Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

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Availability of phosphorus in plant and soil

Some case studies from the forestry section

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Jede weise Forstdirektion muss daher die Waldungen (...) so hoch als möglich, doch so zu benutzen suchen, dass die Nachkommenschaft wenigstens ebenso viel Vorteil daraus ziehen kann, wie sich die jetzt lebende Generation zueignet.

Georg Ludwig Hartig (1804)

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I hope you enjoy your reading.

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II. SUMMARY

Phosphorus (P) is a vital nutrient for living plants, and its plant available forms are often not available in sufficient quantities in natural ecosystems. Over the past decade, high Nitrogen (N) emissions have raised the N supply of forests. Meanwhile, P shortfall is likely to be a very important restrictive factor for tree productivity. Thus, new insights into the P cycle (absorbed from the soil into tree biomass) are necessary for a comprehensive knowledge in forest nutrition. In addition to the limited availability of P in forests, high P export via intensive tree harvesting and biomass removal has increased the concerns of forest researchers with regard to the health of forests. The results of biomass analyses in many European forests have shown a decline in the concentration of P in tree foliage. Furthermore, the outcomes of the Second German National Forest Soil Inventory (BZE II) indicated that 25% of Norway spruce and 50% of European beech trees in German forests suffer P deficiency.

For sustainable nutrition management in common forests, P availability in soils is a fundamental prerequisite. Due to the strong tendency of phosphate (PO_4^{3-}) to selectively bind with mineral and organic substances in soils (depending on soil pH), measuring the amount of plant-available P is difficult. In contrast to agricultural lands, in unfertilized soils, there is a lack of efficient soil extraction methods to evaluate the plant available P fraction in various types of soil. The results of strong acid methods, representing the total quantity of soil P, are no appropriate indicators to estimate tree P nutrition, since most P forms in soil are not available for tree uptake. Hence, employing methodologies, which can quantify bioavailability of P in highly developed soils, should lead to a better understanding of the dependency of tree P nutrition on slowly running P pools at managed and unmanaged forests. The objective of this work is to use the results of simple P extraction methods from soil (PEMs) **I)** to estimate the quantity of easily extractable P in soil and present an appropriate indicator for describing sites' P status, **II)** to expand knowledge of P availability in mature forests and explain the interaction between plant-available P in soil and P nutrition of Norway spruce and European beech trees, and **III)** to explore the relationship between soil P fertility and P uptake, tree P nutritional status, site productivity, and the tendency of P internal cycling.

Accordingly, water, double-lactate, citric acid and sodium bicarbonate methods were employed. The extracted amount of P per mass unit of soil increased in the order of $P_{\text{water}} <<< P_{\text{double-lactate}} < P_{\text{sodium bicarbonate}} < P_{\text{citric acid}}$, decreased with soil depth and was higher in acidic soils. Among the results of PEMs, along with other soil parameters, the linear regression models selected the stocks of citric acid and sodium bicarbonate plant-available P as a first predictor, which positively explains a substantial part of the P nutrition of trees. The aggregation of soil depth levels down to 40 cm and stratification of soil pH of sub-collectives ($pH < 6.2$ and $pH > 6.2$) improved

the results of the regression models. The stocks of P extracted using citric acid and sodium bicarbonate methods in topsoil (down to 40 cm) at each plot represented the best correlation with tree P foliage. Compared to previous soil tests, these PEM methods are relatively simple, cost effective, and practical for a large number of samples.

Using PEMs, we assessed the impact of soil P availability at mature stands on P nutrition and productivity of Norway spruce trees as well as P internal cycling in adult Norway spruce trees. Our observations identified that the value of readily extractable P from mineral soil is strongly correlated with P stored in tree aboveground biomass (notably needles), and is an appropriate predictor for evaluating the rate of trees' P uptake and forest productivity. In contrast, the total and plant-available amount of P extracted from organic layers did not indicate a significant relationship with the concentration of P stored in the aboveground biomass of Norway spruce trees. A high accumulation of P was found in the first and second year needles as well as in twigs of adult trees, but the strongest relationship was detected between stocks of citric acid extractable P down to 40 cm of soil depth and P in first year needles and stem-bark. For this reason, we suggest a stem-bark analysis as a supplementary or alternative method for needle analysis to evaluate the nutritional P status of trees.

Regarding the distinct variations in concentration of P in the first and second year needles (interpreted as an indication of P internal cycling), the amount of P extracted using the citric acid method is employed to assess the relationship between soil P fertility and differences in concentration of P between needles (P-difference $_{\mathrm{Ny1-Ny2}}$) of adult Norway spruce. It was hypothesized that these differences result from P re-translocation from older organs in order to support younger ones. Due to the low availability of P for root uptake, this phenomenon could be a supplementary strategy for Norway spruce trees to cope with soil P deficiency in early growth or under critical conditions. This study detected no significant relationship between stocks of P extracted using citric acid and P-difference $_{\mathrm{Ny1-Ny2}}$, even when tree P nutritional level was below the normal range. From intensive tree sampling, we determined that the typically lower concentrations of P in second year needles compared to first year needles derive from an increase in the weight of older needles (probably from accumulation of immobile elements such as calcium) in 85% of the examined cases. The net quantity of P re-translocation into growing needles, thus, is of minor importance. Accordingly, the study recommends a precise sampling of needles annually and from the same branch to avoid a systematic error when calculating the net amount of elements re-translocation. Our results lead to the conclusion that the citric acid extract (down to 40 cm soil depth) is a suitable method for the estimation of plant-available P, especially in the context of large soil inventories.

III. ZUSAMMENFASSUNG

Phosphor (P) ist eines der wichtigsten Nährelemente für Pflanzen. Jedoch ist Phosphor in natürlichen Ökosystemen in für Pflanzen verfügbarer Form meist nicht ausreichend vorhanden. Galt früher Stickstoff als der limitierende Wachstumsfaktor in Wäldern, so ist heute bekannt, dass eine allgemeine hohe Stickstoffimmission vorherrscht und P zum limitierenden Faktor in vielen Wäldern geworden ist. Deshalb sind neue Erkenntnisse über den P-Kreislauf (vom Boden zur Baumbiomasse) in der Waldernährung notwendig. Zeitgleich mit dem geringen P-Eintrag in Wäldern findet ein hoher P-Austrag aus Wäldern durch intensive Holznutzung statt. Biomasseanalysen in vielen europäischen Wäldern haben einen Rückgang der P-Konzentrationen in Blättern beziehungsweise Nadeln von Bäumen bestätigt. Zudem zeigten Ergebnisse der zweiten bundesweiten Bodenzustandserhebung in Deutschland (BZE II), dass 25% der Fichten und 50% der Buchen in deutschen Wäldern mangelernährt sind.

Für eine nährstoffnachhaltige Waldbewirtschaftung ist eine ausreichende P-Verfügbarkeit für die Bestände jedoch eine Grundvoraussetzung. Aufgrund der starken Neigung von Phosphat sich an mineralische und organische Partikel im Boden zu binden sowie der starken Abhängigkeit seiner Verfügbarkeit vom pH-Wert, ist die Bestimmung des pflanzenverfügbaren P schwierig. Im Gegensatz zur Landwirtschaft fehlt bisher leider eine einheitliche Methode für Waldböden zur Abschätzung von pflanzenverfügbarem P und zur Bewertung der P-Anteile bei verschiedenen Bodentypen, welche zudem einfach durchzuführen ist und eine hohe Durchsatzzahl erlaubt. Zu berücksichtigen ist auch, dass die P-Gesamtvorräte im Boden, wie sie aus quantitativen Bestimmungsmethoden mit starken Säuren ermittelt werden, nicht direkt mit der Phosphorversorgung eines Standortes korrelieren. Grund dafür ist, dass viele Phosphorverbindungen im Boden nicht bioverfügbar sind. Die Entwicklung von Methoden, die die P-Bioverfügbarkeit in Böden quantifizieren können, führt folglich zu einem besseren Verständnis des P-Ernährungszustands der Bäume. Diese würden auch dazu dienen, die Abhängigkeit des Ernährungszustands der Bäume von langsamen P-Quellen in bewirtschafteten und unbewirtschafteten Wäldern untersuchen zu können. Die Hauptziele dieser Arbeit waren mittels einfacher P-Extraktionsverfahren (PEMs) **I)** die Menge an leicht verfügbarem P zu bestimmen und einen geeigneten Indikator für den P-Status des Bestands zu finden, **II)** zu einem besseren Verständnis der P-Verfügbarkeit in Beständen beizutragen und die Zusammenhänge von pflanzenverfügbarem P im Boden und dem P-Ernährungszustand von Fichte und Buche zu identifizieren und **III)** die Beziehung zwischen pflanzenverfügbarem P im Boden, P-Aufnahme, der Standortproduktivität und des internen P-Kreislaufs (P-Verlagerung) im Baum zu untersuchen.

Dazu wurden Wasser, Doppel-Lactat, Zitronensäure und Natriumbikarbonat als Extraktionsmittel verwendet. Die Menge des extrahierten P pro Masseneinheit Boden nahm in der Reihenfolge $P_{\text{Wasser}} <<< P_{\text{Doppel-Lactat}} < P_{\text{Natriumbikarbonat}} < P_{\text{Zitronensäure}}$ zu, nahm mit der Bodentiefe ab und war in sauren Böden höher als in basischen. In linearen Regressionsmodellen unter Einbeziehung von PEMs und anderen Bodenparametern wurden Zitronensäure und Natriumbikarbonat als beste Vorhersageparameter für pflanzenverfügbares P identifiziert. Eine Aggregation der Bodentiefenstufe bis 40 cm und eine Einteilung des Boden-pHs in Subgruppen verbesserte die Ergebnisse der Regressionsmodelle zudem. Die beste Korrelation zwischen dem P-Vorrat im Boden und den Nadel-/Blattspiegelwerten des Baumes fand sich bei Verwendung von Zitronensäure und Natriumbikarbonat im Oberboden (bis 40 cm). Im Vergleich zu anderen Extraktionsverfahren sind PEM-Methoden relativ einfach, kostengünstig und leicht anwendbar für eine große Anzahl von Bodenproben.

Mit PEMs untersuchten wir die Auswirkungen der P-Verfügbarkeit im Boden auf die P-Ernährung, die Produktivität und den internen P-Kreislauf von alten Fichtenbeständen. Unsere Beobachtungen ergaben, dass leicht extrahierbares P aus dem Mineralboden stark mit dem in der oberirdischen Biomasse (insbesondere Nadeln) gespeicherten P korreliert und ein geeigneter Prädiktor für die Bewertung der P-Aufnahmerate von Bäumen und der Standortproduktivität ist. Im Gegensatz dazu, zeigte die Gesamtmenge und des pflanzenverfügbaren P im Humus keinen signifikanten Zusammenhang mit der P-Konzentration der oberirdischen Biomasse in Fichten. Eine hohe Anreicherung von P wurde im ersten und zweiten Nadeljahrgang sowie in Zweigen ausgewachsener Bäume festgestellt. Zudem fand sich die stärkste Korrelation zwischen dem mit Zitronensäure extrahierten P aus 40 cm Bodentiefe und dem P-Gehalt im ersten Nadeljahrgang sowie der Stammrinde. Aus diesem Grund wäre eine Stammrindenanalyse als ergänzende oder alternative Methode für die Nadel/Blatt Analyse in der Ernährungsdiagnostik vielversprechend.

In Bezug auf den unterschiedlichen P-Gehalt des ersten und zweiten Nadeljahrgangs (als Parameter des internen P-Kreislaufs) wurde die mit Zitronensäure extrahierte P-Menge verwendet, um die Beziehung zwischen der P-Verfügbarkeit im Boden und dem unterschiedlichen P-Gehalt zwischen den Nadeln (P-Differenz Ny1-Ny2) der Fichte zu bewerten. Es wurde die Hypothese aufgestellt, dass diese Unterschiede auf eine P-Verlagerung von älteren zu jüngeren Kompartimenten zurückzuführen sind. Im Falle einer geringen P-Verfügbarkeit könnte dieses Phänomen eine ergänzende Strategie der Fichten sein, um den P-Mangel des Bodens im frühen Wachstum oder unter kritischen Bedingungen zu bewältigen. In dieser Studie wurde keine signifikante Beziehung zwischen dem mit Zitronensäure extrahierten P-Vorrat und der P-Differenz Ny1-Ny2 festgestellt, selbst wenn der P-Gehalt in der Nadel unter dem Normalbereich lag. Mit jährlichen Baumproben (Nadel) haben wir festgestellt, dass die im Vergleich zur Nadel des ersten Jahres typischerweise niedrigeren P-Konzentrationen in Nadeln des zweiten

Jahres auf eine Gewichtszunahme älterer Nadeln von bis zu 85% zurückzuführen sind (wahrscheinlich aufgrund der Ansammlung von unbeweglichen Elementen wie Kalzium). Somit spielt die Nettomenge für die P-Verlagerung in jungen Nadeln eine untergeordnete Rolle. Dementsprechend empfiehlt die Studie eine genaue Stichprobe von Nadeln aus demselben Ast pro Jahr, um einen systematischen Fehler bei der Berechnung der Nettomenge der Umlagerung von Elementen zu vermeiden. Unsere Ergebnisse führen zu der Schlussfolgerung, dass der Zitronensäureextrakt (bis zu 40 cm Bodentiefe) eine geeignete Methode zur Bestimmung von pflanzenverfügbarem P, insbesondere im Rahmen von großen Bodeninventuren, ist.

IV. PREFACE

Forest productivity is controlled by environmental factors such as light, water, temperature, and nutrient availability (Binkley 1986). Although nutrition deficiency is definitely not the only influencing factor on forest productivity, sites development is openly associated with soil fertility. Regarding site parent material, water availability, and alteration of natural mineral cycles, forest soils are noticeably more varied in the case of nutrient availability compared to agricultural soils. Hence, it is necessary that forest researchers more focus on soil fertility with the objective of better understanding the transport of nutritional elements from forest sites. In this regard, the availability of phosphorus (P) and nitrogen (N) is more dominant for the forests health.

The Professorship of Forest Nutrition and Water Management at the Technical University of Munich has been concentrating on the subject of sustainable forest nutrition management for many years. The focus of recent projects has been on nutrient balance, considering different harvesting systems, P cycling in the forest, and development of methods to determine plant-available P in soil. The concern about an increase of the P deficiency in forests made researchers be more focused on the assessment of tree P nutrition and forest health. Our imagination about the pattern of soil P shortage in forest ecosystems is too general, and concerning its impact on tree health our knowledge thereof is especially limited (Falkengren-Grerup et al. 1994). Hence, the effects of P on forest productivity have been identified as a fundamental future research area for our understanding of ecosystem functioning.

This study addresses an issue for both, forest ecologists and forest managers, namely, the identification of an appropriate soil P assessment (fraction) that permits a reliable evaluation of the nutritional status of forest trees. The main objective here is to increase the knowledge about the impact of plant-available P in common forests on tree P nutrition in Bavarian forests, southern Germany. Accordingly, the first and second German Forest Soil Inventory (BZE I and II) provide useful information about the P status of main European tree species, and their findings motivated the application of the current study. BZE campaign is a part of the forest environmental monitoring in Germany for regularly reporting on soil conditions that assessed the tree nutrition on 1014 and 1900 forest sites, in the first and second inventory, respectively (Ilg 2009 and Wellbrock et al. 2016).

V. GENERAL INTRODUCTION

1. Biological Importance of Phosphorus

P is a life-supporting element and is vital to all living organisms (Syers et al. 2008). It is essential in the composition of nucleic acids, thus in the structure of DNA and RNA as well as being involved in energy transfers inside cells via molecules such as ATP. Moreover, P contributes to composition of phospholipids, which control the stability and properties of cell membranes (Marschner 2012). Therefore, P has a fundamental role for cell function and plant nutrition. In plants, P also plays a vital role in many biological processes, e.g. photosynthesis. Plants absorb the P only as dissolved form in the water from the soil and cannot grow without an adequate supply of P (Ahmed et al. 2011). Biologists often present the P in their classification as a main macro element for plant nutrition, which is why the low concentration or lack of P leads to a decrease in yield, and it is required by plants in relatively great quantities. In addition, P promotes the development of plant roots in soils and improves the success rate of plant establishment (Brady and Weil 1999). Apart from this, plants gain the soil P typically via mycorrhiza, absorbed by root hairs, root tips or the cortex of the roots (Sultenfuss and Doyle 1999), and thus, the development of the root system directly influences the tree P uptake. The biological importance of P for many natural ecosystems is widely known (e.g. Hoffmann 1991; Smith and Read 2008).

