Distribution of phosphorus fractions of different plant availability in German forest soils and their relationship to common soil properties and foliar P contents

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Abstract. Repeated, grid-based forest soil inventories such as the National Forest Soil Inventory of Germany (NFSI) aim,
10 among other things, at detecting changes in soil properties and plant nutrition. In these types of inventories, the only
information on soil phosphorus (P) is commonly the total P content. However, total P content in mineral soils of forests is
usually not a meaningful variable to predict the availability of P to trees. Here we tested a modified sequential P extraction
according to Hedley to determine the distribution of different plant available P fractions in soil samples (0-5 and 10-30 cm
depth) from 146 NFSI sites, capturing a wide variety of soil conditions. In addition, we analyzed relationships between these
15 P fractions and common soil properties such as pH, texture, and organic carbon content (SOC). Total P content among our
samples ranged from approximately 60 to 2800 mg kg^{-1}. The labile, moderately labile, and stable P fractions contributed to 27
%, 51 % and 22 % of total P content, respectively, at 0-5 cm depth. At 10-30 cm depth, the labile P fractions decreased to 15
%, whereas the stable P fractions increased to 30 %. These changes with depth were accompanied by a decrease in the organic
P fractions. High P contents were related with high pH-values. Whereas the labile Hedley P pool increased with decreasing
20 pH in absolute and relative terms, the stable Hedley P pool decreased in absolute and relative terms. Increasing SOC in soils
led to significant increases in all Hedley P pools and in total P. In sandy soils, the P content across all fractions was lower than
in other soil texture types. Multiple linear regression models indicated that Hedley P pools and P fractions were moderately
well related to soil properties (r² mostly above 0.5), and sand content of soils had the strongest influence. Foliar P contents in
Pinus sylvestris were reasonably well explained by the labile and moderately labile P pool (r² = 0.67) but not so for *Picea abies*
25 and *Fagus sylvatica*. Foliar P contents in all three species could not be related to specific Hedley P pools. Our study indicates
that soil properties such as pH, SOC content, and soil texture may be used to predict certain soil Hedley P pools of different
plant availability on the basis of large soil inventories. However, foliar P contents of tree species cannot be sufficiently well
predicted by the soil variables considered here.

1   Introduction

Insufficient or even critical phosphorus (P) nutrition in forest trees has been repeatedly observed in Europe during the last decades (e. g. Jonard et al., 2015). A large proportion of forest trees which were examined within the framework of the Second National Forest Soil Inventory in Germany (NFSI I-II) showed an insufficient P nutrition (*Picea abies* L. H. Karst and *Pinus sylvestris* L. both 20 % and *Fagus sylvatica* L. 60 % of all sampled trees) (Ilg, 2007; Wellbrock et al., 2016). In contrast to agriculture, where permanent P export is compensated by fertilization, forest sites in Germany have received no or only very limited amounts of P fertilizer in the past (Ilg et al., 2009). There has been some P fertilization to accelerate stand establishment after planting and also admixing of P to dolomitic lime that has been broadcast to compensate soil acidification through acid rain (Hoecke, 2006; v. Wilpert et al., 2013). In undisturbed forest ecosystems, P cycling is not dominated by input (e.g. deposition) and output (e.g. seepage) processes but by internal recycling (transfer) processes (Newman, 1995). However, even undisturbed forest ecosystems in temperate regions develop in the long term a negative P balance (Smil, 2000; Walker and Syers, 1976). In anthropogenically influenced forest ecosystems, the ongoing acidification and nitrogen deposition may lead to nutrient imbalances affecting P nutrition in trees (Duquesnay et al., 2000; Prietzel and Stetter, 2010; Talkner et al., 2015). Furthermore, high levels of ongoing harvesting and export of forest biomass may aggravate P malnutrition in trees (Berndes et al., 2003; Kangas and Baudin, 2003).

It has been shown that total P content in mineral forest soils is not a significant predictor of tree nutritional status, expressed as foliar P content, in different tree species (Ilg et al., 2009). This indicates that most soil P is not or not directly plant available. Correlations between total soil P and foliar P contents have been observed in a few studies, e.g. for *P. abies* (Rs = 0.54) or *F. sylvatica* (Rs = 0.38) (Ilg, 2007). It has been assumed that foliar P may be more closely related to plant available soil P fractions (Ilg, 2007). However, in forests, unlike in many agricultural systems with annual crops, it has been difficult to identify a single measure or fraction of plant available soil P that can predict tree nutritional status sufficiently well. This may be related to the many mechanisms that trees developed to cope with nutrient poor soils, including mycorrhizal symbioses, root architecture and root exudates supporting uptake of apparently unavailable P stocks and internal recycling (Fox et al., 2011; Hinsinger, 2001; Hinsinger et al., 2011; Lang et al., 2017; Schachtman et al., 1998).

Other approaches that comprise the quantification of a number of different P fractions in mineral soils have been successfully employed for forest soils to describe potential sources of P uptake by trees. One analytical approach that allows for the partitioning of total P in mineral soils into fractions of different (plant) availability is the Hedley fractionation method (Cross and Schlesinger, 1995; Hedley et al., 1982; Tiessen and Moir, 2008). The original method (Hedley et al., 1982), which was modified by Tiessen and Moir (2008), provides all in all seven inorganic and four organic P fractions. Often these P fractions are grouped into pools of distinct plant availability. A labile, fast cycling pool (labile P), which is considered to supply short-term P demand of plants, a slow cycling pool (moderately labile P), which can be converted into labile P forms, and a pool of occluded P (stable P), which is assumed to hardly contribute to plant nutrition in the short-term (Guo & Yost, 1998; Stevenson & Cole, 1999; Johnson et al., 2003). There are a number of studies that have examined changes in P stocks in forest ecosystems

using the Hedley fractionation method. Some of them followed the development of P fractions over time to gain information on the relevance of these P fractions for tree nutrition during ecosystem development (Richter et al., 2006; De Schrijver et al., 2012). In other studies, the approach was used to investigate influences of different forest management systems on the distribution of P fractions in soils (Alt et al., 2011). These were case studies at single sites or only at few different sites and

5   thus had only a limited population of inference (the population to which the results from the sample can be extrapolated) (Binkley and Menyailo, 2005). To our knowledge, no studies so far have addressed the distribution of Hedley P fractions and P pools in forest soils on the basis of large scale inventories. Thus, there is little information on how different soil variables such as pH-value, C and N content or soil texture, which have been found to influence P availability (Alt et al., 2011; Franzluebbers et al., 1996; Prescott et al., 1992; Silver et al., 2000; Stevenson and Cole, 1999; Thirukkumaran and Parkinson,

10   2000; Turner et al., 2007) affect the distribution of different P fractions across a variety of forest soil types. Therefore, we determined the Hedley P fractions in mineral soil samples from 145 sites of the National Forest Soil Inventory of Germany, covering a wide range in P content and many different soil parent materials (Niederberger et al., 2015). With this study we addressed the following questions:

15   1)   How do commonly measured soil properties such as pH-value, soil organic carbon content, and soil texture influence the distribution of Hedley P fractions, representing different P pools believed to have different bioavailability?

2)   Are foliar P contents of trees related to specific Hedley fractions or pools of soil P or other soil variables?

2   Material and Methods

2.1   Sites and Samples

20   For the purpose of our study, we used archived soil samples from the National Forest Soil Inventories of Germany (NFSI I and II) including samples from the state of Baden-Wuerttemberg which originated from the first NFSI I in 1990, samples from the states of Hesse, Lower Saxony and Saxony-Anhalt which originated from the second NFSI II in 2006. In total, 285 archived soil samples from 147 sites (Figure 1) were included in this study. In most cases, two depths, 0-5 cm and 10-30 cm, were analyzed for each site. For 0-5 cm depth, 145 samples and for 10-30 cm depth 140 samples were available. The selected

25   samples represented a wide range of total P contents (Table 1). Additional soil and site data as well as foliar element concentrations were provided by the Thünen-Institute, the Forest Research Institute of Baden-Wuerttemberg, and the Northwest German Forest Research Institute. Here, we used pH-value, C and N content (Table 1) and soil type, forest floor type, soil texture and dominant tree species as predictor variables. Sampling approaches and analytical methods used in the NFSI have been described in detail by Wolff and Riek (1996).

