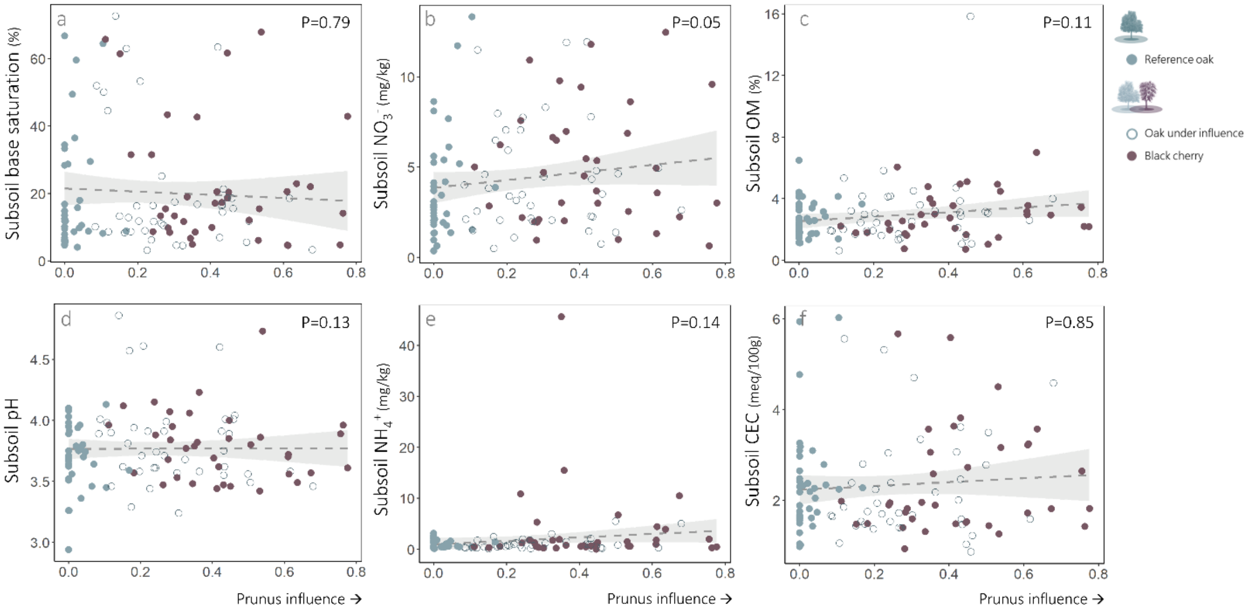

Figure S7: Subsoil base saturation, NO$_3^-$ concentration, organic matter (OM), pH, NH$_4^+$ concentration and CEC with Prunus influence. None of the relations is significant. Observations are indicated per type of selected tree: the reference oak (full dark green circle), the oak under influence (full light green circle) and the black cherry (pink circle).

Table S3: Standardized coefficients, standard deviations and P-values of fixed effects (intercept, Prunus influence, fine particle content and prunus*fine particle content interaction) of mixed models accounting for site as a random effect explaining different topsoil response variables.

Response	Intercept	Prunus influence	Fine particles	Interaction
OF+OH layer	**5.44 (±0.79) $^{P<0.001}$**	**-1.07 (±0.21) $^{P<0.001}$**	-1.13 (±0.75) $^{P=0.14}$	**-0.57 (±0.22) $^{P=0.009}$**
Topsoil base saturation	**22.35 (±2.72) $^{P<0.001}$**	**2.99 (±0.93) $^{P=0.001}$**	4.43 (±2.63) $^{P=0.09}$	**1.97 (±0.98) $^{P=0.05}$**
Topsoil pH$_{(NaCl)}$	**3.10 (±0.05) $^{P<0.001}$**	0.02 (±0.01) $^{P=0.15}$	-0.009 (±0.05) $^{P=0.97}$	-0.01 (±0.01) $^{P=0.35}$
Topsoil Al	**35.62 (±4.86) $^{P<0.001}$**	1.70 (±1.00) $^{P=0.09}$	1.19 (±4.50) $^{P=0.79}$	-1.07 (±1.07) $^{P=0.79}$
Topsoil OM	**7.02 (±1.20) $^{P<0.001}$**	**0.55 (±0.20) $^{P=0.009}$**	1.42 (±1.08) $^{P=0.18}$	**0.53 (±0.22) $^{P=0.018}$**
Topsoil CEC	**4.33 (±0.45) $^{P<0.001}$**	0.16 (±0.11) $^{P=0.15}$	-0.09 (±0.43) $^{P=0.83}$	**0.28 (±0.12) $^{P=0.018}$**
Topsoil NO_3^-	**23.17 (±4.62) $^{P<0.001}$**	**4.14 (±1.20) $^{P<0.001}$**	**14.59 (±4.39) $^{P=0.001}$**	**4.53 (±1.27) $^{P<0.001}$**
Topsoil NH_4^+	**6.40 (±0.98) $^{P<0.001}$**	0.24 (±0.48) $^{P=0.62}$	-1.39 (±0.96) $^{P=0.15}$	0.38 (±0.51) $^{P=0.46}$