2. Phosphorus in Natural Ecosystems

Generally, soil P availability for plant uptake in natural ecosystems is not high (0.1% of total P content (Paul and Clark 1996)). Hence, natural ecosystems, such as forests, have adapted themselves using certain strategies e.g. by changing root architecture and mycorrhiza activities to promote specific biological processes like growth and adaption rate, which increase the plant's uptake capacity (Schachtman et al. 1998). Plant absorb the available soil P via a dynamic process (interaction between root and soil, depending on the plant age and soil P status) by dissolving different P compounds (Marschner et al. 2001). Thus, the physical and chemical characteristics of soils strongly affect the availability of soil P for plants (Karaman et al. 2001). Accordingly, site parent material, the rate of weathering, and climatic conditions usually control the soil P supply (Rademacher et al. 1999). However, numerous studies have already argued that the high availability of N, due to high atmospheric input or fertilization treatment (in experimental investigations), may cause a deficiency of plant-available P in soil (e.g. Flückiger and Braun 1998). Prietzel and Stetter (2010) also claim that high accumulation of N in forest stands together with low P supply in topsoil leads to a decline in P nutrition of trees (due to an imbalance of N/P ratio). Nevertheless, in addition to site N and climate change, variations in tree P nutritional status are mainly explained by the following factors: site P supply, tree age, biomass removal, mycorrhiza activities, and soil pH, which in the long-term for tree growth, influence the P nutrition more (Jonard et al. 2010).

Previous investigations of forest ecosystems have corroborated that the mineral P supply in stands is basically dependent on the characteristics of bedrocks (Prietzel and Stetter 2010; Prietzel et al. 2013; Walker and Syers 1976). The available form of P for plant uptake (phosphate ion) makes strong bonds with soil cations (especially with Ca^{2+}, Al^{3+} and Fe^{3+}), therefore, it is not easily available for root uptake (Chien et al. 2009). Nevertheless, in mature forests, the uptake of P by trees often corresponds to the structure of roots of individual species, presence of mycorrhiza, as well as the accumulation of fungal and their activities in the main rooting zone in upper soil levels (Kölling et al. 2009). The association between P nutrition of trees and root architecture shows the importance of P availability in different mineral soil layers, particularly for adult trees with developed root system. With the development of forest science, especially the field of nutrition management, the importance of P is well established. In this regard, Lang et al. (2016, 2017) stated that the P cycling in common forests appears to be an ideal model to demonstrate the concept of nutrition cycling in forests. In the past, researchers have mostly focused on N as the main factor for controlling forest growth and tree productivity. Hence, the P status in forests has only recently been viewed as a serious object for forest researchers. It should also be noted that the most relevant information about plant-available P derives from agricultural surveys, which are barely comparable to mature forests.

2.1 Phosphorus Availability in Soil

In natural ecosystems, inorganic P in soils, depending on pH values, exists as a negatively charged phosphate ion ($H_2PO_4^-$ or HPO_4^{2-}). The chemical structure of apatite rocks as a main source of soil P is M-(PO_4)-X, and commonly, the cation (M) is Ca (common in calcareous soils), and anions (X) according to which assessable form, could be F^-, Cl^-, OH^- or CO_3^{2-}. In other P minerals, Al and Fe are likewise the cations, which might participate in the aforesaid structure (mostly in acidic soils) (Paul and Clark 1996). Hence, phosphate ions are basically fixed on positively charged surfaces. Generally, most P compounds appear in various inorganic forms and derive primarily from calcium phosphate (apatite group minerals) in calcareous soils or iron phosphate (Strengite) and aluminum phosphate (Berlinite + Variscite) in non-calcareous soils (Augusto et al. 2017). In natural ecosystems, beside organic P pools, these minerals are believed to be the main inorganic sources for providing plant P requirement (Schachtman et al. 1998). Therefore, the concentration of plant-available P in soil is additionally governed by presence and activity of $Al^{3+}$and Fe^{3+} in acidic soils, as well as Ca^{3+} in alkaline soils, which is controlled by soil pH (**Fig.1**) and environmental factors, e.g. redox potential and mineral solubility

(Renneson et al. 2016). Moreover, the role of soil parent material is known in the P cycle in forest sites, since the weathering of primary minerals is the main source of P for forest vegetation and trees (Augusto et al. 2017; Cross and Schlesinger 1995; Prietzel et al. 2013). The supply of organic forms of P in soils, e.g. inositol phosphates or monoester phosphates are also presented by Fox et al. (2011) as an important source of tree P nutrition in forest ecosystems. Jones and Oburger (2011) explained that the organic P forms cover up to 65% of total soil P content in forests, while in a study by George et al. (2011) no direct uptake of organic P by plant roots was reported. It seems that there is very low agreement between researchers about the short-term contribution of organic forms of P in soils to P nutrition of adult trees in mature forests.

Commonly, element solubility in soil occurs over a certain pH range (Marschner et al. 2001). The quantity of soil P availability is normally linked to the lime potential and the variation of soil pH, which are used to estimate the solubility rate of different P compounds (Khanna et al. 2007). Thus, evaluating the pH values in different soil depth is necessary for determining plant-available P. The solubility of phosphate in soil solutions is also affected by the presence of minerals, competing to build stable complexes in the soil. The stability of these complexes is also directly related to soil pH (Hinsinger 2011). A pH range between 6 and 7 is presented by Brady and Weil (1999) as the optimal range for availability of P in forest soils and for plant uptake. As shown in **Fig 1**, when the soil pH rises (greater than 7), large quantities of P ions react with Ca^{2+} (as Ca-phosphates), which diminish the available amount of P for uptake (Sentenac and Grignon 1985). On the other hand, complexes of Al^{3+} in acidic soils, as well as Fe^{3+} in very acidic soils with phosphate ions also reduce the available amount of P in soil.

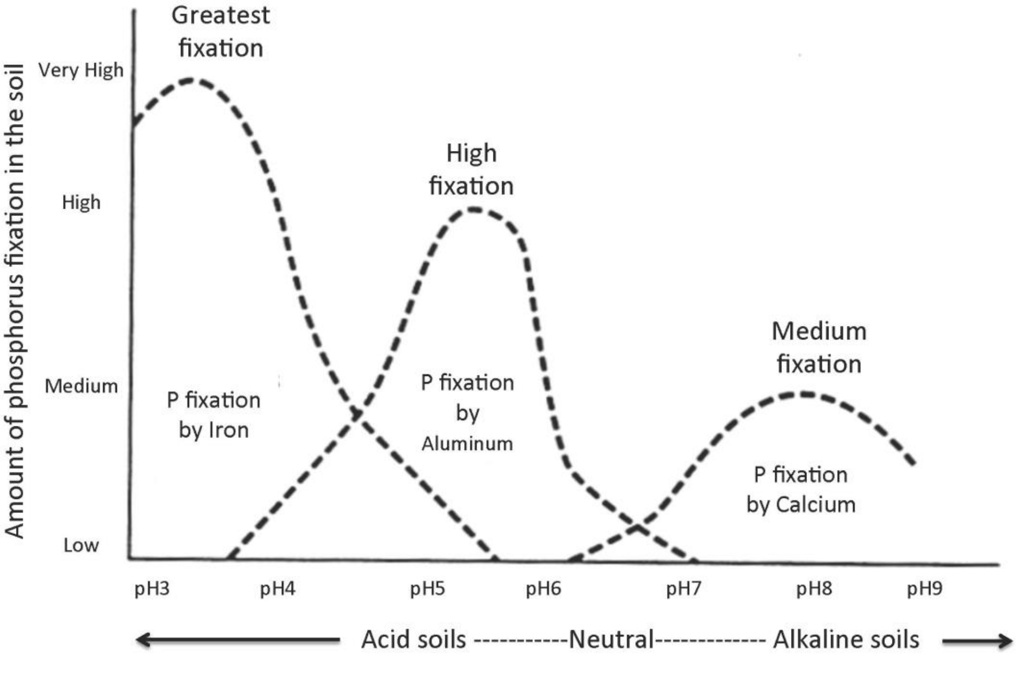

Figure 1: The peaks and valleys of phosphorus fixation across pH ranges, adopted from Stevenson and Cole (1999).

2.2 Role of Rhizosphere and Mycorrhiza Activities

Marschner (2012) emphasized that the part of the soil, directly influenced by root secretions, or associated with soil microorganisms and mycorrhiza, plays a major role in uptake of nutritional elements by plants. Depletion of different sources of P from the rhizosphere has also been linked with the activities of enzymes (e.g. phosphatase) in the main roots' growing area (Nannipieri et al. 2011). In addition, exudation of organic substances by roots in this area might promote the development of rhizosphere microorganisms. This promotion appears to happen via progressions like chelation or indirectly by increasing microbial activity in the rooting zone, and to raise the availability of P in soils in order to improve plant P acquisition (George et al. 2011). As a response to the small portion of available P forms in soils, plants' adaption to enhance the efficiency of P uptake seems to be controlled by soil P status in the rhizosphere region (Belyazid and Belyazid 2012).

Besides the microbial hotspots in topsoil that are naturally made by plants during short-term growth (Kuzyakov and Blagodatskaya 2015), the change in root morphology is often presented by plant biologists (e.g. Marschner 2012), as a mechanism that increases the uptake capacity of P. In this regard, Jansa et al. (2011) explained that although the form and structure of roots are important for P acquisition, increasing the plant capacity to uptake the soil P is probably more affected by association of soil fungal, in the presence of mycorrhiza. Moreover, compared to roots penetration, mycorrhiza has more access to soil pores, and thus, facilitate the uptake of P for plants. Mycorrhiza are also supposed to participate in the process of nutrient mineralization as well as in the weathering of site parent material (apatite group minerals) (Jansa et al. 2011), showing the undeniable role of these associations in P nutrition in common forests. In soils with low P availability, many plants cannot survive without mycorrhiza assistance (Brady and Weil 1999), especially in forests with very low soil pH, mycorrhiza activity and fine root exudations become less effective to release the soil P and impair the process of P uptake by trees. Accordingly, tree P deficit, resulting from these phenomena, is commonly detectable from foliage analysis (Khanna et al. 2007). In an investigation by Gundersen (1998) at temperate forest sites, the low concentration of P in needles of adult Norway spruce trees has been related to a reduction in mycorrhiza activity in the rooting zone, as a result of high N stress at the stand. Marschner (2012) later confirmed this observation.

2.3 Impact of Biomass Removal in Forests on Nutrient Cycle and Phosphorus Balance

Increasing utilization of forest biomass as an energy source has caused a discussion about intensifying the usage of crown biomasses (Ettl et al. 2007). However, forest managers must consider the nutrient exports and the future development of site productivity for nutritionally sustainable forest management. For this reason, site-specific nutrient availability (e.g. nutrient deposition and exchangeable nutrient pools) has to be compared to the nutrient losses through biomass export (tree harvesting) and seepage output. In the context of biomass removal, the availability of essential nutrient elements such as P at sites has become more crucial for sustainable forest management, since the accumulation of P stored in tree crown biomass is high (Weis et al. 2009). For example, evaluating P stored in the aboveground biomass of European beech trees, Jacobsen et al. (2003) showed different P accumulation in the bark (6 kg/ha*a), in branches (26 kg/ha*a), and nearly 6 kg/ha*a, in tree leaves, while for Norway spruce trees, this amount was 9, 18 and 20 kg/ha*a, respectively. Different amounts of P stored in adult European beech and Norway spruce trees are also reported by Zhang and Mitchell (1995), but their outcomes highlight the great accumulation of P stored in tree foliage and bark (considering the volume of bark). Göttlein et al. (2013) and Weis et al. (2011) demonstrated that the crown biomass of adult Norway spruce and European beech trees contain 25% of the total tree production, which cover a high portion of P stored within tree, notably in foliage and in bark. Accordingly, the authors strongly warn against the export of crown biomass from sites exploited for wood utilization **(Fig.2)**. In addition, Fäth et al. (2019a) concluded that with tree biomass removal, the amount of plant-available P would decline in the mature forest (see also Appendix B).

Figure 2: With developing mechanization, trees are used more. Subsequently, more crown materials as valuable nutrient resources are removed from forest surface (Weis 2009).

3. Forest Sites Phosphorus Balance

Generally speaking, the nutrient balance in forest stands is determined by calculating the difference of nutrient input (atmospheric deposition + mineral soil weathering), and the nutrient depletion (loss from the seepage water + biomass organs export) (Pretzsch et al. 2014). If the depletion is less than the entry, the system is considered nutritionally sustainable. Subsequently, measuring balances between nutrient input and output assist in estimating the site-specific nutrient availability to manage potential forest nutrient deficit. An adequate supply of P is a prerequisite for plant growth. In a common forest, this P supply has to be provided by soil mineralization (Ettl et al. 2007), which normally depends on site history and is generally regulated by the tree community at a site (Hooper and Vitousek 1998). Therefore, for plausible quantification of the P balance in a site (**Fig.3**), in addition to the intensity of tree harvesting, further information about the content of P in tree components must also be considered. If this information reveals that intensification of biomass removal from forest surface decreases the site P supply, consideration of the other respective growth limiting factors (e.g. soil P status) at sites is necessary. A long-term perspective in our study is also to specify, whether the P export through intensive biomass removal diminishes the site P fertility or threatens forest health in the next generation. For this reason, detailed information about the storage of plant-available P in soil at investigation sites, using reliable soil extraction methods, is one of the important prerequisites. However, this general statement about the negative impact of whole tree harvesting on site nutrient fertility is not new and has already been proved by Krapfenbauer and Buchleitner (1981) and Kreutzer (1979) at mature forest sites.

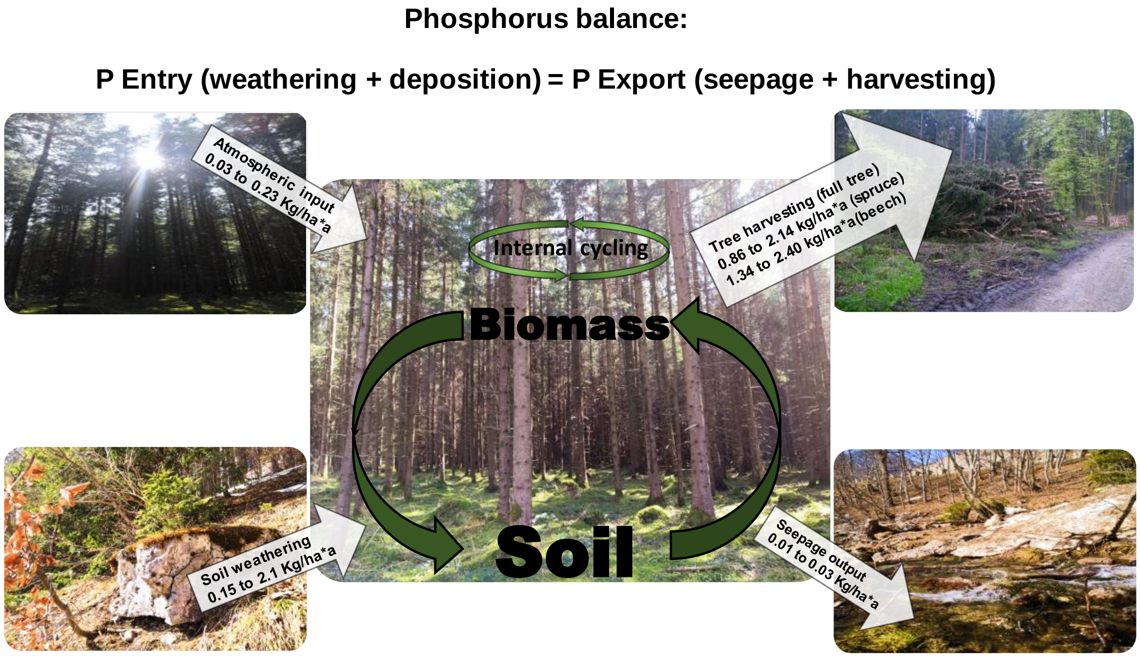

Figure 3. The general pattern for the P cycle in a managed forest. The size of arrows indicates the importance of P entry and export into and from forest sites. The values are obtained from Fäth et al. (2019a).

3.1 Phosphorus Input into Forest Site by Atmospheric Deposition and Soil Weathering

Inputs of P into the forest ecosystem are commonly present through soil weathering, soil treatment by fertilizer, and atmospheric deposition. Compared to N, atmospheric P entries into forests are very low (Brady and Weil 1999) and might be derived from various sources such as dust or organic particles. Yanai (1992) reported that the total P inputs from the atmosphere span between 0.07 and 1.7 kg/ha*a. Technical difficulties in quantifying atmospheric P inputs into the forest ecosystems have been discussed by Newman (1995). The author explained that the content of P in tree foliage is partly affected by suspended particles in aerosols and varies considerably in different forests. Although Vitousek (2004) and Prietzel and Stetter (2010) hypothesized that atmospheric deposition of P in the forest is a source of P for trees, according to Richter et al. (2006), this portion is negligible and not sufficient for forest growth.