Table 1: Variation in selected variables of soil samples from the National Forest Soil Inventory of Germany.

Figure 1: Location of the 147 sample sites from the National Forest Soil Inventory of Germany (NFSI) data set; B: Baden-Wuerttemberg (n=70); H: Hesse (n=23); L: Lower Saxony (n=34) and S: Saxony Anhalt (n=20).

5 To analyze the effects of soil variables on distribution of P across fractions of different plant availability, we classified the samples by their variation in soil properties. To classify them by pH-value, we used the buffer ranges suggested by Ulrich (1981). In relation to SOC content of mineral soil, samples were grouped into classes of "low" (< 1.2 % SOC), "medium" (1.2-2.8 % SOC), "high" (2.8-5.6 % SOC), and "very high" (>5.6 % SOC) content following the German soil assessment protocol for forest soils (Ad-hoc-Arbeitsgruppe Boden, 2005). Furthermore, we grouped samples into the broad texture classes sand

10 (s), loam (l), silt (u) and clay (t), following the German soil assessment protocol for forest soils (Ad-hoc-Arbeitsgruppe Boden, 2005).

For 118 NFSI sites, foliar P contents of the main tree species (*F. sylvativa, P. sylvestris,* and *P. abies*) were available. Foliar P contents for broad leaved trees were measured in leaves from the upper crown. In conifers, current year needles from the seventh whorl were used. Leaves and needles were collected in the same year as the soil samples.

2.2   Phosphorus Fractionation

The P fractionation was done using the Hedley method (Hedley et al., 1982) modified by Tiessen and Moir (2008). For this purpose, 0.5 g soil was repeatedly extracted by different extractants with increasing chemical strength (Figure 2). A detailed description of the fractionation procedure used in this study is provided in Niederberger et al. (2015, 2016).

Figure 2: Sequential P fractionation schema according to Hedley modified by Tiessen and Moir (2008); grey boxes indicates fractions with organic and inorganic P forms; dashed line separates Hedley P pools of different availability, after Niederberger et al., (2015).

2.3   Total phosphorus

25 The NFSI provides total P contents for individual soil samples, which is determined in different labs employing different analytical methods for its measurement. In a preliminary study, we found considerable differences between this total P (of the NFSI) and the sum of our Hedley fractions. Therefore we carried out an additional, independent analysis to determine total P. For reasons of comparability with the Hedley fractionation procedure we used the nitric acid digestion to quantify this additional measure of total P. It should be kept in mind though that this analytical procedure might underestimate the real total

30 P content in mineral soils (BMEL, 2014; Schwartz and Kölbel, 1992). This measure of total P content served also as a control to verify the recovery rate of the sum of Hedley P fractions, see also Niederberger et al. (2015).

2.4   Statistical analyses

In a first step, data were analyzed using descriptive statistics. Since most of our soil and site data were not normally distributed (Shapiro-Wilk-Test, p<0.05), we used non-parametric tests to identify significant differences in Hedley P pools or P fractions related to soil properties.

To compare variables between soil depths, we used the paired non-parametric Wilcoxon test. To compare variables among different soil classes within the same soil depth, for instance classes of different SOC content, we used the non-parametric Mann-Whitney-U-test.

In addition, we used linear regression models to explain Hedley P pools and P fractions with the predictor variables depth, pH, SOC, and soil type. For modelling soil P content, we applied a log transformation to the Hedley P fractions and P pools. Transformations of the major soil types (sand, loam, silt and clay) into grain size distribution (expressed as sand content) led to considerable model improvements. To transform soil type information in this way, we used mean values of sand content found in specific soil types based on the German soil assessment protocol for forest soils (Ad-hoc-Arbeitsgruppe Boden, 2005). To assess further model improvements we separated our sample set into calcareous and non-calcareous soils, since we expect here strong differences in processes affecting P availability (Prietzel et al., 2104). Despite the large number of sites included in our survey, there were only 8 out of 143 with pH > 6.5. Since this number is too low to develop robust statistical models for this collective of samples, we could only test whether model results for the group of soils with pH < 6.5 (non-calcareous soils) did change when calcareous soils were excluded. However, we found only some minor improvements as well as some minor deterioration of model quality. Hence, for all further analyses, calcareous soils were not separated from the other soil samples. Furthermore, we used linear regression models to test whether foliar P contents of *F. sylvatica, P. abies,* and *P. sylvestris* could be explained by the predictor variables pH, SOC, soil texture as well as the soil content of different Hedley P pools and fractions. In addition we calculated models with stocks of total Hedley P and P Hedley P pools as predictor variables, to see whether these might improve the statistical models. However, these models based on P stocks were of consistently lower model quality. For that reason, they will not be reported in the results section. Predictor variables used for model building were checked for correlation with Pearson correlation coefficients (r<0.7), for multiple collinearity with VIF (variance inflation factor, <10) and condition number test (<30) as well as for auto correlation (Durbin-Watson). For all regression models, we used the stepwise backward method where nonsignificant predictors (p > 0.05) were progressively excluded. All statistical analyses were performed with SPSS 24 (IBM, 2011).

3   Results

3.1   Total P

The total P content calculated as the sum of all Hedley P fractions ranged from 58 to nearly 2800 mg kg^{-1} across the 285 NFSI samples. The independently determined total P values (nitric acid digestion) ranged from 42 to nearly 2300 mg kg^{-1} and were

closely related to Hedley P sums (Spearman rs = 0.98, α<0.001). The difference between the two measures of total P was not statistically significant (Wilcoxon paired rank sum test, α=0.05) (Niederberger et al., 2015).

3.2 Distribution of P fractions with soil depth

The sum of stable P fractions (P HCl$_{conc}$ and Pi residual) increased with increasing depth, whereas the total P content (as sum of all Hedley fractions) at 10-30 cm depth was lower than at 0-5 cm depth (Fig. 3). The proportion of total P in the stable Hedley P pool increased with depth (from 22 % to 30 %) while the portion of the labile Hedley P pool decreased (from 27 % to 15 %) (Table S1). The portion of moderately labile Hedley P, although decreasing significantly in absolute values (Figure S1), showed no distinct change with depth.

Figure 3: Boxplots of Hedley P fractions and P pools in mineral soil samples from 0-5 and 10-30 cm depth (all values in mg kg^{-1}); asterisks indicate significant differences between depths, paired non-parametric Wilcoxon test, *** α<0.001, ** α<0.01.

Organic P forms were the largest single fractions within labile and moderately labile Hedley P pools at both depths. At 0-5 cm depth, organic P forms contributed even more than the sum of the inorganic forms to these two Hedley P pools (Fig. 3). At 0-5 cm depth, contents of all labile P fractions were significantly higher than at 10-30 cm depth. While organic P in the moderately labile pool (Po NaOH) decreased with soil depth, this was not the case for inorganic P in this pool (Pi NaOH and Pi 1M HCl). The stable fractions P HCl$_{conc}$ and residual Pi showed no significant change with soil depth.

3.3 The influence of soil pH on distribution of P fractions

Figure 4: Total soil P and P in pools of different plant availability (means), grouped by pH-classes and soil depths; lower case letters indicate significant differences between pH-classes within P pools and per depth (non-parametric Mann-Whitney-U-test, α < 0.05).

Total P decreased with increasing soil acidity (Fig. 4). This decrease was mainly attributable to a significant decline in the pool of stable Hedley P fractions, which decreased both in absolute as well as relative terms. The portion of stable P dropped from 48.7 % to 16.0 % of total P at 0-5 cm depth and from 56.8 % to 26.0 % at 10-30 cm depth (Fig. 4). In contrast, the labile P pool in surface soils (0-5 cm) increased significantly in absolute as well as relative terms with increasing acidity. At 10-30 cm depth, absolute quantities of labile P remained relatively constant, whereas its relative share of total P increased with increasing acidity (Fig. 4). The moderately labile Hedley P pool showed comparatively small differences between pH classes at both depths. Only at 10-30 cm depth, this pool was significantly smaller in the most acidic soils when compared to other pH-classes. Considering individual P fractions, we found for all labile P fractions an increase of P content with decreasing pH-value at 0-5 cm depth (Table S2), but this was significant only for the Po HCO$_3$ fraction. At 10-30 cm depth, labile P fractions also increased with decreasing pH-value up to a maximum at pH 4.2-5.0 but then declined for the most acidic soils (pH 3.0-4.2).