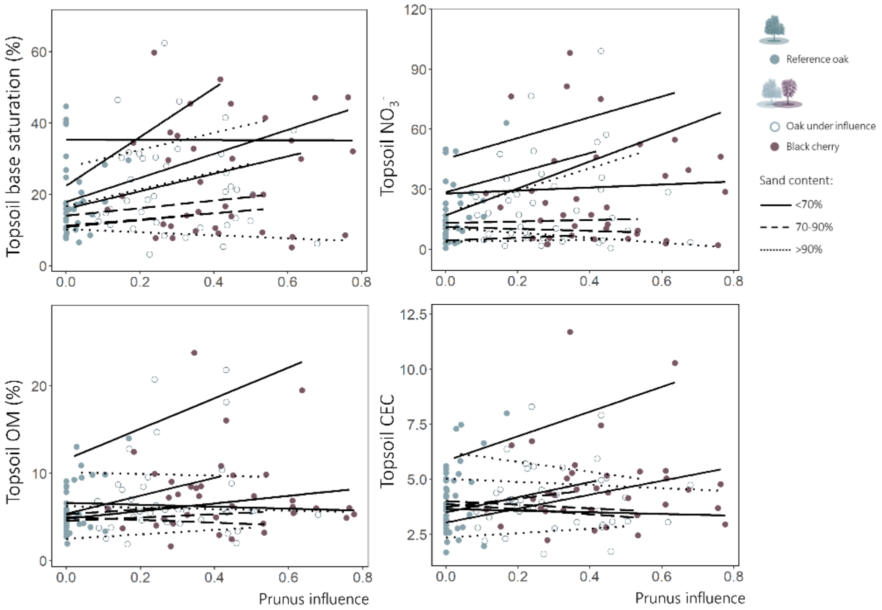

Figure S8: Linear relations of topsoil base saturation, topsoil NO_3^- concentration, topsoil organic matter (OM) and topsoil CEC with Prunus influence per site. Sites with a sand content lower than 70% are indicated by full lines, sites with a sand content between 70 and 90 % are indicated by dashed lines and sites with a sand content higher than 90% are indicated by dotted lines. Observations are indicated per type of selected tree: the reference oak (full dark green circle), the oak under influence (full light green circle) and the black cherry (pink circle).

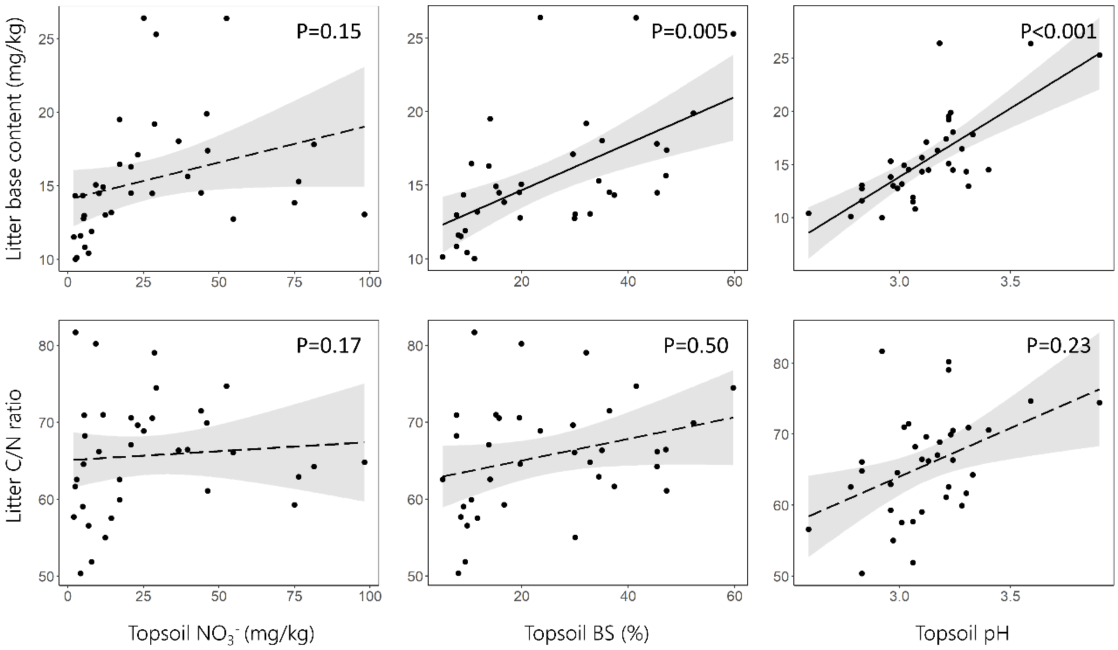

Figure S9: Linear relations of topsoil NO$_3^-$ concentration (mg/kg) (left), topsoil base saturation (%) (middle) and topsoil pH (right) with prunus litter quality variables litter base cation content (top) and CN ratio (bottom). The significance of the relationship wheb accounting for site as a random effect is indicated in the top right corner. Significant relations are indicated in full lines whereas relations that are not significant are indicated by dotted lines. This analysis is based on the cherry target trees (N=38).