Soil chemical weathering contains the decomposition of site bedrock into a smaller unit. The release of P in soil depends on the rate of physical weathering, which positively impacts the rate of chemical weathering (Newman 1995). The effect of this weathering on the accessibility of major nutrient elements such as P in soil has received more attention recently as it can limit the forest development (Achat et al. 2018; Prietzel et al. 2016). In highly weathered soils, the presence of ion oxides causes a greater chemical fixation of P and decreases the soil available P, while in younger soils, organic compounds improve the soil P availability and are a major reservoir of plant-available P in soil (Augusto 2008; Sanchez et al. 1982). However, Newman (1995) presented several factors, which alter the rate of chemical weathering, e.g. bedrock type, temperature, water availability, and the availability of soil microorganisms. The physical, chemical, and biological weathering of bedrocks in a natural ecosystem releases a number of nutritional elements into the soil solution. Basically, the P from the weathering process is also the main resource of P inputs in forest ecosystems (Prietzel et al. 2013), and due to the difficulty of measurements, this has not been estimated effectively (Payn et al. 2000). Furthermore, with regard to the replenishment of P from the soil weathering, preparing the site P balance sheet is complicated and includes some uncertainties in the results. Therefore, an alternative method, such as employing the result of reliable soil extraction to evaluate the amount of site P supply that positively correlates with stand development, is more appropriate (Fäth et al. 2019b, see also Appendix B).

3.2 Phosphorus Output from Forest Site by Soil Erosion, Seepage Water, and Biomass Removal

Brady and Weil (1999) identify soil erosion, seepage water, and biomass removal as the main pathways by which natural ecosystems lose their P. However, in forests with high lush vegetation, the portion of P lost by soil erosion may be ignored (Jones and Oburger 2011). In agricultural land, considerable amounts of P fertilizer yearly must be used to enrich soils and to increase yields. In contrast, forest soil fertility is commonly associated with nutrients stored in tree biomass (Belyazid and Belyazid 2012). According to Tiessen et al. (2011), the lack of atmospheric P input, the limitation of the solubility of soil P, and the low rate of soil erosion in forest sites are the main causes for P shortage at forest sites. Nevertheless, some other disturbances such as full tree harvesting and fires also amplify the trend of P loss from the forests (Brady and Weil 1999).

The loss of P via leaching is normally very low and is sometimes even insignificant, since available inorganic P compounds in soil rapidly fix on the surface of other mineral compounds in soil (Attiwill and Adams 1993). Recently, Fäth et al. (2019b) confirmed the findings of Brady and Weil (1999) and Newman (1995), who found the value of P output via leaching as well as soil erosion in forests is low, fluctuated from stands, and mostly correspond to cultivated land. In an old common forest in Sweden (100 year Norway spruce and Scots pine), Löfgren et al. (2009) calculated that yearly 0.06 to 0.07 kg/ha*a of P is exported through leaching. However, P leaching from forest stands is still not well investigated, but the observations in the studies above seem to confirm that the quantity of P output via seepage water is not important for the sustainable management of P in forests (see also Appendix B).

Generally, the output of P from forest stands by tree utilization is much higher than other pathways such as seepage water. Therefore, direct P export by removal of P rich biomass from sites could also negatively impacts site P fertility, due to the high accumulation of P in tree components (mainly crown biomass) (Mann et al. 1988; Weis and Göttlein 201; Pretzsch et al. 2014). Moreover, significant relationships between site nutrient supplies, usage of woody productions and forest growth, were thoroughly investigated by Kreutzer and Weiss (1998) in Bavarian forests. They reported that nearly half of P stored in tree compartments is accumulated in crown biomasses of Norway spruce and European beech (for Norway spruce, more specifically in foliage and bark). For this reason, they concluded that the whole tree harvesting might lead to a deficiency in the supply of P **(Fig.4)**. Mann et al. (1988) observed that the harvesting of adult conifers (only stem-wood) removed up to 56 kg/ha*a P from a site, while for complete tree harvesting this value rose up to 96 kg/ha*a. Recently, Weis and Göttlein (2016) fairly proved the negative impact of essential nutrient removal via full tree harvesting on forest development.

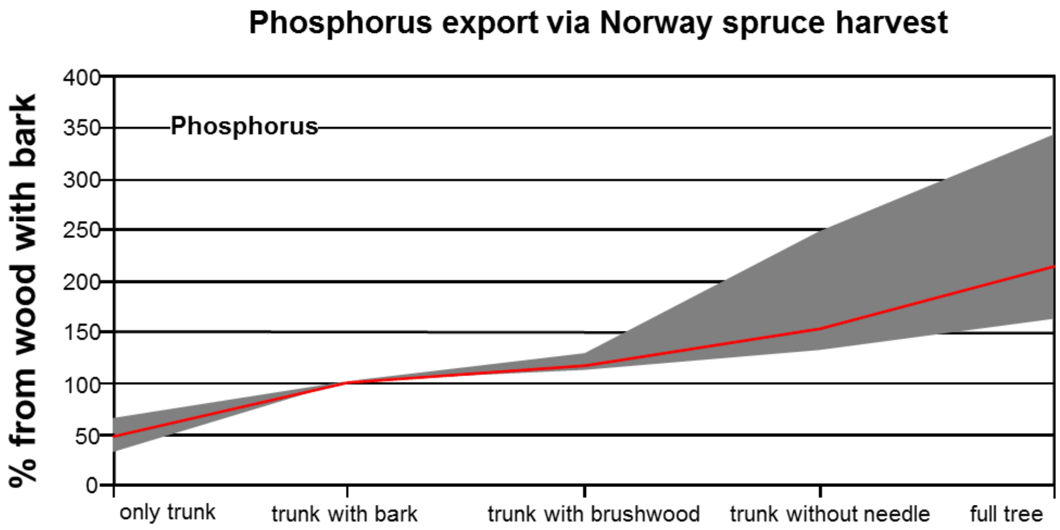

Figure 4. The average portion of P exported via harvesting Norway spruce trees (the red line). Gray area represents the minimum and maximum values of P export (reprinted and adapted from the results of Weis and Göttlein 2011, and Pretzsch et al. 2014). Data used in our study are also included in this graph.

Consequently, due to the high P demand of adult trees at mature sites and limited P input into forests, the P stored in the tree crown biomass is a wealthy pool to support site P fertility in unmanaged forests. Therefore, reducing the export of tree biomass via intensive forest harvesting would result in more stable P levels in forest ecosystems. As a consequence, without supporting the P stored in rich aboveground biomass, and only relying on the P input through mineral soil weathering or P released from site organic matter, a decrease in tree P nutrition and in the rate of site growth in the long-term are also expected (Blume et al. 2010).

Accordingly, the discussions about the protection of soil P fertility in central European forests have gained significance, following a continual decrease in the concentration of P in the foliage of Norway spruce and European beech trees, monitored by the Institute of Plant Biology (IAP) in Switzerland (Flückiger and Braun 2009). The research group reported that in 1984, P levels of 12% of European beech and 11% of Norway spruce trees were below normal nutrition, but these percentages had changed by 2007 to 71% and 67%, respectively. Almost similar observations are reported in Wellbrock et al. (2016) from the result of BZE II inventory in German forests. These outcomes were linked to the relationship between site P supply and tree P nutritional status. Flückiger and Braun (2004) argued earlier that the low P status in leaves and needles indicated the low rate of tree growth. The results showed that the usual harvest of biomass only as trunk wood with a relatively low nutrient accumulation has a lesser effect on the removal of nutrient from forest surface. This strategy in the long-term leastwise helps the sites to keep their initial fertility. On the other hand, branches and foliage removed from the forest led to a multiplication of nutrients removal. These organs represent a small proportion of the biomass, but usually contain a high accumulation of nutrients.

4. Phosphorus Availability as Interaction of Soil and Biomass in Mature Forests

The productivity of mature forests generally varies between sites that are different in soil attributes (Augusto et al. 2008). However, lower number of studies in forestry have been advanced, concerning how P in tree biomass affects the site P fertility. Still there is a lack of plausible indicators to assess the interaction between trees aboveground organs and soil P richness and to consider relationships between P rich crown biomass and P in developed forest soils. In unmanaged forests, most of the attention by researchers to this interaction was emphasized on the supply of plant-available P in the mineral soil. The availability of P normally is determined by competition among biological and geochemical sinks in upper soil levels with a high accumulation of fine roots, microorganisms, minerals and organic matter (Prietzel and Stetter 2010). However, compared to other essential elements, the interaction of soil available P on site productivity in mature forests has not been thoroughly investigated. For example, Marschner (2012) and Ilg et al. (2009) explained that forests with a calcareous soil background, where the quantity of plant-available P is lower than on acidic soils, trees are more affected by the site P deficiency. Observations by Augusto et al. (2002) previously confirmed the impact of soil characteristics on the variation of P accumulation in tree components (aboveground biomass). Mellert and Ewald (2014) also claimed that the plant-available amount of P in forest soils governs tree productivity.

4.1 Soil Properties

The importance of soil available P for site growth highlights the importance of soil properties, which typically control the accessibility of plant-available P in forests (Achat et al. 2013; Hinsinger 2011). The supply of P in soils normally derives from an organic and inorganic fraction of P compounds in soil. Hence, mineralization of organic P forms and microbial P turnover in the soil, in addition to chemical reactions of P compounds in soil lead to an increase in the rate of tree P uptake (Morel et al. 1996). Soil characteristics, like age and physical and chemical properties, were used in studies by Prietzel et al. (2013) and Regelink et al. (2015) to present the capacity of soil P solubility. The distribution of Fe-(hydr) oxides and SOC (soil organic carbon), besides soil pH, were specified by Regelink et al. (2015) as a control factor in this regard.

Ewald (2000) estimated the impact of soil characteristics on tree nutrition levels at European beech stands and highlighted that soil properties strongly influence P values in tree foliage. The level of P concentrations in the foliage of investigated trees in high-developed soils was higher than in soil of undeveloped carbonate sites, where the presence of Ca reduces the P availability in soils. Ewald (2000) concluded that P is a critical element in the nutrition of European beech forests in the Alpine region. Khanna et al. (2007) interpreted this outcome from the poor vitality of European beech trees in mixed mountain forests. Considering the geologic substrate of forests at Bavarian Alps, Khanna et al. (2007) discussed that the low P nutritional status of trees on some calcareous bedrock is probably derived from the buffering power of carbonate ions that deliver less protons available for silicate weathering (presumably at forest sites having mixed carbonate-silicate soils, e.g. Marl containing various amounts of clay, carbonate, and silt in soil horizons). However, environmental factors like location climate, site vegetation, as well as soil biological activities can also strongly affect the availability of nutrients at common forests. Poor P nutritional status for European beech trees, considering concentrations of P and N/P ratios in foliage in the study by Prietzel and Stetter (2010), is related to low P content in soil at sites with limestone or dolomite parent material (alkaline) as well as in soil at sites with quartz-rich substrate, e.g. dune or quartzite (acidic). In contrast, the greatest P quantities in the study of Khanna et al. (2007) were reported in the needles of Norway spruce and pine trees on sites with basalt parent material. Recently, Niederberger et al. (2018) demonstrated that P pools and P fractions were highly associated with soil properties, and soil with higher SOC and lower sand content had the highest impact on P nutrition of trees. The results of BZE I and BZE II also revealed that the P nutritional status of Norway spruce and pine forests is much higher at sites containing basalt bedrocks (Ilg 2009; Riek et al. 2016). This additional information on soil attributes is essential in assessing the long-term influence of gradual release of P resources on site P fertility and forest development.

4.2 Site Organic Matter, Humus layer, Organic Phosphorus, and Plant Available Phosphorus

Generally, soil organic matter is a complex of organic substances with high nutrient accumulation and greatly influences the functions and properties of soil in natural ecosystems. In the common forest, site organic matter has little impact on availability of P in soils (Brady and Weil 1999). Accumulation of carbon (C) in the litter of healthy forests is often high, and if the ratio of C/P at site highly rises, the decomposition of organic matter decreases, diminishing the rate of P release from litter (Belyazid and Belyazid 2012). From monitoring two fertilized mature pine forests, Prietzel and Stetter (2010) observed that the amount of plant-available P in topsoil with lower C/P ratio was relatively high. However, the changes in C/P ratio were linked to the yearly net sequestration of P in tree woody biomass in their study. An increase in the content of N in forest litter (via atmospheric input) enhances the decomposition of litter, but concurrently via fixation of organic matter on forest floor and top mineral soils, indirectly diminishes the availability of soil P (Meiwes et al. 2002). Therefore, the long-term presence of organic compounds at sites often reduces the soil P fertility. Correspondingly, at sites with higher N atmospheric input in the study of Prietzel and Stetter (2010), concentrations of P in needles were lower. Accordingly, it seems that the high values of N in soil negatively influence the soil microbial community or enzyme activities, and by altering the soil C/P and N/P ratios, also change the nutrients availability in soil sites. This assumption was beforehand discussed by Belyazid and Belyazid (2012) and Jonard et al. (2009).

Although Achat et al. (2009) reported that P in organic matter covers more than 50% of total P supply in forest soil, they concluded that most P becomes gradually available for tree uptake. Accordingly, Khanna et al. (2007) argued that evaluating the amount of plant-available P, using typically strong acid tests or sequence methods is not suitable in forests and often leads to systematic errors in final outcomes. Nevertheless, from a long-term perspective and continuous P cycling in mature forests, the authors explained that the supply of P in forest litter modifies the P status of mineral soils. Thus, with reducing the mineralization rate of soil organic matters at sites, possibly the availability of P from site organic pools was decreased. Prietzel and Christophel (2014) also comprehensively defined the role of site organic matter on availability of macronutrients and micronutrients in the soil of mountain forests. This impact was highly associated with site geological substrate, e.g. their parent material, climate changes, and intensity of tree harvesting in previous decades (see also Baier 2006, and Mellert and Ewald 2014). The only concern about the accuracy and certainty of outcomes came from the variety of soil extraction methods (reliability of soil indicators) used. Furthermore, employing these tests on a few soil levels at dissimilar soil depths, e.g. mostly were conducted in most upper layers in their study.

Releasing the nutrients from organic layers into the mineral soil enhances the soil fertility (Waring and Running 1998). On the other hand, regarding the high accumulation of microorganisms in organic layers, humus seems to play a prominent role for the P status of sites. Studies by Bauhus and Khanna (1999) and Turner et al. (2004) demonstrated that the concentration of microbial biomass P in the humus is higher than in mineral soils. This points to the important role of microorganisms in the organic layers to support the tree P uptake, as well as to participate in mineralization processes (Khanna et al. 2007). Nevertheless, Bauhus and Khanna (1999) clarified that the impact of microbial growth and activity is relatively different at sites with various substrates. In addition, the positive impact of P in organic layers on the development of young trees has been reported by Talkner (2010b). However, in such experimental studies, the higher P uptake from the organic layers than from the mineral soil probably derives from the limitation in the root architecture of saplings. According to Belyazid and Belyazid (2012), the low potential of the humus to retain inorganic P also causes more inorganic P to be available for uptake. However, great amounts of organic P forms in humus as well as in mineral soils (monoester phosphates, inositol phosphates, nucleic acids, and phospholipids) are not easily accessible for plant uptake. Between these forms, inositol phosphates are commonly available in sufficient amounts (Jones and Oburger 2011). In an investigation on mature forests, Ilg et al. (2009) reported that the organic layers significantly influence the input-output of P in stands. The authors demonstrated that the values of P in the organic layers are dependent on the form of humus at site. For example, in sites containing the mull-humus form (pH= 3.8), P is more available in the rooting zone. In this regard, Ilg et al. (2009) explained that the growth of deciduous forests in sites with mull-humus is greater, while conifer forests are more developed in sites with mor-humus. Nevertheless, the impact of plant-available P stored in humus on P nutrition of trees in mature forests is not well investigated, and the results of most studies, in this regard, are linked to pot experiments or young trees.

4.3 Phosphorus Internal Cycling in the Tree Compartment

Internal cycling of mobile elements such as P in tree components supports the trees at different stages of growth (Proe and Millard 1995; Turner and Lambert 1986). P reuse in tree via internal cycling between organs is mainly expected in critical climatic conditions (e.g. cold winter, drought) or during early growth when uptake of nutrients by roots is limited (Nambiar 1985; Proe and Millard 1995). In this regard, the re-translocation of P between tree organs e.g. needles of conifers, might be a possible pathway for this phenomenon. Khanna et al. (2007) reported that up to 50% of P in first-year needles of adult Norway spruce trees shifted into younger needles during the new growth season. The element shift from older organs into the younger ones probably derives from tree adaption, supporting active organs, as well as coping with soil nutrition deficiency. Accordingly, although Belyazid and Belyazid (2012) documented that the rate of P withdrawn from tree foliage increases in abscission time, the rate of re-translocation is not related to soil P fertility.