At both soil depths, the proportion of the Pi NaOH fraction increased from neutral to acidic conditions, except for the most acidic soil group. Whereas the size of the Po NaOH fraction was unrelated to soil pH at 0-5 cm depth, it declined in the most acidic soils at 10-30 cm depth. For the Pi 1M HCl fraction we found inconsistent but significant differences among pH classes at 0-5 cm and 10-30 cm depth. At both depths, the lowest content was found in the most acidic soils. The two stable P fractions P HCl_{conc} and P residual showed clear and consistent significant decreases with decreasing pH at both depths (Table S2 and S3).

3.4 The influence of soil organic carbon on distribution of P fractions

Total P as well as P in all Hedley fractions increased strongly and significantly with increasing SOC content in mineral soil at both depths (Fig. 5). In contrast, the relative proportions of Hedley P pools showed no or only minor changes with increasing SOC at both depths (Fig. S2, Table S4 and S5).

Figure 5: Hedley P pools and total P (mean values), grouped by SOC content in % and depth; n = number of observations, lower case letters indicate significant differences in P pools among SOC classes and per depth, non-parametric Mann-Whitney-U-test, α < 0.05. The column with no letters had too few observations for statistically valid tests for differences.

3.5 The influence of soil texture on P fractions

Total P and in particular the stable Hedley P pool increased with decreasing particle size from sand to clay. The lowest contents of total P as well as P in the stable and moderately stable fractions were found in sandy soils at both depths (Fig. 6). In particular, the 1M HCl soluble P fractions showed extremely low P contents in sandy soils (Table S6). Accordingly, the highest proportion of labile P was also found in sandy soils; 40 % at 0-5 cm and 35 % at 10-30 cm depth. The proportion of labile P decreased with decreasing grain size. At 10-30 cm depth, the increase in total P with increasingly finer soil texture was mainly caused by stable P forms.

Figure 6: Hedley P pools and total P (mean values) grouped by soil texture and depth, n = number of observations, lower case letters indicate significant differences in Hedley P pools among soil texture groups, non-parametric Mann-Whitney-U-test, α < 0.05.

3.6 The combined influence of soil variables on Hedley P pools and P fractions

Table 2: Adjusted R^2 values and standardized regression coefficients of linear regression models between predictor variables and log transformed Hedley P pools and P fractions for soil samples from 0-5 cm depth.

The best linear regression models were found between soil variables and organic P fractions in labile and moderately labile and stable Hedley P pools, whereas model quality for the inorganic P forms were considerably lower (Table 2). Sand content was a negative predictor in all cases, whereas SOC was always a positive predictor. In contrast, pH value was a negative predictor for labile P and in particularly labile organic P, but positive for stable P forms.

5 For labile Hedley P pool and the organic P fractions, the SOC had a stronger influence than the sand content, whereas the reverse was true for stable Hedley P pools. For moderately labile P, both predictors were similarly important, except for the 1M HCl soluble P fraction, where SOC content was not a significant predictor.

Models with a goodness of fit above 0.4 (Table 2) were only obtained for organic P fractions (Po HCO$_3$, Po NaOH) or P fractions with high portions of organic compounds (P HCl$_{conc}$) and fractions which are dominated by soil parent material (P
10 HCl$_{conc}$, P residual). As an exception, the 1M HCl soluble P fraction was the only inorganic P fraction with a model quality above 0.4.

In samples from 10 to 30 cm depth (Table S7), we found in general lower model qualities but comparable patterns to those observed at 0-5 cm depth.

15 **3.7   The influence of soil variables and Hedley P pools and P fractions on foliar P contents**

Total soil P as well as Hedley P pools of different availability varied considerably between NFSI plots dominated by different tree species (Figure 7). Under *P. sylvestris,* all soil Hedley P pools were significantly lower than under *F. sylvatica* or *P. abies*, yet the relative proportion of labile P was greatest under *P. sylvestris*. The differences in Hedley P pools between *P. abies* and *F. sylvatica* were mostly small and significant only for the stable Hedley P pool.

Figure 7: Boxplots of Hedley P pools and sum of all Hedley fractions in mineral soils of analyzed NFSI plots, separated by main tree species. Different letters indicate significant differences between P pools resp. Hedley P sum in subject to tree species (non-parametric Mann-Whitney-U-test, α < 0.05).

25 The quality of the linear regression models for foliar P content varied considerably amongst the examined tree species. For *F. sylvatica* and *P. abies* the adjusted r² of models did not reach 0.5. In contrast, models to explain foliar P content of *P. sylvestris* through Hedley P pools and soil variables at 0-5 cm depth were of considerably higher quality. Here Hedley P pools were the most important predictors, whereas soil variables played only a minor role. Interestingly, the moderately labile P pool had a negative influence on foliar P content in *P. sylvestris* at 0-5 cm depth. In all multiple linear regression models, at least one of
30 the three soil Hedley P pools was found to be a significant predictor of foliar P content (Table 3), however no specific Hedley P pool was significant in all cases. Remarkably, SOC content in soils under *F. sylvatica* was a negative predictor for foliar P content, whereas in contrast, SOC content was always a positive predictor for mineral soil Hedley P pools including labile P

(see chapter 3.4). With the exception of *P. abies* soil samples from 0 to 5 cm depth, Hedley P pools had a stronger influence on model quality than the other soil variables in all other models.

However, the vast majority of the relatively low number of needle samples of *P. sylvestris* originated from sites with very similar soil properties (same forest floor type, soil texture, soil type, and pH class) and in general very low total P contents (significantly lower than in *P. abies* and *F. sylvatica* (Table 2)).

Table 3: Model quality, regression constants and standardized, significant regression coefficients of linear regression models to explain foliar P content with Hedley P pools of different availability and other soil variables (pH, SOC and sand content) determined at 0-5 and 10-30 cm soil depth.

Multiple linear regression models to predict foliar P content in the three tree species with soil variables and P pools from 0-5 and 10-30 cm depths achieved a moderate quality when applied across the three species (Fig. 8). However, they were not suited to predict foliar P contents when datasets were considered for each of these species separately.

Figure 8: Linear regressions to predict foliar P content in *P. abies*, *P. sylvestris*, and *F. sylvatica* (see Table 3) with soil variables (pH, SOC and sand content) from 0-5 (left panel) and from 10-30 cm depth (right panel), x-axis measured and y-axis modelled foliar P content in mg g^{-1}.

4 Discussion

4.1 The influence of soil properties on Hedley P pools and fractions

Our results show that soil properties like acidity, SOC content, soil texture and depth have an important influence on the quantity and distribution of plant available P in forest soils. Yet there have been very few studies that investigated this issue (Augusto et al., 2017; Buckingham et al., 2010; Shang et al., 1992; Zederer and Talkner, 2018).

In our analysis there was no single soil variable that was consistently the best predictor of the different Hedley pools or fractions. However, there were consistent patterns such as that SOC content always had a positive and sand always a negative influence. In contrast, the influence of pH, which was never a stronger predictor than either SOC or sand, could be positive or negative. Labile Pi fractions could not be sufficiently well explained (r^2>0.4) with the chosen soil variables. They may be more influenced by soil biological processes, which were not captured in our study. In contrast, organic P fractions were well described by SOC content. Sand content was the strongest predictor of variation in moderately labile and stable Hedley P fractions and pools. This reflects the influence of soil clay content, which is inversely related to sand content, on these fractions (e.g. Zederer and Talkner, 2018). The magnitude of stable soil P pools was strongly and positively related to pH at both soil depths, whereas the moderately labile pool was, in absolute terms, little affected by soil pH.

In the following discussion, we first address the general assumptions regarding the influence of these variables on P distribution in mineral soils and relate them to our results. Secondly, we discuss the results of the regression models that were used to examine the relationship between Hedley P pools or fractions and foliar P content of *F. sylvatica, P. abies,* and *P. sylvestris*.

4.1.1 Soil depth

The vertical distribution of P in the soil profile is dominated by biological turnover processes. Plant P uptake and transformation of inorganic into organic P in combination with microbial activity lead to an enrichment in organic and labile P and hence also in total P in the topsoil and forest floor layers (Jobbagy and Jackson, 2001). This could be clearly demonstrated by our results which showed significantly higher amounts of organic P forms as well as labile Hedley P in the upper soil layer. Furthermore, our findings of significant decrease in organic P fractions (Po NaHCO$_3$, Po NaOH) with decreasing soil depth are in accordance with earlier studies (Condron et al., 2005; Turner et al., 2003) which described a strong influence of microbial activity on organic P accumulation in the topsoil layers, and a concomitant decrease of Po and SOC with soil depth (Jobbágy and Jackson, 2000).

Our results are also in agreement with the observation of a relative accumulation of more stable inorganic P forms in deeper soil layers by P fixation for instance as secondary P minerals or in clay minerals (Buckingham et al., 2010; Vitousek et al., 2010). This increase of moderately labile and stable Pi forms was, however, not significant, which may be related to the limited profile depth investigated.

4.1.2 Soil pH

Solubility and fixation of soil P is strongly affected by soil acidity (pH) (Hinsinger, 2001; Shang et al., 1992; Stevenson and Cole, 1999). Optimum availability of P to plants occurs typically around pH 6.5. At pH below 6, P is being fixed as Fe or Al phosphates or adsorbed to oxide surfaces (Shang et al., 1992; Stevenson and Cole, 1999) and above a pH of 7, P is being fixed in the form of Ca phosphates (Stevenson and Cole, 1999). It has been shown that there are considerable changes in the relative importance of P fractions with pH even if there is only a minor influence of pH on total P (Turner and Blackwell, 2013). For example, phosphonates were only found in acidic soils and the amount of P in DNA increased with increasing soil acidity (Turner and Blackwell, 2013). However, specific organic P forms can unfortunately not be picked up by the Hedley fractionation and thus we could not analyze these pH-related shifts.

In accordance with other studies, the highest portion of labile P was found in the most acidic soil samples (Alt et al., 2011; Turner and Blackwell, 2013). The decrease in labile organic P with increasing pH might be caused by its enhanced mineralization in soils with more favorable acid-base status for microbes (Stewart and Tiessen, 1987). In contrast to Turner and Blackwell (2013), we observed a positive influence of pH on total P contents at both soil depths. This disagreement between the studies may be attributed to the much larger and more variable data set used in our study.

The contrasting effects of pH, negative on labile P and positive on stable P forms, might be explained by the different processes that influence P availability and fixation in mineral soils at different pH (Hinsinger, 2001; De Schrijver et al., 2012). The negative impact of increasing pH on labile P might be caused by enhanced decomposition of organic matter by microorganisms at higher pH and increased mixing of organic matter with the mineral soil matrix (Paré and Bernier, 1989; Scheffer and Schachtschabel, 2010). Likewise the positive effect of pH together with higher portions of clay minerals on stable P may be explained by increasing fixation of P by clay minerals(Sugihara et al., 2012) and occurrence of primary and or secondary P containing minerals in soils at higher pH (Hinsinger, 2001).

4.1.3   Soil organic Carbon content

Since organic P forms can account for more than 50 % of total P in mineral soils (Fox et al., 2011; Stevenson and Cole, 1999; Turner, 2008), we assumed a strong influence of SOC on the distribution of P in mineral soils. In agreement with expectations, total P and all P fractions increased with increasing SOC content, whereas the relative contribution to total P of P in pools of different availability remained stable (Fig. 5). Like other studies, we found a strong positive correlation between SOC and total organic P content (rS = 0.77) in mineral soils (Cleveland and Liptzin, 2007; Perakis et al., 2017; Zederer and Talkner, 2018). In accordance with Johnson et al. (2003), we found an increase in inorganic P fractions with rising SOC content. This increase with SOC may be caused by higher microbial turnover as a source of labile Pi (Condron et al., 2005; Johnson et al., 2003). In our dry, archived samples, the relationship between SOC and Pi, in particularly in the labile Hedley P pool, might have been more pronounced owing to microbial P released during the soil drying process (Johnson et al., 2003; Tiessen and Moir, 2008). Our analyses indicated that SOC is a strong positive predictor of labile and moderately labile Hedley P and to a lesser extent also for the stable Hedley P pool.

The rather constant relative proportions of stable, moderately labile, and labile Hedley P pools across soils with different SOC contents (Fig. 5) and the close relationship between SOC and P (Johnson et al., 2003) suggests that these pools may be predicted by SOC content.

4.1.4   Soil texture

The significantly lower P in all Hedley fractions in sandy soils when compared to other soil texture types may be related to lower organic matter content, fewer possible fixation opportunities e.g. at clay minerals and higher acidity in these soils. Strong negative correlations between sand content and organic P and strong positive correlations with inorganic P were found in agricultural soils, whereas silt content had the opposite effect (O'Halloran et al., 1985). These were explained by sorption of phosphate monoesters at clay minerals. Likewise, we interpret the negative influence of sand content on total P content in all significant models of our study as the decreasing amount of surfaces to which P could be adsorbed or fixed. Since 2:1 clay minerals are able to fix P, the absence of clay minerals can lead to considerably lower P content in sandy soils (Buckingham

et al., 2010). Further, it has been shown that sand content had a direct negative influence on P content in soils of all climate zones worldwide (Augusto et al., 2017). To our knowledge, the effect of texture on P distribution in forest soils has been described so far only in one publication (Zederer and Talkner, 2018). In forest soils of northern and central Germany, strong positive effects of clay minerals on Po content were identified (Talkner et al., 2009; Zederer and Talkner, 2018). In soils from

5   NFSI plots under *P. sylvestris* (Figure S3), which were located mostly on sandy soils, labile and moderately labile P forms were most strongly influenced by SOC content and in some cases pH, indicating a dominance of microbiological processes, whereas stable P forms were solely influenced by soil type. With increasingly finer soil texture, increased higher total P contents were observed, but this was largely attributable to increases in the stable fraction, whereas there were no or only minor increases in the labile or moderately labile Hedley pools, confirming results from earlier studies (Tiessen et al., 1983,

10 Tiessen et al., 1984). These results show that in particular the proportion of stable Hedley P pools may be influenced by soil texture.

4.2   Foliar P content in relation to soil variables and Hedley P pools

Nutrient content in leaves and needles are subjected to strong spatial and temporal (inter- and intra-annual) variability (Netzer

15 et al., 2017; Rennenberg and Herschbach, 2013). Therefore, statistical models to explain the foliage nutrient content based on soil properties should be based a large number of replicate foliage samples to capture the spatial heterogeneity as well as the temporal variation (Wehrmann, 1959), which may be caused climatic conditions or mast years. Unfortunately, the NFSI provides data on foliage nutrient content for only one point in time, and based on a small sample from three trees per plot (Wellbrock et al., 2016). Therefore, the low quality of our statistical models may be partially caused by the sampling design

20 of the NFSI, and could be improved by collecting foliage samples in several consecutive years (Zederer and Talkner, 2018). The mean values of Hedley P pools of different availability in forests soils stocked with different main trees species (Figure 7) indicated considerable differences in P availability. Whereas for *P. abies* and *F. sylvatica*, no significant difference in P pools were observed, except for a significantly lower stable Hedley P pool under spruce, there was significant less P in all pools under *P. sylvestris*. This raises the question whether low foliar P contents in trees can be linked to insufficient amounts

25 of labile P, which is assumed to be plant available in the short term. A rough calculation of labile P in profiles of the NFSI sites suggests that this is not the case. Based on mean stone content and typical bulk densities for these depths, the calculated average stocks of labile P in topsoil (0-30 cm depth) were 340 kg P ha^{-1} in *P. abies* and *F. sylvatica* stands and about 200 kg P ha^{-1} in *P. sylvestris* stands. The estimated average annual uptake demand of about 4 kg P ha^{-1} by *P. abies* or 6 kg P ha^{-1} by *F. sylvatica* (George and Marschner, 1996) would be easily matched by the P in the labile Hedley pool in all cases. This

30 suggests that either not all labile P is available to trees in the short term or that the foliar P concentrations are not chiefly controlled by P uptake.