Riek et al. (2016) already observed the fluctuations in the concentration of P in the needles of adult Norway spruce trees. The authors theorized that the differences in the concentrations of P between needles of different ages derive from tree P internal cycling via re-translocation at sites with low P fertility. However, according to Nambiar and Fife (1987), soil amendment by chemical fertilization increases the content of immobile elements in older needles and leads to an increase in the weight of the needles. Therefore, besides net P re-translocation, an increase in the weight of needles (organs) is likely an important factor to explain the differences between concentrations of P in the needles of conifers from different years that are seldom considered in similar studies. Göttlein et al. (2012) concluded that the low concentration of P in older needles at least partly resulted from the accumulation of immobile elements, such as Ca in older needles. Though the evaluation of the annual P shift between conifer needles has also been investigated in former studies, most of these studies examined seedlings or saplings over a short growing period. Hence, monitoring this phenomenon in developed sites for adult trees yields more reliable results than experiments on younger trees.

5. Tree and Site Phosphorus Nutritional Status Estimated by Foliage Analyses

For decades, forest researchers used the results of foliar analyses as an indicator to specify tree nutrition and site fertility. Regarding the higher P demand and the indispensable requirement of foliage for photosynthesis, foliage is a more appropriate organ for accumulating P than other tree components. Thus, the P nutritional status of trees can be evaluated by determining the P concentrations in needles and leaves. Flückiger and Braun (2003) previously emphasized that the results of foliage analysis are a suitable indicator for the nutrient status of adult trees in relation to site health. On the other hand, the impact of soil P fertilization on tree P nutrition and forest productivity has already been evaluated by analyzing the biomass (e.g. Augusto et al. 2008; Nilsson and Wiklund 1995). Although above-mentioned investigations sometimes reported significant differences in content P in tree foliage or tree productivity, these studies frequently reported an increase in concentration of P in the foliage and in the bark of trees. Concentrations of P in tree foliage as an index have already been used by forest researchers to predict the current site P fertility and optimum supply of P for the main forest tree species (e.g. Krauß and Heinsdorf 2005; Mellert and Göttlein 2012; Rothe and Binkley 2001).

Nevertheless, each above-mentioned study used a specific nutritional range for interpreting the tree nutritional status. These dissimilarities between nutritional ranges probably derive from the classifications of forest sites conducted by researchers, or according to tree age. For example, Krauß and Heinsdorf (2005) did not pay attention to the dissimilarity between the responses of young and adult trees to site fertility in developed or un-developed forests (details are available in Khanna et al. 2007). Consequently, applying the various evaluation systems, when creating a foliage database in order to define an adequate level for the nutritional status of trees, partly results in great differences in the outcomes of similar studies to represent tree species reference systems. In the current study, we decided to employ the newest foliage nutrition classification by Göttlein (2015), which in the majority of cases is more cautious compared to other reference systems. Göttlein (2015) specified a new range of threshold values (.25 percentiles, median, .75 percentile) for the concentrations of the main macro elements in foliage such as P. These threshold values were applied for the statistical data analysis in the current investigation to i) specify P nutrition of adult Norway spruce and European beech trees ii) compare the P nutritional status of trees in mature stands iii) identify the tendency of P internal cycling in trees with the amounts of soil extractable P at individual sites. These thresholds should be plausible as they were previously used to analyze the BZE II investigated plots throughout Germany, as well as recently by Mellert et al. (2018) and Fäth et al. (2019a, b) for the Bavarian part of the BZE II survey.

VI. STUDY JUSTIFICATION AND MAIN TARGETS

Soil N supply and soil pH as the two main site nutrient control factors in common forests are widely documented by researchers (e.g. Mellert et al. 2004; Weis et al. 2009). Nevertheless, the study of P resources and of soil P availability as a restrictor for site productivity was neglected for several decades in temperate forests (vs. tropical forests) (Vitousek 1984). Janssens et al. (2010) and Mellert et al. (2004) reported that the N deficiency in terrestrial ecosystems has been diminishing in recent decades. From the observations of Mellert and Göttlein (2013) and Vitousek (2010), the P shortage appears to be becoming the most significant limiting element in common forests. This issue is currently getting ever more important, because many forest stands in central Europe are apparently drifting from former N limitation into P limitation (e.g. Mellert and Göttlein 2013; Niederberger et al. 2018). As earlier noted, a sufficient supply of P is a precondition for plant growth, and its availability in forest soil has been shown to be linked to tree growth. Thus, information about soil P supply (notably, plant-available P) and the content of P stored in trees are required to clarify the current P status of sites, as well as to manage forests sustainably for the future.

In addition to the results of IAP, Braun et al. (2010) and Talkner et al. (2015) detected a continuous decrease in P nutrition in adult Norway spruce and European beech trees in central Europe. This decrease is mainly linked to the low availability of P in the soil. The results of BZE II by Wellbrock et al. (2016) also revealed that approximately 25% of Norway spruce and 50% of European beech in German forests are below the normal range of P nutrition. This percentage is raised to 70% in Bavarian mountain forests (Mellert et al. 2017). Mellert et al. (2018) explained that this P decline in deciduous species is more widespread than in conifers. The authors argued that it might indicate that stocks of soil P in sufficient quantities cannot be provided only from the P supplied in certain soil layers. The present work will answer some of the open questions concerning the different P pools in the soil of mature forests (study aims are individually and precisely noted in the next section). Here, special emphasis will be placed on measuring the concentration and stock value of readily extractable P in soils to determine which of these sources and which levels of the soils are more important for tree nutrition (see also Appendices A and B).

The current supply of P in trees is normally determined by P concentration in leaves or needles of tree crowns. However, sampling foliage from tree crowns (7th whorl) is relatively complicated, and thus, is limited for large numbers of trees. Moreover, using foliage diagnosis as a standard parameter leads to some inconsistencies e.g. differences in tree age or variations in foliage P concentration (Talkner et al. 2010a). Owing to the variability of P accumulation in tree components during annual growth (Wyttenbach et al. 1995), relying only on the results of biomass analyses is not sufficient to estimate site P fertility. Therefore, it was necessary to find other reliable parameters (e.g. soil parameters), which are easy to survey and that help to estimate the P supply of trees at a site. Hence, regarding the relatively high consistency over time of the soil P supply in mature forests, the results of soil analyses should also be trustworthy. In total, the above descriptions once again justify the arrangement to use particular P extraction methods for forest soils. Moreover, the results of soil analyses may more accurately explain the effects of soil chemistry on the tree P resorption. According to Khanna et al. (2007), merely taking into account concentrations of nutritional elements in tree foliage does not completely predict tree nutrition status. The authors additionally documented, despite the fact that several complicated P extraction methods have been developed, none is appropriate as a standard method for analyzing a large number of samples in forests. Finally, gradual soil weathering is known to be responsible for site P cycling, but the most investigations only use short-term indexes of P supply to identify the sites' P availability (Richter et al. 2006). Our study was conducted in mature forests, where adult trees commonly attain their P requirement gradually and over long-term soil development.

During the BZE I and II inventories, for many nutritional elements (e.g. C, N, Ca, Mg, Na, and K) a suitable test or an extraction method has been established to evaluate plant-available pools at forest sites. For example, elemental analysis for C, N, Aqua regia method for stocks of Ca, Mg; the $BaCl_2$ and NH_4Cl methods for CEC of Ca, Mg, K, (details are available in Ilg 2009; Welbrock et al. 2016). Unfortunately, there is still a methodological problem for quantifying the values of plant-available P in forest soils (Ilg 2009). Since most portions of P supplied in forest soils are not available for tree uptake (Prietzel et al. 2013), the quantity of total P in soils may not be a suitable indicator for predicting site P fertility. Marschner (2012) similarly acknowledged that the total soil P is not a good predictor of plant-available P in soils. Therefore, applying simple extraction methods that quantify the easily available P in sites is necessary. With regard to the simple and economic features of simple soil tests to extract P **(phosphorus extraction methods, PEMs)**, these are potentially suitable methods to use in large forest soil inventories and may be of great interest to the BZE III preparation committee. In addition, the low practicability of the Hedley method (1982) to estimate the P nutritional status of main tree species in German forests was affirmed in the study of Niederberger et al. (2018). Although abundant knowledge of the substantial mechanisms of P uptake by plants and influencing factors exists, most studies have been conducted on fertilized soils (e.g. in agricultural lands or at managed forest sites). There is still sparse knowledge about the fundamental processes concerning the P uptake and a lack of practical relevant studies on common forests, covering different aspects of P extraction from unfertilized soils.

On the other hand, P absorbed by trees, as well as its subsequent fate in the biomass, has not been well investigated in a broad variety of soils with differing P levels and properties. This subject becomes more significant when sites lose their main source of P input (P stored in rich organs) via full tree harvesting, which in long-term site development, probably negatively affects the supply of P in soils. It is worth mentioning, investigations in this field, by BZE I and II, have strengths and weaknesses. During BZE I, different nutritional ranges and critical P nutrition values were used to evaluate the nutritional status of tree foliage (Khanna et al. 2007). Further, there was no indication of whether the values were only valid for mature forests, and the thresholds were solely defined based on symptoms of foliage P deficiency. The authors claimed that employing the critical ranges for the concentrations of P in leaves/needles had some limitations. For example, these values did not represent a particular tree P status for all species, all ages, stand chemical and biological processes or biological factors like P re-translocation. Moreover, P nutrition of most investigated trees was evaluated at controlled forests, which may not realistically explain the optimum tree nutrition. Briefly, during BZE II, only three trees per plot in each sampling year were investigated. Hence, the BZE II dataset is, on the one hand, the largest available forest soil dataset in Germany, but on the other hand, due to sampling size, the results based on foliar nutrient contents have relative uncertainty. Furthermore, the results of most studies on P availability in forests have mainly been from pot experiments or were limited to saplings. Hence, there is a lack of studies, focusing on the efficient use of P by adult trees through P acquisition from soils (uptake efficiency) and on high forest utilization (intensive harvesting) in common forests. The current study, however, does not aim to assess the fundamental process of chemical fractions of available P compounds in the soil solution.

The aims of this thesis are to:

I) expand knowledge of P availability in mature forests to explain the interaction between sites P supply and P nutritional status of adult Norway spruce and European beech trees. The initial aim here is to identify the current supply of P in stands to quantify the accessibility of P in different soil levels for trees and its relationship with P foliage, representing for tree P nutrition (Appendix A).

II) present a simple P extraction method to estimate the quantity of easily extractable P in soil and determine an appropriate indicator for describing the site P status. The purpose is to develop a protocol that optimizes plausible, inexpensive, rapid, and simple soil tests for assessing the relationships between readily soil extractable P and the concentration of P in aboveground organs of adult Norway spruce trees (Appendices A and B).

III) demonstrate the importance of P stored in tree crown biomass for site growth. Removal of crown biomass from the forest surface could lead to a site P deficiency. Using PEMs predictors, our study also assesses the important impact of plant-available P distribution in soil on the rate of tree P uptake at developed sites (Appendix B).

IV) explore tree P internal cycling through P re-translocation between needles of adult Norway spruce and to clarify the relationship between differences in concentrations of P in needles using the results of PEMs. Here the aim is to specify whether the P supplied in older needles supports the new needles or a decrease in concentrations of P in older needles derives from an increase in weight of needles via accumulation of other immobile elements (Appendix C).

Accordingly, the present work was undertaken to answer the following questions:

1) How did the applied PEMs behave in the face of soil available P?

2) Is there a routine and suitable soil extraction method that properly mirrors the reservoir of P in the tree needles/leaves? Accordingly, is the P nutritional status of adult trees also predictable?

3) If such methods exist, which criterion shall be used for prediction (concentrations or stocks of soil extractable P)? Which soil level provides the most portion of P for tree nutrition?

4) How do the other tree compartments respond to different P availability in soil? Is the site productivity also associated with soil P fertility?

5) Does an adult tree react to critical quantities of available P in soil by internal cycling of P via re-translocation among organs?

To achieve our purposes, trees were facetiously asked about their health at the sites, at which they were growing. The trees' response was more serious than we expected, and their health was reflected in P concentrations in their biomass organs. If these reflections are positively correlate with the plant-available P in their soil, we can be reasonably certain about tree health. Correspondingly, in the result and discussion section, the above questions will be individually answered.

VII. OVERVIEW OF APPLIED METHODS

1. Simple Soil Tests to Evaluate the Readily Extractable Phosphorus

According to Schick et al. (2013), complicated extraction methods do not lead to the best measurements of plant-available P. Therefore, employing simple extraction methods, and thereby identifying the amount of soil readily extractable P may be more meaningful to assess the actual P availability. Besides this, different extraction methods yield dissimilar diagnoses for P availability in plant growing areas (Maguire et al. 2005). Accordingly, Hinsinger (2001) and Ilg (2009) emphasized that the determination of soil extractable P in developed soils (like mature forests), especially in rooting zones (topsoil), should be considered more than other soil levels (subsoil). However, regarding the strong dependency of P availability on soil pH, along with the high tendency of phosphate ions to bind with soil cations, evaluating whole amounts of plant-available P is relatively difficult (Khanna et al. 2007). Further, many previous soil P extraction methods are either available for alkaline or acid soils, they are partly complicated (sequential approaches, e.g. Hedley test, 1984), time-consuming (ion exchange resin membranes), or their results did not accurately represent the amount of plant-available P (strong acid tests). Therefore, these methods are not applicable for large numbers of soil samples. Employing PEMs in the current study modifies the above-mentioned complications. Since Dyer (1894) applied the citric acid method to extract the plant-available P from soils, to date several different soil tests have been suggested. Thus, some reasons for selecting the employed **"PEMs"** are briefly elucidated. The water, double lactate, sodium bicarbonate, and citric acid extraction methods have been used to extract readily extractable soil P.

The **"Water method"** Paauw (1987): Mixing 10 g dry and sieved soil with 200 ml distilled water, shaking time 12 hours. This method is the simplest test to measure the amount of nutritional elements in any ecosystem. In addition, the relationship between P extracted values using the water method might be closer to plants uptake of P than the other common tests (Paauw et al. 1971). Applying the water method would also be most useful, when the extraction amounts of P are basically low (considering the low extractive power of water), especially if other solvents are more acid or alkaline than the soil solution (Self-Davis et al. 2000). The value of extracted P differs considering several factors such as pH of soil solution, extraction time, temperature and concentration of active agents in the solution (Schick et al. 2013; Sibbesen 1983). In this regard, mild solvents probably do not highly change the soil chemically and possibly better mirror the above-mentioned effects than employing solvent in strong acid methods. Moreover, the water as a solvent is not harmful to the environment and more accurately, simulates the release of P to soil solution than other stronger solvents (Moore et al. 1998).

The **“Lactate method” (developed later to Double lactate)** Hoffmann (1991): Mixing 4 g dry and sieved soil with 200 ml Double lactate solution, shaking time: 90 minutes. Double lactate is a solvent with relatively strong solubility, which quickly forms chelates with Ca, Al, and Fe cations (Vanderdeelen 1994). Hence, it is an appropriate solvent to extract P from soil compounds (e.g. hydroxides and oxides of Fe and Al, as well as Ca-phosphate). However, Riehm (1942) had modified this method by doubling the lactate concentration leading to an incremental increase in the acidity and the buffering capacity of this solvent.

The **“Sodium bicarbonate method”** (Olsen 1954): Mixing 5 g dry and sieved soil with 100 ml 0.5 M sodium bicarbonate, pH = 8.5, shaking time: 30 minutes. This test is one of the common techniques to extract the plant-available P from the soil. In principal, the method employed to diminish the concentration of soluble Ca^{2+}, Al^{3+} and Fe^{3+} cations in the soil solution by precipitating $CaCO_3$ or forming Al- and Fe-oxides and hydroxides with HCO_3^-, CO_3^{2-}, and OH^- in calcareous and non-calcareous soils. This method is also as a part of Hedley fractions often employed by forest researchers to evaluate the site P fertility. It should be noted that the outcomes of these methods in agricultural land are highlighted more than in forest ecosystems.

The **“Citric acid method”** Dyer (1894): Mixing 10 g dry and sieved soil with 100 ml 1% citric acid solution, shaking time: first, for 3 hours, and the next day before filtering, for 30 minutes. This solvent has rarely been used to quantify the amount of plant-available P in forest soils (only in a few studies such as Gulder and Kölbel 1993; Schubert 2002). The experimental and positive outcomes of former research in mature Bavarian forests (e.g. Prietzel and Stetter 2010; Schubert 2002), concerning the results of P extracted by using the citric acid method as a predictor for plant-available P in forest sites was the main reason to employ this technique in the current investigation.

Finally, it is worth mentioning that the applied PEMs in our study were formerly tested in a pilot study by Lang (2009) on a small number of soil samples. Bedsides these simple soil tests, the values of total soil P is measured by the **“aqua regia”** method, according to König et al. (2005). For more details, kindly refer to Appendix A.

2. Abstract of Soil and Biomass Sampling and Employed Data

Initially, it should be mentioned that this study partly used the available data at the Professorship of Forest Nutrition and Water Management, which are thoroughly referenced in Appendices A, B, C. Secondly, the meaning of topsoil throughout the manuscript is a range of soil depth from 0 to 40 cm of mineral soil. Procedures of soil and biomass sampling and their chemical analysis methods in all experimental parts were applied according to the Handbook Forest Analytics, HFA (König et al. 2005).