Yet, some earlier studies indicated that there was a correlation, albeit not strong, between total P content in soil and tree nutrition for *P. abies* (Rs 0.54) and *F. sylvatica* (Rs 0.38) (Ilg et al., 2009; Khanna et al., 2007). Other studies showed that P

fertilization led to a significant increase in foliar P content (Prietzel and Stetter, 2010). In our study there was no single mineral soil Hedley P pool or soil variable that was consistently the best or unique predictor of foliar P content in the different tree species. There are several studies using other P extraction methods to explain P foliar content (Manghabati et al., 2018; Prietzel and Stetter, 2010). Prietzel and Stetter (2010) found P extractable with citric acid to be a good predictor to explain P foliar

5   content of *P. sylvestris*. Manghabati at al. (2018) compared a series of different extractants, from pure H_2O, over lactate, sodium bicarbonate, citric acid to aqua regia. They found that needle P content in *P. abies* was most closely related to soil P extracted with citric acid and sodium bicarbonate. For P leaf content in *F. sylvatica*, total P content was also good predictor variable, at some soil depths even the best (Manghabati et al., 2018). Similarly, total organic P and soil clay content were best predictors (r^2=0.6) to model foliar P content in *F. sylvatica* (Zederer and Talkner, 2018). However, in these studies, the

10   collective of analysed soils was much less heterogeneous regarding soil types and soil chemical and physical properties. Thus it is unlikely that those extraction methods or identified P fractions would be strong predictors of P nutrition in trees growing on a wide variety of soils as found in national inventories.

Foliar P contents in *F. sylvatica* and *P. abies* were related differently to Hedley P pools and soil properties. Foliar P content in *F. sylvatica* was explained by SOC content and stable as well as labile Hedley P pool, whereas in *P. abies*, foliar P content

15   was a function of sand content and the moderately labile Hedley P pool. The reason for this might be that the average sand content in mineral soil was twice as high under *P. abies* as under F. sylvatica. Thus, sites dominated by *F. sylvatica* had a considerably higher portion of stable organic P forms (P HCl_{conc}) which could lead to a negative influence of SOC on P nutrition. The finding that SOC has an important influence on foliar P content of *F. sylvatica* corresponds with findings of other studies and furthermore it indicates that the forest floor mass or thickness, or nutrient ratios like C_{org}/P_{org} should be

20   included as a variable to improve model quality (Talkner et al., 2015).

Our best multiple linear regression models for foliar P in *P. sylvestris* reached quality levels (r^2=0.67 at 0-5 cm and r^2=0.52 at 10-30 cm depth) that were comparable to the best model by Zederer and Talkner (2018) for *F. sylvatica*.

The model results for *P. sylvestris* indicated that the labile Hedley P pool could have a strong influence on P nutrition. Yet, the moderately labile P pool for *P. abies* and *P sylvestris* and the stable Hedley P pool for *F. sylvatica*, were also important

25   predictor variables to describe foliar P content. This indicates an important difference between forests and agricultural systems. In forests, P uptake may be not only from the labile but also from moderately labile or even the stable Hedley P pool (Niederberger et al. 2016). The latter may also replenish the labile Hedley pool during phases of reduced plant P uptake.

The results of the study of Magnhabati et al. (2018) are remarkable because total soil P was as good a predictor of P nutrient status in *F. sylvatica* as the P extracted with citric acid or sodium bicarbonate or as the labile Hedley P pool (Zederer and

30   Talkner, 2018; and this study). This suggests that the concept of P fractionation with specific extractants to quantify plant available pools of P is at least questionable. The notion that certain soil P pools or fractions are not suitable as a major or even single predictor of P availability in forest ecosystems is in accordance with recent advances in our understanding of more complex ecosystem processes as important drivers of P nutrition (Lang et al., 2016, 2017). At the same time, a recent study on tropical trees showed that foliar P content may have only limited indication strength for the physiological performance of

leaves (Mo et al., 2019). Hence it may be necessary, if we want to relate soil properties to tree growth, not only to identify soil P fractions crucial for plant nutrition but also P fractions in leaves, such as metabolic P and nucleic acid P, that are sensitive to changes in P availability and closely related to physiological performance.

5 Conclusions

Using the Hedley fractionation approach, we assessed the distribution of soil P forms of different availability in a range of German forest soils and analyzed relationships between these fractions and selected soil properties. Although our data set was not representative for German forest sites, it clearly showed that approximately half of the soil P is contained in moderately labile fractions, whereas stable and labile fractions contribute to approximately one quarter of total P in the upper mineral soil. With increasing depth, the labile Hedley soil P pool declines in favor of the stable Hedley pool. Common soil properties such as pH, SOC, and soil texture may be used to predict certain Hedley P pools in large forest soil inventories. However, additional soil and site variables should be considered to improve these models.

Despite high quantities of P in labile fractions in mineral soils, which greatly exceed the annual uptake demand of trees, correlations between these fractions and foliar P contents of *P. abies* and *F. sylvatica* were not stronger than for moderately labile fractions. Current statistical models using several soil properties and soil Hedley P pools of different plant availability are not capable to adequately explain the P nutrition status in tree foliage. However, these models may be developed further through use of larger and more balanced data sets, incorporation of other important variables such as the forest floor, or by separate analysis of soils types with very different properties related to P availability (e.g. carbonate soils).

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Table 1: Variation in selected variables for soil samples from the German Forest Soil Inventory

		n	Mean ± Stdv	Min	Max
0-5 cm	pH-H_2O		4.35 ±0.79	3.29	7.47
	SOC[g kg^{-1}]		66.04 ±35.04	11.42	178.0
	N_{tot} [g kg^{-1}]	143	4.00 ±2.13	0.13	12.35
	C/N		19.76 ±35.18	10.00	436.72
	P [g kg^{-1}]		0.61 ±0.37	0.09	2.22
10-30 cm	pH-H_2O		4.67 ±0.76	3.56	8.20
	SOC [g kg^{-1}]		19.29 ±17.55	0.21	115.00
	N_{tot} [g kg^{-1}]	140	1.38 ±1.15	0.11	8.13
	C/N		14.66 ±6.53	1.94	60.50
	P [g kg^{-1}]		0.48 ±0.35	0.04	2.29

Table 2: Adjusted R^2 values and standardized regression coefficients of linear regression models between predictor variables and log transformed Hedley P pools and P fractions for soil samples from 0-5 cm depth.

depth 0-5 cm	n = 143	predictor variables		
		SOC	sand	pH
		mg kg^{-1}	%	
target	r² [#]	standardized regression coefficients[§]		
log P labile	0.52	**0.518**	-0.374	-0.346
log P moderately labile	0.59	0.408	**-0.539**	
log P stable	0.60	0.132	**-0.566**	0.316
log pi resin	*0.35*	0.378	**-0.387**	-0.238
log Pi HCO$_3$	*0.22*	**0.331**	-0.262	
log Po HCO$_3$	0.61	**0.563**	-0.340	-0.479
log Pi NaOH	*0.35*	0.140	**-0.542**	
log Po NaOH	0.64	**0.505**	-0.488	
log Pi 1M HCl	0.41		**-0.582**	0.134
log P HCl$_{conc}$	0.55	0.146	**-0.544**	0.291
log P residual	0.47		**-0.472**	0.364

adjusted r², Hedley P pools or P fractions with model performance r² below 0.4 are shown in italics. § significant predictors (p < 0.05, F-Test) are shown, strongest predictor are presented in bold.

Table 3: Model quality and standardized, significant regression coefficients of linear regression models to explain foliar P content with Hedley P pools of different availability and other soil variables determined at 0-5 and 10-30 cm soil depth.

		n	r² #	P labile	P moderately labile	P stable	SOC mg kg⁻¹	sand (%)	pH
						standardized regression coefficients §			
Picea abies		61	*0.20*		0.255			**-0.288**	
Fagus sylvatica	0-5 cm	37	*0.28*	**0.507**		0.354	-0.495		
Pinus sylvestris		17	0.67	**1.191**	-0.620				
Picea abies		59	*0.27*		**0.361**			-0.293	
Fagus sylvatica	10-30 cm	35	*0.21*			**0.607**	-0.487		
Pinus sylvestris		16	0.52		**0.832**			0.777	

\# adjusted r², Hedley P pools or P fractions with model performance r² below 0.4 are shown in italics, § significant predictors (p < 0.05, F-Test) are shown, strongest predictor are presented in bold.
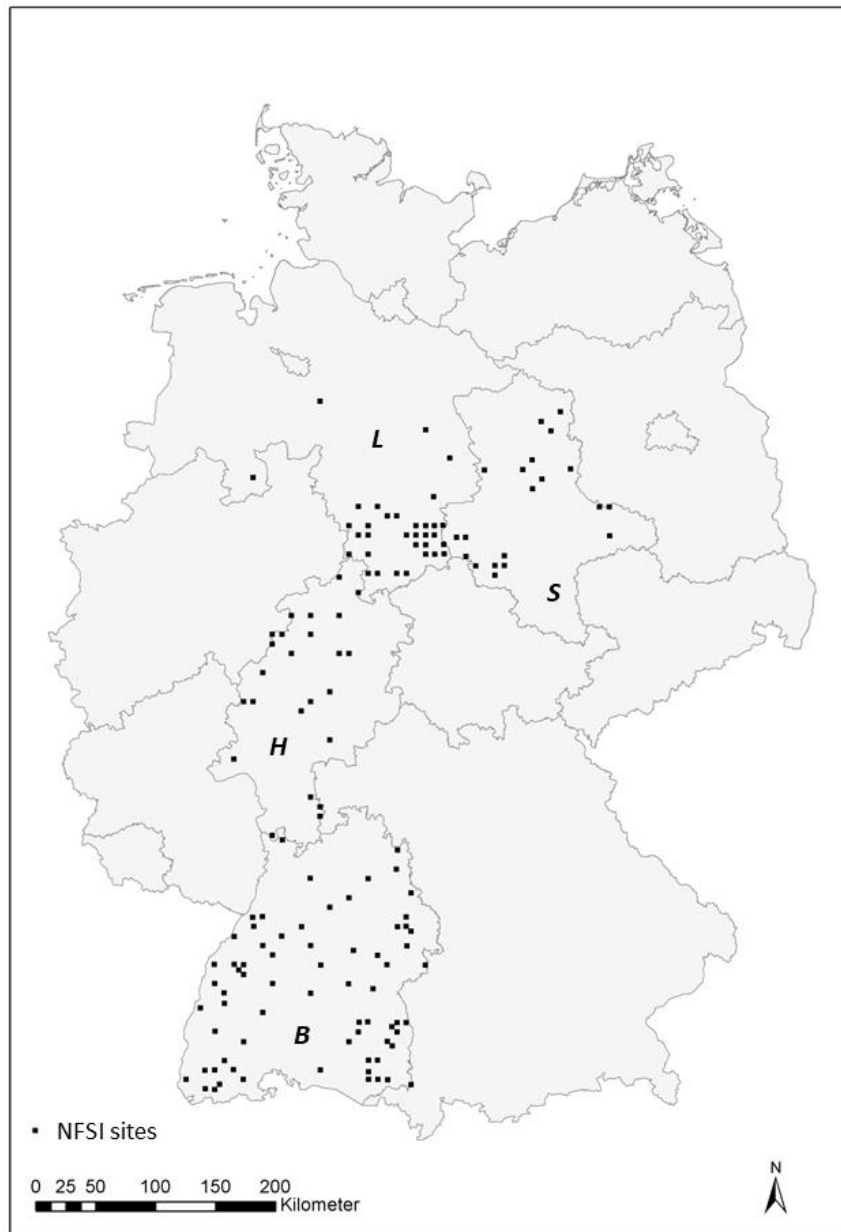
Figure 1: Location of the 147 sample sites from the German Forest Soil Inventory (NFSI) data set; B: Baden-Württemberg (n=70); H: Hesse (n=23); L: Lower Saxony (n=34) and S: Saxony Anhalt (n=20).