We used: **i)** the concentration of P in foliage of Norway spruce and European beech trees for Study A, available data from the BZE II inventory, Bavarian part, **ii)** sites information, and the concentration of P in aboveground biomass of Norway spruce trees for Study B, available data from the research project B67 (Nutrients sustainability criteria for Bavarian forests), **iii)** and the concentration of P in needles of Norway spruce trees for Study C, available data from the project SFB 607 and BDF, conducted in Kranzberger-Forst in Freising southern Germany and other Bavarian forests. To assess the tree P nutritional status, we used the thresholds of P in the first-year needles of the Norway spruce and leaves of European beech trees, according to Göttlein (2015). For more details, kindly refer to the methods and material section in Appendices A, B, C. Stand growth at each site for study B was modeled using the single tree growth simulator SILVA 2.3 (Pretzsch et al. 2002) (Appendix B).

For soil analysis, from available soil samples in the above-mentioned projects (A and B), the author of this doctoral thesis conducted soil analysis (including the extraction process, and pH measurements) in the laboratory. In the study C, besides the soil data for all Bavarian sampling plots in BZE II inventory, we used the soil data from the permanent soil monitoring investigation by the Bavarian State Institute of Forestry (LWF). Accordingly, the depth of soil samples include: 0-5 cm, 5-10 cm, 10-20 cm, 20-40 cm, and 40-80 cm. The depth of mineral soil and humus sampled for P stocks include: 0-5 cm, 0-10 cm, 0-20 cm, 0-40 cm and 0-80 cm. The values of P in each soil depth and for aggregated soil (down to 80 cm depth including the organic layer) were calculated to evaluate the concentration and stocks of P in mineral soils. The soil samples that the author worked on were filtered via a membrane (0.45 μm), and were analyzed at the ICP-spectrometer model genesis of Spectra for determining the P. The stepwise variable selection in the multiple linear regression (statistics package SPSS version 23.0) was carried out with the inclusion criterion $p < 0.05$. For more details, kindly refer to Appendices A, B, C.

VIII. ABSTRACTS AND CONTRIBUTIONS TO THE INDIVIDUAL PUBLICATIONS

1. Correlating phosphorus extracted by simple soil extraction methods with foliar phosphorus concentrations of Picea abies (L.) H. Karst. and Fagus sylvatica (L.)

Hadi Manghabati, Michael Kohlpaintner, Rasmus Ettl, Karl-Heinz Mellert, Uwe Blum, Axel Göttlein (2018): Plant Nutr Soil Sci, 181 (4): 547-556. https://doi.org/10.1002/jpln.20170 0536

Phosphorus (P) concentrations in needles and leaves of forest trees are declining in the last years in Europe. For a sustainable forest management, the knowledge of site specific P nutrition/ availability in forest soils is vital, but we are lacking verified simple methods for the estimation of plant available P. Within this study, four soil P extraction methods [water (P_{H2O}), double-lactate (P_{lac}), citric acid (P_{cit}), and sodium bicarbonate (P_{HCO3})], as well as total P content of the soil (P_{tot}) were tested to investigate which method is best correlated with foliar P concentrations of spruce [Picea abies (L.) H. Karst.] and beech [Fagus sylvatica (L.)]. Mineral soil samples from 5 depth levels of 48 forest sites of the Bavarian sample set of the Second National Forest Soil Inventory (BZE II) were stratified according to tree species (spruce and beech) and soil pH (pH < 6.2 and pH > 6.2), covering the whole range of P nutrition. The extractable amount of P per mass unit of soil increased in the order $P_{H2O} << P_{lac} < P_{HCO3} < P_{cit}$, decreased with soil depth, and was higher in soils with pH < 6.2. Citric acid extracted up to 10% of P_{tot} in acidic soils. Whereas P_{cit} delivers adequate regression models for P nutrition in the case of spruce (R^2 up to 0.53) and beech (R^2 up to 0.58) for acidic soils, P_{HCO3} shows good results for spruce growing on acidic soils (R^2 up to 0.66) and for beech on soils with pH > 6.2 (R^2 up to 0.57). P_{lac} produces adequate models only for beech on high pH soils (R^2 up to 0.64), while P_{H2O} did not produce acceptable regression models. P_{tot} seems suitable to explain the P nutrition status of beech on acidic (R^2 up to 0.62) and alkaline soils (R^2 up to 0.61). Highest R^2s are obtained mostly in soil depths down to 40 cm. As P_{HCO3} and P_{cit} showed good results for both investigated tree species, they should be considered preferentially in future studies.

Contributions: I carried out all procedures of soil P extraction in the laboratory and was responsible for data management, as well as data evaluation. Furthermore, I wrote the text, designed all figures and tables and did all additional work. Michael Kohlpaintner is the equal author. Rasmus Ettl and Karl-Heinz Mellert contributed to the statistic and discussion sections. Uwe Blum gave support for the BZE II data-base and provided supplementary nutritional and soil data. Axel Göttlein designed and supervised the study.

2. Importance of soil extractable phosphorus distribution for mature Norway spruce nutrition and productivity

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Phosphorus is an essential nutrient for forest growth. In this study, we assessed the impact of soil extractable phosphorus using two simple extraction methods on nutrition and productivity of Norway spruce in sixteen mature forest stands on different bedrocks and soils in Bavaria, Southern Germany. Representative trees were sampled for needles, twigs, branches, stem bark, and stem wood. Total phosphorus content in the tree parts and soil phosphorus stock extractable with citric acid and sodium bicarbonate up to a soil depth of 80 cm were determined. We found that easily soil extractable phosphorus is a suitable indicator for estimating phosphorus uptake and stand productivity in Norway spruce. In contrast, organic layer phosphorus showed no significant correlation with aboveground biomass phosphorus contents. In the biomass, the highest phosphorus contents were measured in young needles and twigs, but the highest correlation with soil phosphorus was detected for phosphorus contents in needles and bark. The stock of phosphorus extracted by citric acid down to 40 cm soil depth revealed the best correlation with phosphorus in needles and bark. Therefore, as a supplemental or alternative method to needle analysis, our study suggests the use of phosphorus contents in stem bark to evaluate tree phosphorus nutrition. These results highlight the suitability of the citric acid soil extraction method to characterize plant available phosphorus in Norway spruce ecosystems.

Contributions: I was responsible for data evaluation, writing the manuscript, and for the design of figures and tables. Axel Göttlein and Wendelin Weis designed the study, provided access to the data, and supported me in writing the manuscript, particularly in the discussion section.

3. Changes in phosphorus concentration in needles of adult Norway spruce - nutrient re-translocation or dilution effect?

Hadi Manghabati, Wendelin Weis, Axel Göttlein (2019): Eur J For Res, 138 (3): 539-546. https://doi.org/10.1007/s10342-019-01188-0

Regarding the low availability of phosphorus in soil, tree internal cycling of phosphorus through re-translocation among needles would be a good strategy for conifers to cope with soil phosphorus deficiency and to support new needles in annual growth. Therefore, the relationship between the amount of plant-available phosphorus in the soil and the differences in concentrations of phosphorus among first- and second-year needles (P-difference $_{\mathrm{Ny1-Ny2}}$) of adult Norway spruce was examined. No significant correlation could be detected between the stocks of available phosphorus extracted using citric acid and P-difference $_{\mathrm{Ny1-Ny2}}$, even for trees with deficient nutritional status. The temporal variations of P-difference $_{\mathrm{Ny1-Ny2}}$ at single plots showed the same order of magnitude as the variability between plots. The typically lower concentrations of phosphorus in second-year needles result mainly from an increase in needle weight of older needles. The net phosphorus re-translocation into younger needles appears to be of minor importance.

Contributions: I was responsible for data evaluation, writing the manuscript, and for the design of figures and tables. Axel Göttlein and Wendelin Weis had the initial idea for the study and provided access to the data. Axel Göttlein designed the study and supported me in the statistic section and writing the manuscript.

IX. RESULTS AND DISCUSSION

In the following chapter, after discussing the results and behavior of employed PEMs in soils, the findings of three published studies (Appendices A, B, C) and preliminary questions are set in a broader perspective. Additionally, general outcomes are argued as a global discussion, and hints to future directions are mentioned.

1. PEMs' behavior at investigated plots (Paper A)

The results reveal that the quantity of P extracted per mass unit of soil clearly differs when using different PEMs, and the values of P increase in the order of water <<< double lactate < sodium bicarbonate < citric acid. This sequence is in accordance with and similar to the outcomes of studies by Csatho et al. (2005) and Kulhanek et al. (2009) (except that citric acid was not tested). Wuenscher et al. (2015) argued that solvents, having different extraction powers, dissolve different P forms; thus, the quantity of extracted P from soil is expected to be unequal. In line with their argument, PEMs with dissimilar extractive power in our study extract various amounts of P from soil. Accordingly, Sibbesen (1983) reported the positive impact of several factors, e.g. activity of HCO_3^- or H^+ ions, on absolute P concentration in extract solutions. However, besides these factors, uptake of P by plants in nature was also linked to the activity of organic anions exuded by fine roots, and to the altering activity of the cations that precipitate the phosphate in soil (Schick et al. 2013).

As expected, the lowest extractable values of soil P were obtained using the water method. Marschner (2012) similarly noted that a very low portion of P stored in forest soils is extractable using water. Correspondingly, Wuenscher et al. (2015) justify that ionic strength and the application of saturation in water extract (lower soil-to-solution ratio) in their study was the main reason for reducing in the percentage of absorbable P from the solid phase. Considering the values of colloidal-size P in water extraction, the low ionic strength of a high soil-to-solution ratio leads to detachment of soil colloids and to diminishing the amount of P in solution (Koopmans et al. 2005). However, in our study after filtration by a 0.45-µm membrane small colloids are still present in solutions. According to Missong et al. (2017), mostly in acid soils a high percentage of water extractable P is bound to colloids, nevertheless, this portion of P is not easily available for plant uptake (Fäth et al. 2019b).

On the other hand, due to the highly complexing feature of double lactate versus available cations, e.g. Ca, Fe and Al in soil solutions (Schick et al. 2013), our study expected high extractive power of this solvent for releasing P from different soil layers. The amount of P extracted, using double lactate, was higher than the water method, but contrary to our expectations, the extracted P concentration was not high and still much lower than the citric acid and sodium bicarbonate extractants, particularly in deeper soils and in calcareous sites. In an agricultural experiment, Schick et al. (2013) reported that the solubility of soil extractable P decreases with rising pH values. Therefore, the authors claimed that the amount of P extracted using the double lactate method underestimates the extractable amount of P in calcareous soils. Werner (1974) also argued that the buffering capacity of the double lactate solvent is insufficient for chalky soils (soil with high pH and alkalinity due to excessive amounts of lime and $CaCO_3$), which accounts for the uncertain results of this test for calcareous sites. Nevertheless, regarding the high availability of P in agricultural lands, the water and double lactate soil tests are commonly used in routine analyses to predict and determine the P balance assessment for different fertilization treatments (Schick et al. 2013).

Employing the double lactate extraction test, in a comparative study on forest and agricultural soils Leinweber et al. (1993) indicated that this solvent contains lower extractive power in forest soils. Comparing the efficiency of PEMs in fertilized soils, Otabbong et al. (2004) showed that the sodium bicarbonate method better explained the P distribution in plots than the double lactate method. In accordance with Bortolon and Gianello (2012) and Wuenscher et al. (2015), the results of our study and the findings of the above-mentioned research demonstrating some dissimilarity for the amount of P extracted, are probably derived from variations in physical and chemical parameters of soils and site attributes. Depending on study aims and regarding the type of soil (e.g. agricultural or forest soil, at managed or unmanaged sites, with poor or rich parent material, geologic substrates), extracting the different P forms from the soil likely influences the interpretation of soil test result (Menon et al. 1989). Hence, the current study aimed to identify the amount of **"readily extractable soil P"** in common forests. To the best our knowledge, no recent study in forestry has recommended applying the water or double lactate methods to evaluate the plant-available P in mature forests.

It is worth mentioning that at sites examined, the percentage of total P extracted in calcareous soils was generally higher than in non-calcareous soils, while the amount of P extracted by PEMs was greater in non-calcareous soils. These outcomes likely result from the high tendency of phosphate ions to match with the available cations in calcareous soils. Principally, the existence of Ca^{2+} ions in calcareous soil decreases the mobility of soluble forms of P (organic and inorganic P forms) (Wang et al. 2015). Further, the applied PEMs may not be able to dissolve such P forms, which strongly bind with other soil particles. This is in line with the interpretation of Prietzel et al. (2016), who reported that rather 50% of the total amount of P in alkaline soils (dolomite, sedimentary carbonate rock) is present as Ca bound organic P (calcium inositol hexakisphosphate) and Apatite-P (**Appendix A**). Therein, the citric acid solvent, which can extract that part of organic P for plant uptake, might dissolve a larger portion of labile organic P in soils (Darch et al. 2016; Hayes et al. 2000). Prietzel et al. (2014) observed that in mature Norway spruce sites with calcareous soils on limestone, the value of soil extractable P (plant-available P) using the citric acid test is lower than for non-calcareous soils. However, the authors reported that this low amount in shallow alkaline soils on dolomite-stone bedrock is usual in Alpine regions.

Correspondingly, the extracted amount of P, using the citric acid solvent in our study, was substantially higher than other PEMs and showed the highest extractive power, especially at acidic sites. Though the mean value of P extracted, using the citric acid and sodium bicarbonate method, was almost the same in the topsoil (down to 40 cm), this value in the subsoil was almost two times higher using the citric acid method. The similarity in the results of both methods in upper soils was previously demonstrated by Khanna et al. (2007) and was linked to the high accumulation of soil organic matter and the high accessibility of organic P compounds. An explanation for this alteration in deeper layers, using the citric acid method, might derive from the greater tendency of citrate anions to form strong complexes with cations, especially at lower pHs (Abdu 2006).

In total, quantifying the value of plant-available P, using organic acids, is more appropriate in sites with low P availability, such as stands with very acidic and alkaline backgrounds (Ström et al. 2002; Palomo et al. 2006). Employing such solvents probably mimics the behavior of roots through dissolution, desorption, or chelation reactions (Renneson et al. 2016). In the study by Beylazid and Belyazid et al. (2012), it was argued that the exudation of organic acids by plant roots in critical climate conditions (excessive drought or soil freezing in long winters) highly increased to cope with soil P deficiency. Grayston et al. (1996) also acknowledged this for forest trees. For this reason, organic acid soil tests (e.g. citric acid) by Attiwill and Adams (1993) are recommended to extract the plant-available P in forest soils. Fox et al. (2011) confirmed that the solvents such as citric acid with pKa > 4 (acid dissociation constant) affect the P release from soils more than solvents with pKa < 4. From another aspect, the chemical structure of citric acid is relatively stable in soil solution, particularly in acidic soils, where the presence of Al cations strongly governs the soil pH and negatively impacts on degradation of organic acids (Beylazid and Belyazid et al. 2012). This stability documented by Jones et al. (2001) from the complexing of Al^{3+} with citrate anions in the soil solution. The authors have stressed that tree roots usually produce organic acids when a high number of Al cations is available in the soil, but most of these organic acids exuded are quickly decomposed by soil microorganisms.

Furthermore, compared to the sodium bicarbonate solvent, citric acid contains a higher number of negative binding places to trap the soil available cations and release their anions (Göttlein 1998). Wuenscher et al. (2015) reported that the amount of P extracted, using the sodium bicarbonate method was not always associated with the pH of the soil or the content of carbonate in soils. This observation is not consistent with our results, where in carbonate sites a lower quantity of P is extracted by applying the PEMs. This difference might be due to the typical formation of a relatively rigid bond between the Ca and phosphate ions in lime soils. Hence, Prietzel and

Stetter (2010) decided to use the citric acid extraction method for quantifying the amount of plant-available P in the topsoil of pine forests with acidic specifications. Prietzel et al. (2014) also monitored the site-related patterns of essential nutrients (for P, they used the results of citric acid extraction method) in soil and the nutritional status of adult Norway spruce trees, which represent the applicability of this extractant to evaluate the amounts of plant-available P in the soil of mature forests.