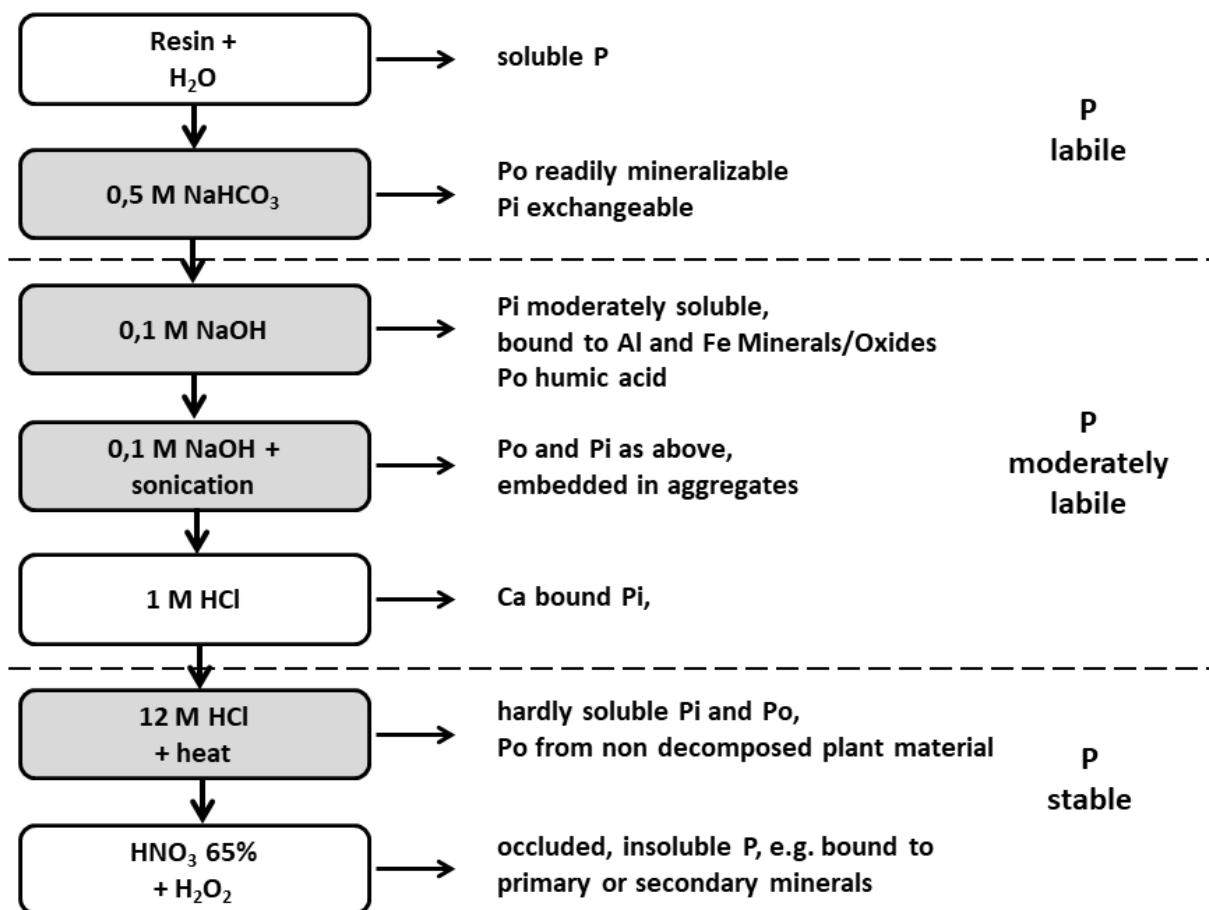
Figure 2: Sequential P fractionation schema according to Hedley modified by Tiessen and Moir (2008) ; grey boxes indicate fractions with organic and inorganic P forms; dashed line separate Hedley P pools of different availability, after Niederberger et al., (2015).
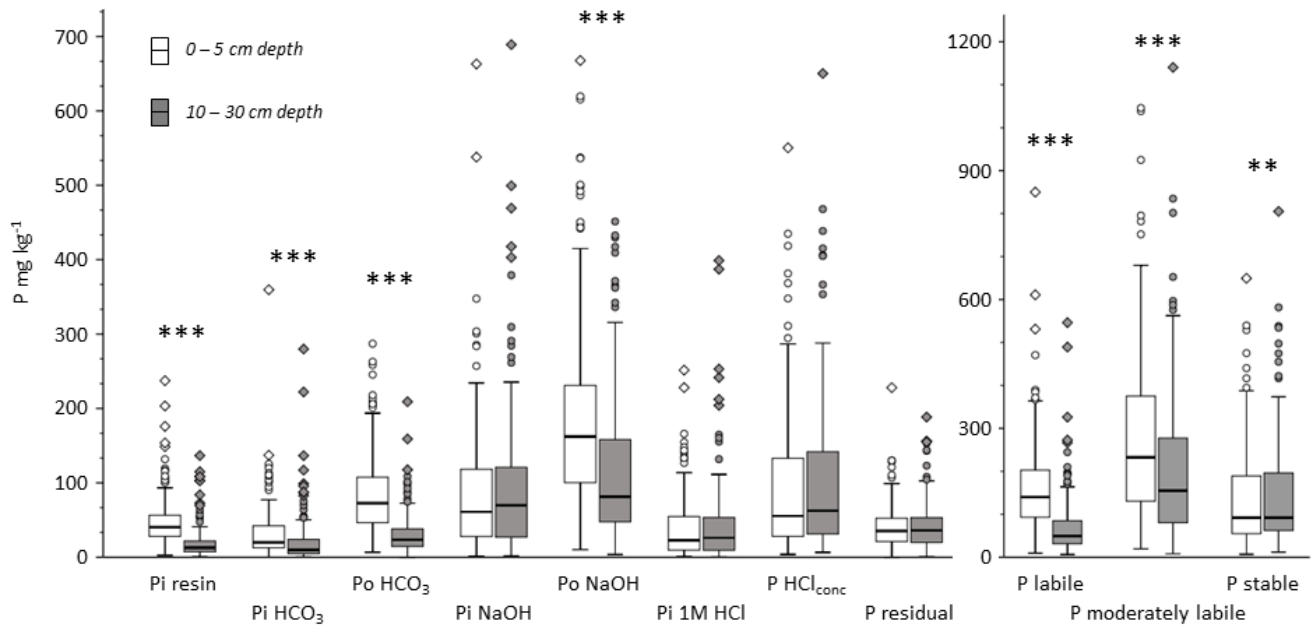
Figure 3: Boxplots of Hedley P fractions and P pools for all analyzed mineral soil samples separated by depth (all values in mg kg⁻¹); asterisks indicate significant differences between depths, paired non-parametric Wilcoxon test, *** α<0.001, ** α<0.01.
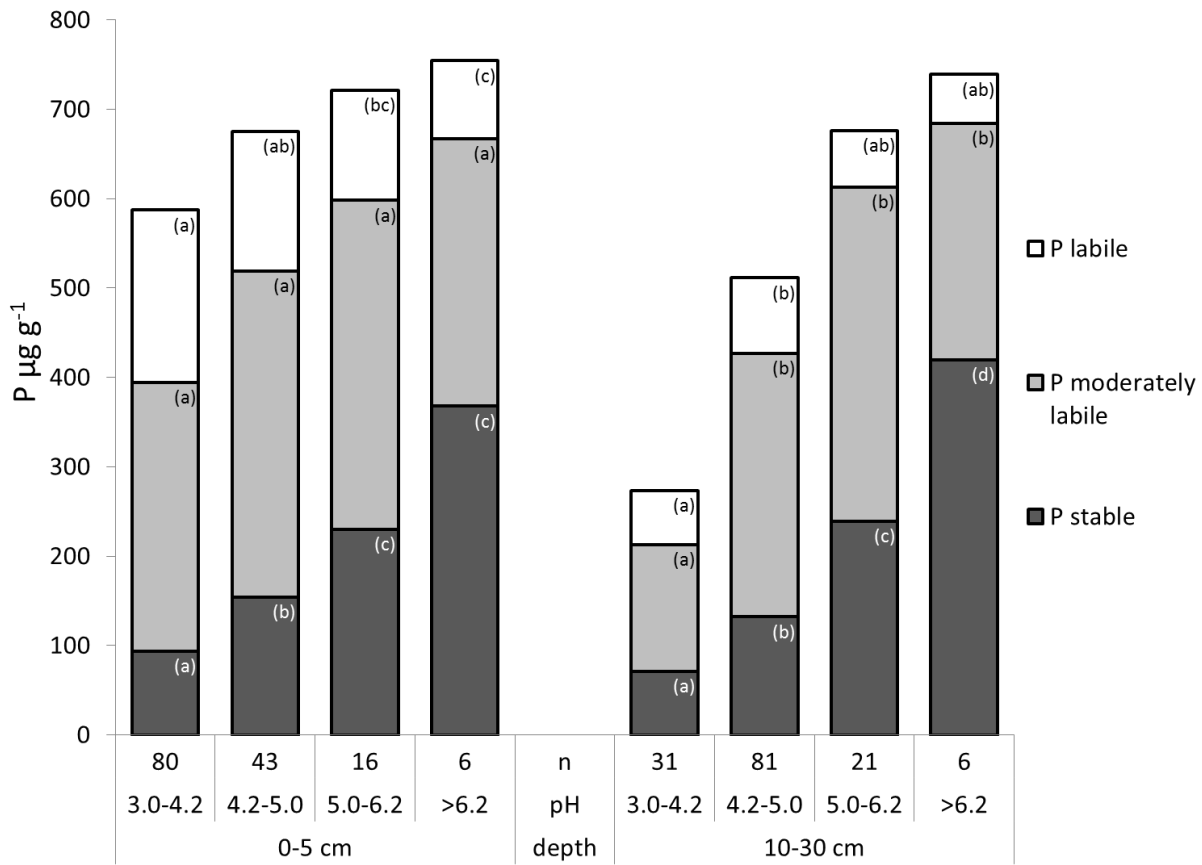
Figure 4: Hedley P pools and total P (mean values), grouped by pH-classes and soil depths; lower case letters indicate significant differences between pH-classes within Hedley P pools and per depth (non-parametric Mann-Whitney-U-test, α < 0.05).
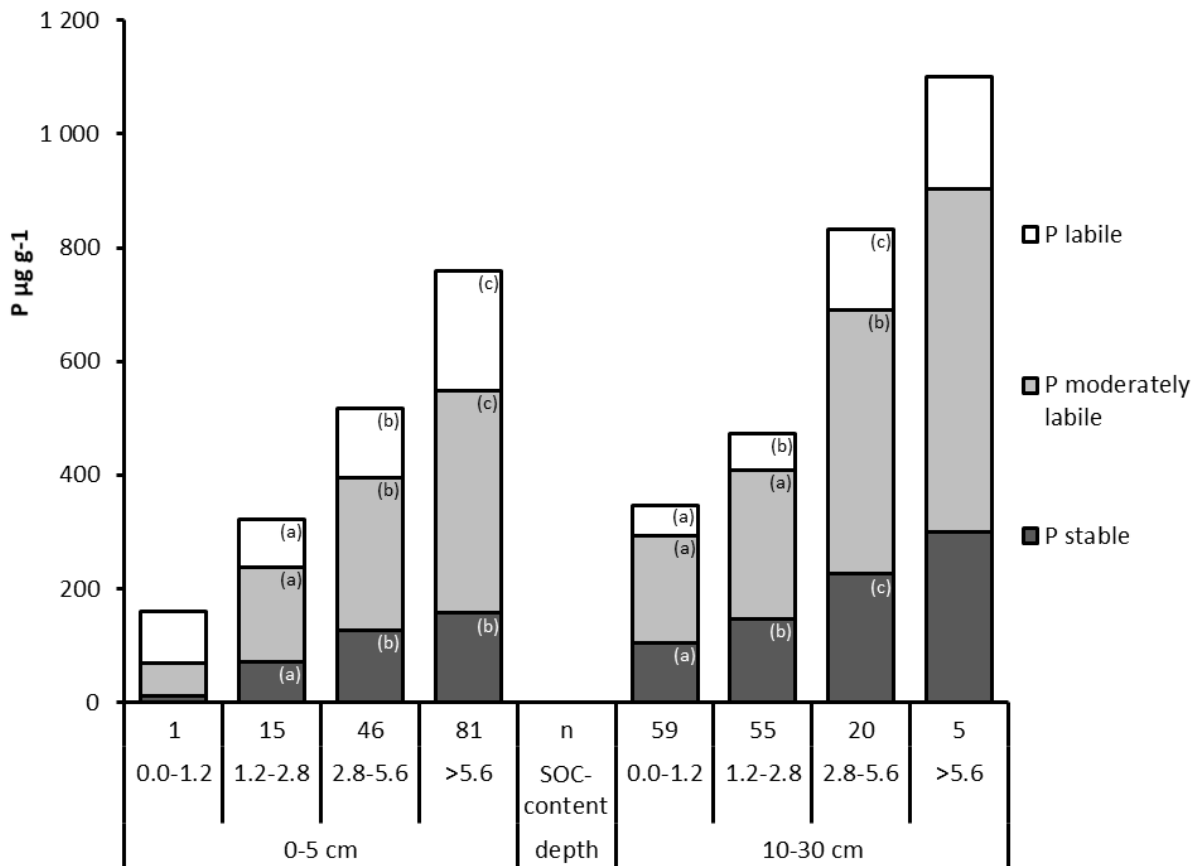
Figure 5: Hedley P pools and total P (mean values), grouped by SOC content in % and depth; n = number of observations, lower case letters indicate significant differences in P pools among SOC