As observed above, the concentration of extracted P using PEMs at acidic forest sites was higher than in forests with alkaline soils, but this concentration was reduced in deeper soil levels at both European beech and Norway spruce sites. Beylazid and Belyazid et al. (2012) reported that in conifer forests, P availability in the topsoil is enhanced owing to an increase in mineralization of organic P forms, as well as high microbial and fungi accumulation and greater root phosphatase activity. It is known that Ca compounds are prevalent in most calcareous sites, whereas Al and Fe compounds are more dominant in acidic sites. In soils with high pH, the $Ca_3(PO_4)_2$ and apatite formation are rather stable and sparingly soluble. As the pH of soil goes down, PO_4^- becomes more soluble and tends to dissolve, leaving acidic conditions. The opposite trend is expected for $AlPO_4$ and $FePO_4$ in non-calcareous soils (Brady and Weil 1999). The authors explain, among soil P forms, the amount of P released from the apatite rock is lower than simpler P compounds, such as mono-calcium phosphate (commonly found as $Ca(H_2PO_4)_2.H_2O$) and di-calcium phosphate (commonly found as $Ca(HPO_4).2H_2O$), also being easier available for plant uptake. On the other hand, Fe and Al-hydroxy phosphates are present as low extractable P forms in acid soils. Nevertheless, Brady and Weil (1999) explained that at acidic sites, these P forms become more extractable as the pH of soil increases. Consequently, our observations are consistent with the statement of (Gerke 1992), who reported a high power of citric acid (concerning complexing properties) to extract the plant-available P in soils with lower pHs than sodium bicarbonate. The higher levels of P extracted using citric acid rather than other PEMs clearly explained this capability. Furthermore, citric acid is a more suitable extract than the other organic acid for simulating P mobilization by tree roots (Gerke 1992; Grayston et al. 1997). As noted in study justification, the biology and adaptation of adult trees versus nutrient deficits at forest sites can indirectly modify P uptake via root expansion and exudation of different organic acids from fine roots. This affects the solubility of nutrition elements in soils. Hence, citric acid might also accurately simulate the changes in P extractability, when using different extraction substances under laboratory conditions, leading to different P values in the soil solution.

The most significant findings:

1. **There is a significant difference between the results of P extraction methods employed in our study at different mature forest sites with developed soils.**
2. **The mean values of P extracted from soils, using PEMs at investigated sites is:**
   Water <<< Double lactate < Sodium bicarbonate <Citric acid
3. **The extracted amount of P using PEMs at acidic sites is higher than at calcareous sites, while total P supplied in calcareous soils is higher than in the acidic sites.**
4. **In acidic soils, P extracted using the citric acid and sodium bicarbonate solvents contained up to 10% of total amount of soil P supply. In calcareous soils, this percentage was almost 5%. These amounts decreased with increasing soil depths at both sites.**
5. **The information on stand parent material and the type of geologic substrates at mature forest sites are more helpful than soil pH stratification for estimating the availability of P in soil.**

2. Do the results of PEMs significantly reflect the P in needles/leaves? (Papers A and B)

In the first statistical analysis, we used a stepwise multiple linear regression to test if the amounts of readily soil extractable P can explain P in tree foliage. As explaining variables, besides the results of PEMs, we also offered other soil parameters (cation exchange capacity: CEC; total digestion: TD for important cations, e.g. Al, Mg, Fe, Ca; SOC: soil organic carbon), measured during the BZE II inventory to improve the prediction of the foliar P concentration, which may influence P availability (unpublished results). Though in some single cases, CEC and TD positively, and SOC negatively predict the foliage P nutrition, the results of PEMs (frequently P extracted applying both the citric acid and sodium bicarbonate methods) using aggregated stocks and concentrations showed a higher number of linear regressions, selecting P extracts as a first predictor (84% of the models, results are not shown). Accordingly, for large dataset analysis, Fäth et al. (2019b) also included the CEC and TD variables to the results of citric acid extract to identify additional predictive soil information for tree P nutrition. Similar to our results, in their data-analysis, P extracted using citric acid and sodium bicarbonate tests were subsequently selected as accurate predictors for P nutrition of sampled trees (main European tree species).

Based on these outcomes, we were convinced we could use the results of the citric acid and sodium bicarbonate extraction methods as diagnostic indicators to assess the relationship between the amounts of easily extractable soil P and P nutrition of adult Norway spruce and European beech trees. An additional advantage of applying the above-mentioned predictors is the applicability of these two methods in forest soils, previously described in the German Handbook of Forest Analytics (König et al. 2005). With regard to the concentration of P in tree foliage, Kohlpaintner et al. (2017) also proposed that PEMs, especially citric acid and sodium bicarbonate methods can estimate the contribution of site plant-available P on P nutrition of adult trees. It should be noted, in contrast to our observations, Paauw (1971) and Jarosch et al. (2018) explained that the concentration of P from water extraction on fertilized soil properly predict the P uptake of plants. Using the results of water and double lactate methods, our study detected a mild correlation with the foliage P nutrition. Sibbesen (1983) argued that forest soils with highly complex P forms often do not contain portions of P easily soluble in water solution, so that perhaps they do not sufficiently provide the P requirement for adult trees.

We indicated that among the PEMs and the aqua regia method (total P content), the P extracted using citric acid and sodium bicarbonate methods positively mirror the concentration of P in the foliage of Norway spruce and European beech trees (significantly, with a high coefficient of determination, $0.60 > R^2 > 0.50$). However, for both species this correlation using both methods in acidic soils was stronger than in calcareous soils. These outcomes demonstrate that tree species may acquire their P requirement from different P fractions in soils (depending on soil chemical properties, such as soil available cations and soil pH). This assumption is also supported by the outcomes of BZE II in the forest nutrition section, where the P nutrition of European beech trees (partly Norway spruce) in calcareous soils was below normal nutrition level, whereas it was the best for oak within the same soils (Riek et al. 2016). The authors reported a decline in P nutritional status of adult trees in oak forests when soil acidification increased. An explanation for this decline might derive from the behavior of oak trees using dissimilar strategies to compensate for their P demand than European beech trees that are still more competitive in German forests. Fäth et al. (2019b) observed that the correlation between the values of plant-available P in soil and P in foliage of trees is clearly different in conifers and deciduous trees. In their investigation, European beech trees noticeably showed a lower level of P nutrition for the same quantity of citric acid extractable P compared to conifers. They reported that the relationship among foliage P nutrition of Norway spruce trees and citric acid topsoil extractable P is stronger than in pine trees. In the study of Riek et al. (2016), above-mentioned correlation was also different for oak and European beech trees, which probably derives from roots competition in the soil of different forest sites. From Fäth et al. (2019b), the content of P in foliage of the European beech is significantly lower than other tree species, with almost the same amount of P extracted from the citric acid in the soil. The explained trend for European beech and Norway spruce trees is in contrast to our observations. Such kinds of dissimilarity correspond to the lower threshold values for the European beech (1200

- 1700 µg/g, normal P nutrition range by Göttlein 2015) compared to the thresholds for Norway spruce (1300 - 2000 µg/g).

According to König (2005), the high chelating capacity of citric acid ions in soil solution is an advantage for extracting the P from acidic soils. Nevertheless, in 50% of the European beech forests, the results of the sodium bicarbonate method appeared to be also a suitable predictor for P in leaves, indicating that this method delivered positive results for both tree species at acidic and calcareous sites. Olsen (1954) earlier documented that his method (sodium bicarbonate) could properly explain P availability in acidic and alkaline soils. However, in a similar study in mature German forests, the results of inorganic P extracted using the sodium bicarbonate (labile P pool, applying the Hedley method) by Niederberger et al. (2018) did not strongly and significantly correlate with P stored in the foliage of adult trees. Using Hedley fractions, the authors could not present any valid soil variables to predict foliage P content in Norway spruce and European beech trees. This clearly explains the great variation between the results of P soil tests in agricultural land and common forests, as well as between fertilized and non-fertilized forest sites. It should also be noted that Niederberger et al. (2018) neither considered the P stored in the mineral subsoil nor P in the organic layers, both of which are important P pools for the nutrition of forest trees, notably at sites with inadequate P supply. Consequently, to identify P nutrition of plants (concerning agricultural soils), Sibbesen (1983) ranked different P availability tests in three groups. The elaborative anion exchange resin was considered the best method, the sodium bicarbonate and water methods were in the second best group, while lactate and citrate tests were placed in the last group.

From literature in a thorough study by Prietzel and Stetter (2010), the reasons for variations in P nutrition of adult trees, with regard to soil P supply in calcareous and acidic soils, are specified. They pointed out the distribution of tree fine roots and bacterial activities on acidic sites with poor P supply and thicker humus are the main biological factors for tree nutrient uptake (with reference to degradation of organic P forms in the humus by mycorrhiza symbiosis and release into the mineral soil, see also Attiwill and Adams 1993; Ewald 2000; Jonard et al. 2009). Likewise, tree P nutrition from mineral soils should be greater in soils with lower pH and at sites with rich P background. Such sites are basically characterized by high P stocks, higher P input via soil weathering, and less limited in the quantity of plant-available P (Prietzel and Stetter 2010). The authors found that at calcareous sites the impact of organic P forms, thus, the role of humus is more crucial for tree P nutrition. This might be the reason why the P nutrition of European beech trees, in the study by Ewald (2000) in the Bavarian Alps, was negatively linked with the total amount of P in mineral soils. In addition, the P nutrition of Norway spruce and pine trees at sites with limestone showed a positive relationship with P in humus. Though in our study the total amount of P measured in both calcareous and non-calcareous soils is much higher than P extracted using PEMs, most of this P is not readily available for uptake (Prietzel et al. 2013). Using the results of the citric acid method for P in humus, our study indicated that the amount of P extracted from organic layers is clearly higher than in individual mineral soil layers. However, with respect to the high amount of P stocks in aggregated soil depths, P values in organic layer were negligible and were not comparable with P extracted from mineral soils. Our results for humus are not consistent with the observations of Priezel and Stetter (2010), since we did not find any significant relationship between concentrations and stocks of total P in the humus, using the PEMs and P in foliage. From their results, it seems that there is a direct relationship between the values of site atmospheric N deposition and the rate of site P amendment using fertilizer, with P nutrition of trees.

In the current study at Norway spruce sites, the results of the sodium bicarbonate test were more decisive for predicting P in needles, whereas at European beech sites, the outcomes of the citric acid test showed significant influence on foliage P nutrition, indicating again that these tree species may use different P fractions in soils. Unfortunately, studies on root architecture and mycorrhiza accumulation were not performed in the current study. Nevertheless, former investigations, such as Marschner et al. (2001) confirmed the vital role of microbial activities in soil for nutrient uptake. Since bacterial and fungal activities in soil besides mycorrhizal symbiosis affect the P nutrition of forest trees (Schachtman et al. 1998 in Priezel and Stetter 2010), the lower P uptake, and thus, the lower P nutrition of European beech trees might result from mycorrhiza associations, and thus, be different from other tree species. Zorn and Krause (1999) explained that the Olsen method is an unsuitable test for estimating the plant-available P for acidic sites, but P extracted using sodium bicarbonate in our study (mostly in deeper soils) demonstrates a significant relationship with the P in the foliage of Norway spruce and European beech trees. An explanation for these conflicting observations may once more depend on tree strategy to gain their P requirement (e.g. root extension and exudation, fungi associations) at sites with various soil properties. As described in the study justification, the fundamental aim of this research was to find a simple extraction method that quantifies the plant-available P in common forests and preferably reflects the P nutrition of foliage. Therefore, in our study we referred to the observations of earlier studies, applied in mature forests including adult trees. Considering positive outcomes, the result of the citric acid extraction method, as presented by Prietzel and Stetter (2010), is an applicable indicator to predict the P nutrition of adult trees. The accuracy of this indicator in mountain forests was also acknowledged by Prietzel et al. (2014) for Norway spruce trees in Bavarian mountain forests.

Recently, Fäth et al. (2019b) employed the citric acid extraction method to predict the P nutritional status of four European tree species (adult Norway spruce, European beech, Scot pine, and Oak). In their study conifer and deciduous species showed different P nutritional status. In this regard, the Norway spruce indicated the strongest response to increasing the levels of readily soil extractable P using the citric acid than other tree species. This might also explain the intensity of variations in Norway spruce productivity in mature forest with different soil P statuses compared to European beech, Scot pine, and oak trees. In contrast, Fäth et al. (2019b) found that concentrations of P in Scot pine needles were not as strongly react to increasing soil P stocks as with other tree species investigated. However, the low nutritional level of pine trees is known (Göttlein 2016), but now this clearly applies to soil P fertility. Although the outcomes of data mining in Fäth et al. (2019b) study showed that P extracted, using citric acid and sodium bicarbonate methods, potentially describes the variability of tree P nutrition, the authors concluded that the citric acid indicator better reflects the P stored in foliage than the other soil variables. Using such a simple P extraction method, ultimately, they suggested thresholds for P deficit ranges of the main European tree species (considering chemical composition of soils), indicating the importance of soil chemistry for the health of mature forests. Consequently, in line with Renneson et al. (2016), who documented that extrapolating the results of extraction methods to other soils is a difficult task, we confirm that the citric acid extraction method provides satisfactory results in forest soils ranging from acidic to neutral.

The most significant findings:

1. **Among all soil variables in statistical analyses like CEC, SOC, etc., the outcomes of PEMs were mostly selected as a first predictor to explain the P nutrition of foliage.**
2. **Among PEMs, the results of citric acid and sodium bicarbonate methods were significantly mirrored by P concentrations in needles/leaves of Norway spruce and European beech trees. Therefore, these valid soil indicators are recommended to predict tree P nutrition.**
3. **In Norway spruce forests, the above-mentioned indicators at acidic sites more accurately explained the P in foliage, while in European beech forests both indicators showed positive results.**
4. **The total amount of P in the humus did not correlate in any case with the P in the foliage.**
5. **The total amount of P only in topsoil of European beech sites significantly (but not systematically) correlated with the P in the foliage.**

3. Which soil variables can better explain the P nutrition of trees: concentrations or stocks of plant-available P? Which soil levels contain more plant-available P? (Papers A and B)

Total and plant-available concentration and stocks of P in forest soils of the Bavarian Alps vary (Prietzel et al. 2014). Therefore, as discussed in the last section, depending on tree adaptation systems at mature forest sites, tree species should achieve their P requirement from various P pools. The results of this study showed that in comparison to the concentration of P extracted from different soil depths, stocks of PEMs [kg/ha] strongly correlated with the tree P foliage. At our Norway spruce sites, stocks of plant-available P, extracted using the citric acid and sodium bicarbonate methods in acidic soils, were highly associated with P in the needles rather than the concentration of plant-available P [mg/g] in soils. At our European beech sites, the concentrations and stocks of P extracted using both methods in topsoil closely correlated with P in foliage, but this relationship for P stocks became stronger with increasing soil depths (down to 40 cm). The heterogeneous distribution of cations in soil layers probably influenced the amount of P extracted by PEMs in the different soil levels.

The results of permanent site monitoring by Richter et al. (2006) showed a substantial dependency on the cycling of P in sites with soil cations. In most previous investigations, the availability of phosphate ions in soil layers were categorized, according to the accumulation of cations, such as Al and Fe in acidic soils, and Ca in carbonate soils (e.g. Augusto et al. 2017; Prietzel et al. 2013). On the other hand, Achat et al. (2016) explained that P stored in the upper soil level is the main P source for tree P nutrition, where variations in soil pH change the dynamics of available P forms in the soil solution. The results of the above-mentioned study justify the outcomes of our study and explain why P extracted from mineral topsoil layers strongly, positively influences tree P nutrition. The biological controls of P in soil are commonly detected in the upper layers, where P uptake via tree roots is strongly affected by soil physical and chemical properties (Lang et al. 2016). As discussed in the last section, mineral topsoil normally contains a wide range of microorganisms that increase the availability of P in soils. Despite the low availability of P in forest soils, adult trees have probably evolved to cope with the low nutrients accessibility at sites by extending the root structure and releasing more organic acids in root areas. These phenomena improve the ability of adult trees to uptake more water and indirectly retain the nutrients within trees. Because high water stress can reduce the rate of nutrient re-translocation between tree organs (mobile elements), and negatively influence tree growth (Nambiar and Fife 1991). Furthermore, changes in root morphology along with soil microbial activity cause an increase in the supply of phosphate from common P pools in the soil around trees (Marschner 2012).

According to Prietzel et al. (2013), low P bioavailability in forest ecosystems (depending on the soil P stock) limits forest productivity. In contrast to agricultural lands, where the soil fertility with chemical fertilization, typically in upper soil layers improve the rate of P uptake by plants, the availability of P for tree uptake in common forests does not seem to be limited to a specific soil layer. This clarifies why in our study aggregated P stocks of PEMs are mostly selected (soil variables) by statistical models as a first predictor to explain the tree P nutrition. Fäth et al. (2019b) confirmed our results that P stocks of aggregated soil (mostly using the citric acid indicator) is the most important variable in upper soil levels. However, using the similar indicator, we found that in European beech plots, P stocks of aggregated soil down to 40 cm (partly deeper) correlated even better with P in leaves than P stocks at the 10 cm of soil depth, which was observed by Fäth et al. (2019). Without considering the stock of plant-available P in deeper soil levels, Niederberger et al. (2018) reported a low predictive power of the Hedley fractions (sodium bicarbonate part) for characterizing the P nutritional status of adult trees. At our Norway spruce sites, though in upper soil layers, the results of PEMs strongly and significantly mirrored the concentration of P in needles, P stocks of citric acid and sodium bicarbonate methods, down to 40 cm positively strongly correlated with P in the needles.

The study outcomes (different impact of P stored in mineral top and sub-soil on tree P nutrition) are here consistent with explanations by Kölling et al. (1996) based on the pattern of soil moisture and roots structure. The vertical distribution of P in developed soils varies, and thus, the dependency of tree P uptake changes along with the penetration of fine roots in different soil layers (Heinze et al. 2001). In addition, varying results in different investigated plots indicate that soil attributes, like acidity rates, soil structure and soil depth, have a critical influence on the quantity and distribution of plant-available P in forest soils. Moreover, in a comparative study in common forests, Achat et al. (2009) observed that the mineralization of organic forms of P in the most upper soil level (down to 30 cm depth), to support soil P fertility is less important. These findings are in line and close to the results of PEMs in our study, which positively predicted the tree P nutrition down to 40 cm, and this might derive from a decline in the amounts of organic P and an increase in portion of plant-available P with increasing soil depth. In total, with regard to the approximate description of tree rooting zone in deeper soils, observations of our study correlated well with the P uptake in this range (from 0 to 40 cm in mineral soil) at sites. Though there is no specific rooting area for adult trees at developed sites (note the role of the rhizosphere for common plants, where the soil chemistry and microbiology govern plant growth, and nutrient exchange), but around 60 cm from forest floor to mineral soils by Wolff et al. (1999), as well as at least down to 40 cm by Borja et al. (2008) and Schmid and Kazda (2002) are defined for adult trees as a rooting zone. This once more refers to the importance of this soil area for nutrition interactions between trees and site soil in common forests.

It should be also noted that after the postglacial period, a great portion of substrate derived P was lost and that P remained has been steadily transformed into organic P forms through plant uptake and accumulation of residuals on the soil surface (Lang et al. 2016). For this reason, we think that soil levels, which cover the main rooting zone in mineral topsoil, contain higher capacities for P reserves (notably the A horizon), and are adequate for evaluating the tree P nutrition. According to Wolff et al. (1999), stock levels of the main nutrition elements in soils, such as N and P, provide essential information about the function of the element cycles in forest ecosystems (e.g. nutrient uptake, mineralization). Recently, Mellert et al. (2018) similarly confirmed that P stocks in upper soil layers can better mirror the nutrient uptake of trees. However, the authors claimed that in sites where nutrient deficiencies are more frequent, this predictor indicates a weak relationship between P in soils and trees P nutrition. Prietzel et al. (2014) also employed the P stocks of the citric acid method to a) quantify the amount of plant-available P in soil b) evaluate stands P status, and c) assess the relationship between site P fertility and Norway spruce P nutritional status in the Bavarian Alps.

Applicability of the stocks of PEMs, which is also used in our study, is considered by Fäth et al. (2019b), who for a broader set of soils with differing P status and diverse properties in Bavarian forests only used the P stocks of citric acid and sodium bicarbonate extraction methods to evaluate the P nutrition of the main European trees. We detected the highest correlation between stocks of plant-available P extracted, using citric acid and sodium bicarbonate methods and P in needles of Norway spruce trees, at 0-40 cm of soil depth (R^2= 0.64 and R^2= 0.61, respectively) (see Appendices A and B). While in the investigation by Fäth et al. (2019b), the highest P in foliage was reflected by the stocks of citric acid method at 0-10 cm (R^2= 0.52). Nevertheless, in their study, the quality of the linear regression models for the content of P in foliage was not dramatically low, down to 40 cm of soil depth (R^2= 0.48). In contrast, at European beech sites, concentration of P in foliage was more associated with the P supply in deeper soil layers. This is explainable according to the statement of Wolff et al. (1999), based on P stocks of available P forms in mineral soil (containing organic and inorganic P), which are mostly but irregularly distributed in the rooting zone. The amounts and stability of these P forms are likely dependent on cations accumulation in various soil levels. This also indicates that even in the rooting zone, the quantity of plant-available forms of P to support tree P nutrition is highly dependent on their bonding at different soil layers. The authors reported that P accessibility in rooting zone is 40 times higher than in the humus at mature sites.

Nevertheless, by the stratification of the P and N stocks in the mineral soil rooting zone, Wolff et al. (1999) concluded that P stored in the biologically active humus forms (e.g. Mull or Moder) is a significant and effective supporter for mineral soil P fertility. This status derives from the presence of organic P compounds which are highly available in the forest litter, as well as phosphate released in the course of mineralization moving into mineral soils. However, due to the number of carbonaceous sites with mull humus, a large part of latter P forms (calcium phosphate, hydroxyapatite) are not available for plant uptake. This might also be the reason why in our study, the total or the plant-available stocks of P in the humus did not positively affect the quality of the relationship between P stocks of PEMs at site and P in the foliage. Employing the concentrations and stocks of total P in topsoil and the amounts of plant-available P (from citric acid extractable P), Prietzel and Stetter (2010) monitored the long-term trends of P nutrition and topsoil P stocks in unfertilized and fertilized mature pine forests. They observed that in sites with high atmospheric N entry and low P supplied in topsoil, P nutrition of pine trees had significantly decreased. On the other hand, the authors found that at sites with acidic soil and thick organic layers, stocks of citric acid extractable P in topsoil positively correlated with the P nutrition of trees.

Although the concentration of absorbable P in soil solutions is normally very low, plants commonly receive their P requirement from upper soil levels (Blume et al. 2010; Wuenscher et al. 2015). This finding once more supports our results, where the highest concentration of P, extracted, using the citric acid and the sodium bicarbonate methods, was detected in top soils. Richter et al. (2006), using the sodium bicarbonate method, also extracted a great amount of soil labile P (one of the Hedley P fractions). The authors detected a relatively strong dependence between the quantity of extractable P in different soil layers and the solvent used. They observed that the value of inorganic P extracted using the Olsen method (1954) in deeper soil layers (down to 35 cm) was up to 75% higher than in the topsoil (7.5 cm of soil depth). Possibly, in this range, the accumulation of Fe and Al ions associated with soil inorganic P forms significantly alters the P availability and is associated with soil dynamics during stand development. These results once more confirm that the supply of P at specified soil levels may not be sufficient for tree P nutrition, when respecting mycorrhiza activity and root extension. Therefore, P saturation and absorption by trees are closely related to soil depth. Moreover, P distribution in different soil depths can be used to estimate soil capacity to retain available forms of P, assuming that the amount of plant-available P in upper soil layers containing Fe and Al oxides is greater than soils with Ca carbonate. This may be why the results of soil extractable P by Prietzel and Stetter (2010) in the topsoil of both fertilized and non-fertilized sites positively reflected the P concentration in foliage. The lack of a significant difference between the total P values in topsoil of fertilized and non-fertilized was linked by these authors to the low amount of P added by fertilization.

Consequently, from the studies on adult trees (mixed forests sites), recently Mellert et al. (2018) and Wellbrock et al. (2016) claimed that the dependency of deciduous trees on soil nutrients fertility (including P) is more than for conifers. This dependency justifies various correlations observed between P availability in soils and tree nutrition in our study, based on the efficient use of P for tree growth (Lang et al. 2017). According to this hypothesis, trees have dissimilar "acquiring systems", and their P nutrition is commonly altered with the stock amount of plant-available P in the upper levels of the soil (Fäth et al. 2019b). Hence, to verify this assumption, our study suggests that further investigations should be carried out to compare soil variables for availability of P in soils (preferably using P stock of citric acid method in topsoil) and tree aboveground biomass (productivity).

The most significant findings:

1. **For two measurements, the stocks of P, extracted using PEMs, strongly explained the tree P nutrition compared to concentration of soil P.**
2. **In total, the relationship between stocks of PEMs and tree P nutritional status for topsoil was stronger than for subsoil. In European beech sites, P extracted from deeper soil layers also positively correlated with P in leaves.**
3. **Stocks of extractable P using citric acid and sodium bicarbonate methods down to a depth of 40 cm in mineral soils were selected as the best variable to predict tree P nutrition and site productivity**
4. **The results of PEMs can explain the current tree nutrition better than total soil P supply**
5. **Applying soil pH stratification (pH < 6.2 and pH > 6.2) systematically influences the prediction for tree P nutrition using PEMs indicators (particularly, at Norway spruce sites).**

4. How do other tree components (older needles, twigs, branches, bark, and stem-wood) and site productivity respond to the PEMs' results? (Paper B)

The study of forest growth and tree productivity is crucial to perform sustainable forest management. Generally, common forests in Germany have not been P fertilized to support site growth and tree productivity. In this regard, along with the intensity of forest harvesting and biomass removal, P export from the forest surface may worsen P malnutrition in trees (Niederberger et al. 2018). Hence, internal reallocation processes at sites dominate P cycling. However, concerning the amount of plant-available P at sites as well as simple P fractions in the soil, there has been very little research investigating this issue.

As argued in earlier sections, the values of soil extractable P, using PEMs, have proven to be good site quality indicators to explain variations in the P nutritional status of trees as evidenced by P in the foliage. Hence, the results of PEMs were employed to specify how other tree components respond to soil P fertility. The stocks of plant-available P, using the citric acid and sodium bicarbonate methods were used to assess the relationship between P in aboveground biomass of the adult Norway spruce trees and soil extractable P. Previously, Achat et al. (2009) emphasized the necessity for suitable diagnostic systems to evaluate the capacity of P supply in the soil and to estimate site biomass production in mature forests. Using stock amounts of organic and inorganic soil P, they investigated the impact of harvest intensity and biomass removal on soil P status in French forests.

Consequently, to manage the essential nutrients in forests, Achat et al. (2011) identified the soil variables as a suitable indicator to clarify the relationship between the amount of plant-available P and forest productivity. In addition to the dissolution of P from the mineral soil surface, releasing P through soil weathering significantly increases the soil P supply. Therefore, P stocks of the citric acid and sodium bicarbonate methods might also in top soils accurately explain the P stored in tree organs, assuming root P uptake in this dimension provides most of the P to meet the demand of single organs (depending on the organs' biological activity like aging and developing in new growth seasons). From the observations in an experimental study by Baier (2006), the results of the citric acid method were efficient to predict the variation of P concentration in the trees (specifically for Norway spruce saplings with active organs). On the other hand, in our study, the results of a crown biomass analysis showed a high accumulation of P in needles, twigs, and bark of Norway spruce trees. However, the first year needles contained higher concentration values of P than older needles. Augusto et al. (2008) detected a range of nutrient concentrations among young (nutrient-rich) and old (nutrient-poor) tissues in pine trees. They theorized that a reduction in physiological activity might explain the variations in the concentration of P in needles of different ages. Marschner (2012) also strongly argued that plant organs with high physiological activity, e.g. growing needles and tissue of inner bark (containing many living cells) require large amounts of P. The high accumulation of P, due to a great P demand in active organs, was closely connected with that part of the soil P supply, which is easily available for uptake. In line with Braun et al. (2010), who acknowledged that the reduction of P in tree foliage derives from a soil P deficiency, the quantity of easily soil extractable P using PEMs in our study, also showed a positive correlation with the concentration of P in tree foliage. In addition, Augusto et al. (2008) reported that P concentrations in living branches (twigs), stem-bark, sapwood, heartwood, and stem-wood were reduced due to thickening of these components. This evidence is linked to nutrient internal cycling through re-translocation of mobile elements between tree components (discussed in the next section).

We detected that the supply of P in stem-wood, branches, and twigs of Norway spruce trees, does not strongly (usually not significantly) correlate with plant-available P stocks, measured using the citric acid and sodium bicarbonate methods. Employing the logarithmic regressions model, the highest correlation was detected between P stocks of both extraction methods in aggregated soil and P stored in needles (of different ages), as well as P in the bark of Norway spruce trees (see also Appendix B). Even the outcomes of the model indicated that P stocks of these PEMs positively explain the P levels in the bark similar to that in the first-year needles.

However, a strong and significant correlation between P stored in the older needles and bark with stocks of plant-available P in deeper soils (coefficient of determination values $R^2 > 0.6$), represent that these components might be frequently regulated by long-term soil reservoirs. Accordingly, young needles may show short-term variations of P availability. In addition, the first year needles, as biologically active organs, have a high nutrient demand at the beginning of the growth season, and this demand is probably met more or less by easily available nutrient sources (Hoffmann 1991; Reemtasma 1966), which appear to be in the upper soil layers and fine root areas. For older needles as well as for the bark, readily accessible P sources are less important, and these organs were highly correlated with slowly running P sources in deeper soils.

The current study detected a relatively high accumulation of P in the bark of Norway spruce trees; hence, in addition to analyzing needles, the stem-bark analysis is thought to be a good alternative method to determine tree P nutrition. Moreover, bark is an integrated organ, which probably can be better used to explain the nutritional status of adult trees during long-term development at sites. An additional benefit for bark analysis is related to the sampling procedure in mature forests, where compared to needles, tree harvesting is not necessary, and we do not use tree climbers or tree pruners, the latter being harmful for forest vegetation. In the long-term site monitoring, Weis et al. (2009) similarly identified decreasing soil P supply in Norway spruce stands had a greater impact on the concentration of P in the bark compared to that in the needles. For this reason, tree bark analyses may also be a promising approach to evaluate tree nutritional status. Although studies confirm the applicability of foliage analyses to explain the nutritional conditions of forests (e.g. Göttlein et al. 2011, Jonard et al. 2015), the standard approach of sampling foliage in forests is time-consuming and costly, rendering it unsuitable for analyses of large numbers of samples. Moreover, concentrations of P in the foliage usually vary between conifers and deciduous species (Wyttenbach and Tobler 1988). The annual fluctuations of P in foliage, particularly in needles, occasionally lead to an error in estimation of tree P nutrition (Vitousek et al. 2010; Yang et al. 2015). Additionally, Khanna et al. (2007) reported variations of P concentrations in European beech leaves and stated that trees with a crown overlap contain a higher P accumulation in the foliage. Similar to first-year needles and bark, we found the best relationship between extractable amounts of P and site productivity as well as the rate of P uptake by trees, using P stocks of the citric acid method down to 40 cm of mineral soil. These findings generally reveal that the P supplied in a specific soil layer is not sufficient to provide the entire P demand for Norway spruce growth. According to Borja et al. (2008) and Schmid and Kazda (2002), trees are able to develop their fine roots down to at least to 40 cm of soil depth. Therefore, the amount of extractable P in this range plays an important role in tree P uptake and biomass productivity. We think PEMs indicators cover common and simple physical and chemical attributes of P bonding in mineral soils (rooting zone) that might be closer to the physicochemical functioning of tree roots than strong acid and sequential methods.

In addition to the main goals of this study, and due to having complete datasets for 16 Norway spruce sites, we decided to assess the impact of site index, which is called **“Location”** in the **Tab.1**, on P nutrition of aboveground biomass. In order to ensure that site characteristics, rather than tree age, dbh, height, and crown length, were responsible for differences in P content, the impact of single tree measurements (seven per plot) were tested in a generalized linear model together with the variable location (including several factors, e.g. P deposition, soil P availability (PEMs’ results), competition between accessible P pools at site, and etc.). On the other hand, PEMs predictors do not completely explain tree P nutrition; therefore, we combined the parameters from each location with further tree variables to inspect the data for the best predictive parameter. Researchers usually employ these variables to estimate a soils’ potential to support tree growth in common forests. We observed that for all tree organs (aboveground biomass), with few exceptions, the influence of the factorial variable “location” - given by the investigated plots - was highly significant. According to Augusto et al. (2008) and Skovsgaard and Vanclay (2008), stand productivity can be also estimated through tree height and tree age, but sometimes data on age or height of trees are not easily available. Thus, the methods based on soil analyses are preferred to predict site production (Sharma et al. 2010). Aertsen et al. (2012) confirmed this preference.