content classes and per depth, non-parametric Mann-Whitney-U-test, α < 0.05. The bar with no letters had too few observations for statistically valid tests for differences.
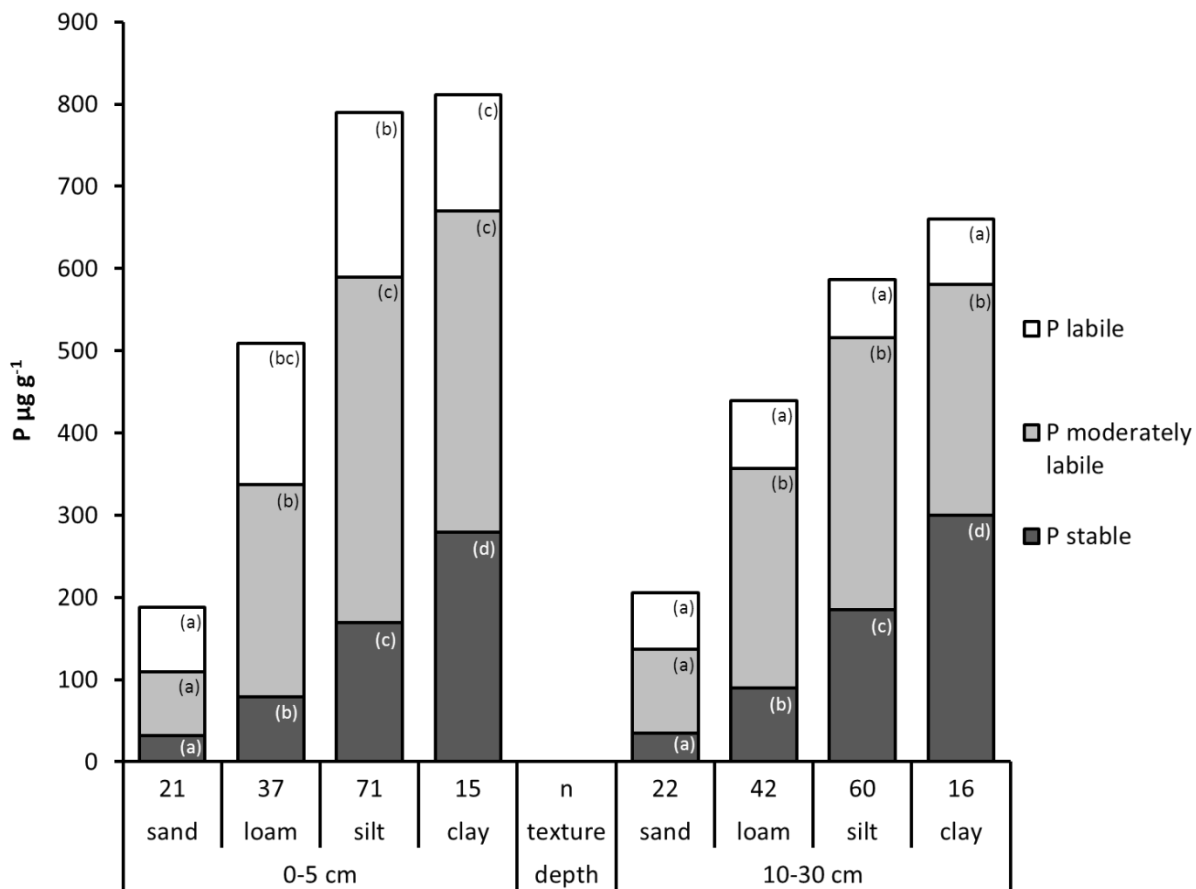
Figure 6: Hedley P pools and total P (mean values) grouped by soil texture and depth, n = number of observations, lower case letters indicate significant differences in P pools among soil texture groups, non-parametric Mann-Whitney-U-test, α < 0.05.
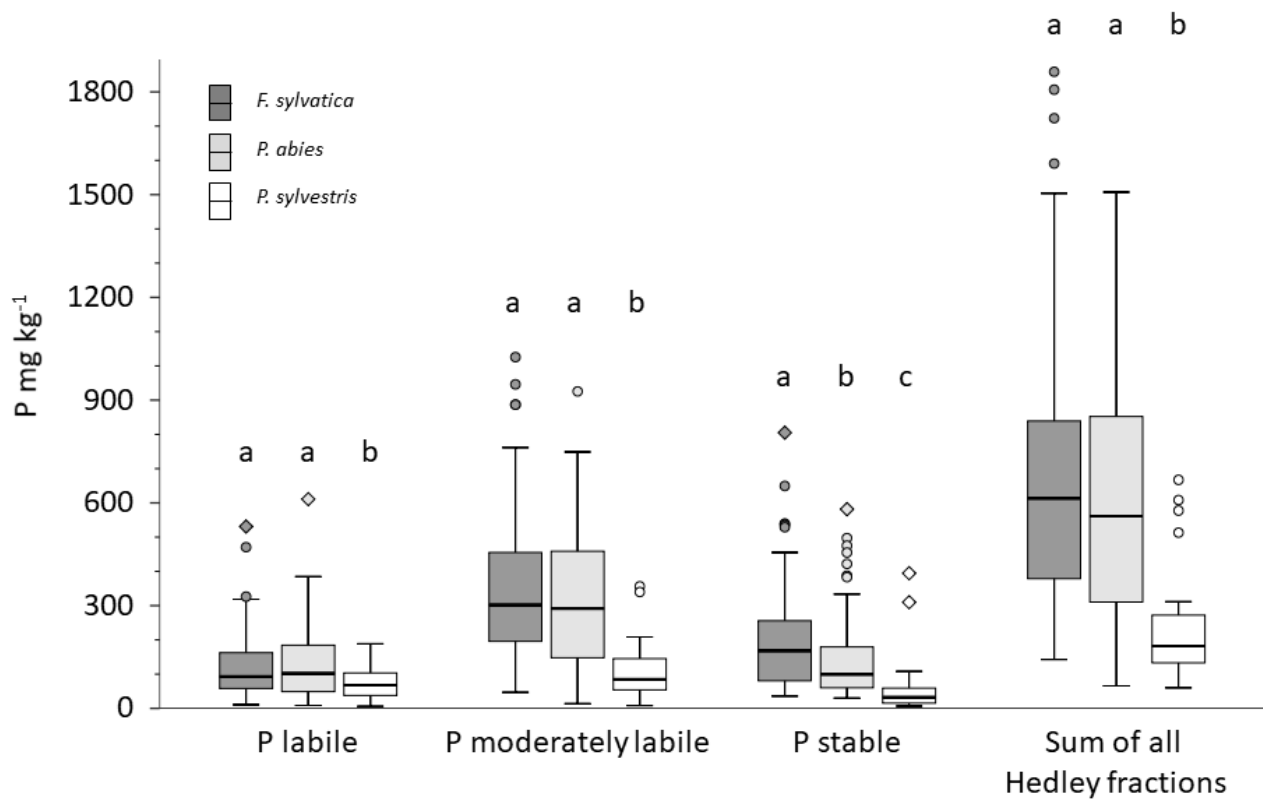
Figure 7: Boxplots of Hedley P pools and sum of all Hedley fractions in mineral soils of analyzed NFSI plots for sites dominated by the three main tree species. Different letters indicate significant differences between P pools resp. Hedley P sum in subject to tree species (non-parametric Mann-Whitney-U-test, α < 0.05).

Figure 8: Results of multiple linear regressions to predict foliar P content in *P. abies*, *P. sylvestris*, and *F. sylvatica* (see Table 3) with soil variables from 0-5 (left panel) and from 10-30 cm depth (right panel), x-axis measured and y-axis modelled foliar P content in mg g⁻¹.