Table 1: Significance of the impact of site and tree biological variables (age, dbh, height, and crown length) on P content in needles and aboveground biomass of Norway spruce (generalized linear model). Underlining displays the variables on the 0.05 level (provided from the data in the Appendix B, unpublished results).

variables	needles whorl seven				aboveground biomass				
	age 1	age 2	age 3	age 4	needle	twig	branch	bark	wood
Location	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
tree age	0.092	0.456	0.837	0.877	0.965	0.002	0.085	0.624	0.084
dbh [cm]	0.026	0.220	0.147	0.216	0.542	0.946	0.002	0.822	0.553
height [m]	0.388	0.511	0.496	0.217	0.532	0.552	<0.101	0.262	0.369
crown length	0.364	0.908	0.610	0.660	0.539	0.230	0.412	0.976	0.960

Consequently, concerning the impact of chemical reactions in the soil on P cycling in forests (via decomposition of organic P forms), the soil specifications are the most important factor to estimate tree nutrition. Long-term management of site fertility and forest productivity are proposed by quantifying the amounts of plant-available P in sites by Achat et al. (2011). In contrast to the results of Riek et al. (2016), who demonstrated that outcomes of soil analyses do not preferably explain tree P nutrition, PEMs' results could significantly explain the tree productivity in our investigated sites. Identifying soil P deficiency in Bavarian forests as a growth limiting factor specified by Klemmt and Ewald (2012) openly revealed that the development of Norway spruce and European beech trees diminished with reduction of soil P fertility. For sustainable nutrition management of forests, in addition to favorable climatic conditions, an adequate supply of nutrient in forest soils is an essential requirement for the vitality of trees. Nevertheless, the priority for selecting the tree species based on their nutrient sensitivity and/or climate conditions is still a speculation about the future of forests. Accordingly, Ammer (2009) and Mellert et al. (2018) argued that the frequent shift from climate-sensitive conifers to climate-tolerant deciduous trees commonly leads to a priority for selecting the tree species with higher nutrient requirements than species with low nutritional demand. Although Mellert et al. (2018) concluded that deciduous trees might be a suitable alternative, but concurrently can conflict with soil nutrient supply. Hence, for developing the forests both climate compatibility and nutrient tolerance of tree species should be considered.

The most significant findings:

1. **Concentrations of P in aboveground biomass of adult Norway spruce trees:**
   First year needles >> second, third, fourth year needles >twigs >bark >branches >stem-wood
2. **Stocks of P extracted, using citric acid and sodium bicarbonate methods, in most cases, indicate the best relationship with first year needles and tree bark. Therefore, bark analysis is suggested as an alternative and supplementary method for needles' analysis to evaluate the tree P nutrition.**
3. **P stocks of citric acid extraction method down to 40 cm of soil depth also revealed the best correlation with Norway spruce site productivity and tree P uptake. Whereas P stock of humus extracted by citric acid and sodium bicarbonate methods were not associated with these parameters, as well as with P stored in tree aboveground biomass.**
4. **In contrast to PEMs' results, except for a few cases, tree biological variables could not be used to positively and significantly explain the P supplied in tree crown biomass.**

5. Is tree P internal cycling in conifers via re-translocation among needles dependent on soil P fertility? (Paper C)

The concentration of P in tree foliage is conditioned to the soil P fertility, P shift into other organs during foliage senescence (P-reuse), and climatic conditions (Chapin and Kedrowski 1983; Helmisaari 1992; Nambiar and Fife 1991). Despite soil P supply commonly provide the P requirement of trees in the growth season (Achat et al. 2013), whether only this P pool (principally plant-available P in soils) are sufficient for annual tree growth still seems to be a question for researchers. As a response to low plant-available P in soils, trees have developed a number of strategies to manage their growth. In this regard, internal cycling of P within the tree components would be a strategy to cope with soil P shortfall. In addition, the largest quantity of P absorbed from soil accumulates in active tree organs and serves as a reservoir of reusable nutrients (Fife et al. 2008).

In line with the observations of BZE I by Ilg (2009), and Riek et al. (2016), we detected a clear difference in concentrations of P between first and second year needles of adult Norway spruce trees. Both authors assumed that this difference resulted from P internal cycling through P re-translocation between needles. Hence, according to the threshold of Göttlein (2015), the tendency of this shift should be higher for trees below the normal range of P nutrition (e.g. in deficiency). Therefore, our study hypothesized that due to the high P demand of growing organs (in this case, first-year needles), P from older needles can be shifted into the younger needles. Although this assumption has often been proposed in former studies, e.g. in Khanna et al. (2007) and Riek et al. (2016), the net value of P re-translocation between needles has not been calculated. Göttlein et al. (2012) claimed that the differences in P concentration in needles are not entirely from the net P re-translocation, but may also derive from an increase in the weight of older needles. We expected that the portion of P withdrawn from the second year needles correlated with the amount of P extracted using PEMs. Therefore, the stock values of citric acid plant-available P were used to explain the differences in concentrations of P between first and second year needles of adult Norway spruce trees. In addition, the amounts of plant-available P in soil might better explain the biological interactions (e.g. P internal cycling) in plants.

According to Riek and Wolf (2007), P re-translocation among tree organs does not increase with decreasing the site P supply. Even Namibiar and Fife (1991) noted that the amount and the rate of nutrient re-translocation between needles of temperate conifers (e.g. N) is enhanced by high soil fertility and quick nutrient uptake. Our statistical analysis also showed no significant relationship between the difference between concentrations of P in first and second year needles with the amount of readily soil extractable P, using citric acid solvent. This result negated our principal hypothesis that in trees with high P nutrition (luxury and normal P ranges), the rate of P re-translocation among needles should be less than in trees below the normal P nutrition. This also follows the observations by Riek et al. (2016), based on the fluctuations of P in needles, which for trees in luxury and normal ranges were greater than in trees with P deficiency. In addition, from the permanent sites monitoring, we found that the temporal variations in concentrations of P between needles is not significantly associated with the values of readily soil extractable P. Temporal variability, in this case, has a similar magnitude to spatial variability. The study assumption supports the explanations of Nambiar and Fife (1991), who argued that the tendency of P re-translocation is related to rate of tree development (shoot growth) rather than P status in soils. Furthermore, it has been stated that nutrient internal cycling and element re-translocation do not play an important role during the early phase of site development but reach significance later (Miller 1989).

The current study used the available data from an intensive tree sampling in order to estimate the impact of an increase in the weight of needles on net amounts of P re-translocation. Since the internal nutrient shift in plants usually occurs during the growth season, or when shoots develop (Marschner 2012), needle sampling was done during vegetation dormancy to represent the maximum values of P shifted in an annual growth. From the results of the needles analysis, changes in weight of needles presented as a main factor in differences of concentrations of P in the needles. This is consistent with the statement by Göttlein (2012) that the lower concentration of P in older needles of conifers compared to younger needles derives from the accumulation of immobile elements such as Ca and the storage of organic substance in older needles. From the Boxplot analysis, approximately 85% of changes in concentration of P between needles resulted from an increase in needle weight, this phenomenon known as the dilution effect. Thus, to evaluate the net amount of P re-translocation distinguishing between P concentration (e.g. mg/kg) and P content (e.g. µg/needle) in organs should be noted. Monitoring a short growth period of pine seedlings, Lim and Cousens (1986) observed an increase in the weight of previous needles. The results of this study also support the statement by Nambiar and Fife (1991) that variations of P values in needles during the primary growth present dissimilar stages of P acquisition e.g. accumulation, re-translocation and replenishment. Reemtsma (1966) stated that the rate of P re-translocation in needles during critical conditions, e.g. drought, cold and long winter, might be higher. However, Turner and Singer (1976) argued that the rate of nutrient shift among organs is linked to requirement intensity of the growing organ, and the initial amount of nutrition in the organ that is withdrawn. We also looked at the portion of Mg re-translocation between needles as a comparison to the results of P re-translocation. For Mg, the percentage of net re-translocation between needles on average is higher than for P, but this portion is not considerable (but almost 10% more than P). The impact of an increase in needle weight was again more prominent (results not shown).

Furthermore, numerous researchers (e.g. Chapin III and Kedrowski 1983; Fife and Nambiar 1984) working on site P fertility determined the tendency of P internal cycling in the tree compartment via re-translocation between needles. The general hypothesis behind these investigations was to specify the influence of soil P fertility on forest growth. This evidence once more supports the hypothesis of Riek et al. (2016) and Göttlein et al. (2012) that tree species seem to use supplemental strategies to compensate the tree P demand. In this regard, perhaps the ability of adult trees to develop their roots in deeper soil layers leads to the high rate of nutrients uptake at mature sites (Kölling et al 2009; Smith and Read 2008). Consequently, Chapin and Kedrowski (1983) documented that the high rate of element re-translocation between tree compartments might not be derived from tree adaptation to cope with its low nutrient status, but a biological characteristic of most tree species.

The most significant findings:

1. **The difference between concentrations of P among first and second year needles of adult Norway spruce trees is not related to the stocks of plant-available P, using the citric acid method.**
2. **These differences did not mainly derive from P re-translocation from second year needles into the first year ones.**
3. **Almost 85% of above-noted differences is based on dilution effect via increasing in the weight of second year needles, and only 15% of that could happen via net P re-translocation.**
4. **In further investigations, instead of considering P concentration in organs, P content should be taken into account as a parameter for quantifying the net amount of P re-translocation.**

X. GLOBAL DISCUSSION

Though trees use supplementary strategies to cope with P deficiency, their productivity is inhibited by low soil P fertility. To detect this fertility, quantifying the amounts of plant-available P in soil is a precondition for evaluating the site P status. In the current study, analyzing BZE II soil samples using PEMs, a comprehensive data set was compiled to test the suitability of simple soil extraction methods to predict the current P nutrition of the two most important European tree species, the Norway spruce and the European beech.

Initially, it is necessary to examine the requirements and benefits of the PEMs employed. The availability of P may be underestimated when the extractant is unable to dissolve the relevant P forms in soil. These forms are normally distinguished as P connected with soil cations, P in primary bedrock minerals, and P in organic matter (Prietzel et al. 2013). The PEMs provide a satisfactory basis to estimate the values of plant-available P in soils. To the best of our knowledge, the results of various soil tests have not provided forest scientist with the data they need. PEMs are easy to handle and can be used for a large number of soil samples in forests with different soil properties. Accordingly, the results of **the citric acid and the sodium bicarbonate extraction methods** significantly positively predicted P nutrition of trees. Therefore, we attained the initial aim of our study by identifying a reliable soil indicator that **i)** correlates well with foliar P concentrations, **ii)** is appropriate for various types of soils at calcareous or non-calcareous sites, and **iii)** functions for both conifer and deciduous tree species. These characteristics of PEMs indicators were recently confirmed in a study by Fäth et al. (2019b), where plant-available stocks of P citric acid and sodium bicarbonate methods were positively linked with the P nutritional status of the main European tree species at all Bavarian BZE II sampled plots.

Using PEMs as an indicator for tree P nutrition, we discovered that soil properties such as acidity (pH), the types of soil substrates at sites (stand parent material), as well as depth/level of soil sampling, have a strong influence on the quantity and distribution of readily extractable P, tree P nutrition, and thus, site productivity (notably at non-calcareous sites). In line with Mellert and Ewald (2014), our results support that both, soil P fertility (plant-available P in soil) and acidification, could be determinative for the growth of Norway spruce and European beech trees. Additionally, aggregated stocks of plant-available P in topsoil (down to 40 cm) can be preferably used to predict the tree P nutrition better than P content in soils. Mellert et al. (2018) claimed that the stocks of nutrients in topsoil better reflect the nutritional status of trees in common forests, but this effect is more dominant at sites with soil nutrient deficiencies. Stocks of plant-available P in the forest subsoil may be lower, since soils with stagnic properties, in the long-term, produce a reduction condition for subsoil cations, leading to an occlusion of phosphate ions by Mn and Fe-oxide (Prietzel and Stetter 2010). In this regard, our results corroborate those of Prietzel and Stetter (2010) and Prietzel et al. (2014), who reported that stocks of citric acid extractable P in topsoil is an appropriate indicator for the stand P quality and P nutrition of trees. These authors also validated the results of Ewald (2000), arguing that the total value of soil P is unsuitable for predicting site P fertility. Though we found a significant relationship between P nutrition of European beech trees and the total value of P extracted from topsoil, no systematic relationship was detected at Norway spruce sites. Niederberger (2018) recently reported the same results in many German forests. Concerning site specifications, e.g. soil pH, mycorrhiza society, and fungi activities, Lang et al. (2017) explained that adult trees gain their P requirement from different P bonding forms in soil (mostly from topsoil). It has not escaped our notice that root architecture in various tree species, as well as the accumulation of fine roots and mycorrhiza in upper soil levels, are also key determinants for nutrient acquisition and growth of trees. From study outcomes, we confirm this assumption that upper soil levels contain higher fine root densities; thus, higher uptake capacities (A-horizon) and water availability, are probably optimal for evaluating tree P nutrition. Mellert and Ewald (2014) and Tichet (2009) reported a positive linkage between an increase in the rate of tree production and an increasing topsoil available nutrient supply at mature sites (more dominant for conifers).

Besides soil pH, forest researchers often claim that the P in organic layers has a positive impact on tree P nutrition. Although the distribution of P supplied in the humus layer governs site productivity (Talkner 2010b), we detected no significant relationship between the total or plant-available amounts of P in the humus and tree P nutrition. Hinsinger (2001) explained that the bioavailability of P in mineral soil layers is more important than P in the organic layers for tree P nutrition. These observations confirm that experimental approaches, based on the determination of plant-available P in mineral soils should be given priority in forest investigations. Furthermore, on the one hand, some researchers describe the reuse of P in plants (like P internal cycling among tree organs) as a globally important mechanism during plant growth; on the other hand, many researchers argue tree growth is more likely affected by the amount of plant-available P in the soil. Nevertheless, identifying the impact of soil P fertility tree growth is essential for evaluating site P status. Hence, we theorized that soil variables (PEMs indicator) would be able to clarify whether the rate of P uptake by trees and the tendency for P internal cycling in the tree components is governed by soil P fertility. Using the outcomes of soil extraction methods, Richter et al. (2006) verified the positive inter-correlation between tree growth and soil P richness. However, Nambiar and Fife (1991) argued that P internal cycling is not clearly related to soil P fertility. The results of the current study also revealed no significant correlation between the rate of P re-translocation between needles of Norway spruce trees and plant-available P in soil, extracted using citric acid. This is consistent with the findings of Chapin and Kedrowski (1983), who acknowledged that in many tree species, foliage P re-translocation is not an important supporter for other growing organs and tree productivity, when the content of P in soils is low. We hypothesized that at sites with low P availability, the tendency of P internal cycling in trees would be higher. Contrary to our expectations, even at sites with poor P nutrition, no strong correlations were observed between the amounts of P extracted and P re-translocation among needles. Lim and Cousens (1986) documented that internal cycling of nutrients within trees in the growing season supports development of active organs, but this is not governed by soil nutrient fertility. We found that the most commonly observed differences in P concentrations among needles are derived from an increase in needle weight. Tree P internal cycling during critical conditions, e.g. drought, cold and long winter, is higher and the rate of P shift corresponds more to the requirements of individual growing organs (Reemtsma 1966). Moreover, those tree compartments that contain a low nutrient content are more capable of withdrawing the elements (Turner and Singer 1976).

Consequently, based on the results of PEMs, we established a quantitative framework to detect the positive impact of P stored in different soil layers on P nutrition of aboveground biomasses of adult trees in common forests. This corroboration is derived from our observation that maximum P accumulated in the tree crown organs, which strongly correlated with the amount of plant-available P in soil. Earlier studies on young trees detected these relationships, but were rarely or only in individual cases detected in mature forests. Similar explanations were documented by Göttlein et al. (2013) and Weis et al. (2009). The authors individually compared the concentration of P stored in the crown biomass of Norway spruce and European beech trees. Both aforementioned studies concluded that intensive site utilization leads to the export of high amounts of nutrient from forests and to soil nutrient deficits. Relying on the results of PEMs, the positive impact of soil P enrichment on site production is confirmed. Hence, full tree harvesting has become a serious concern for sustainable forest P management, thus, we strongly recommend not removing nutrient-rich crown biomass from the forest surface. Moreover, Mellert and Ewald (2014) presented the P as the most critical macronutrient in the Bavarian mountains forests, concerning full-tree harvesting. Ewald (2000) for the European beech and Prietzel et al. (2015) for the Norway spruce sites also revealed that poor soil P fertility diminished the tree productivity and limited the forest development in the Alpine region.

Richter et al. (2006) emphasized evaluating the bio-available supply of P in soil in long-term forest growth. As discussed aforetime, due to the gradual evolution of natural ecosystems, forest soils develop over time, and high portions of P supplied are either absorbed through biological activity by trees or progressively transformed into the unavailable P forms. Applied PEMs in our study covered a large variety of soils containing dissimilar P status (regarding pH ranges), and a wide range of soil properties (regarding parent material) at mature sites. This provides a broader perspective for comparing different soil P extraction methods and their dependency on soil attributes. Thus, PEMs are suitable indicators to estimate P nutrition of trees located in temperate forests with different soil properties. We think that for a large dataset, stratification of soil layers (particularly mineral horizon, from 0 to 40 cm) in a specific pH range does not substantially affect the outcomes of statistical analyses. Finally, we suggest the "**citric acid extraction method"** as a valid soil test in forest ecosystems, in line with the outcomes of Prietzel and Stetter (2010), Prietzel et al. (2014), and Fäth et al. (2019b).

XI. CONCLUSION AND RECOMMENDATIONS

The sampling procedure and analytics applied (PEMs) in the current study offer practice-oriented methods that can be employed in sustainable management planning in temperate forests regarding tree P nutrition by avoiding intensive site harvesting. The results obtained in this doctoral thesis should lead to a better understanding of the bio-available P in forest soils. Study outcomes also indicate how the P distribution at different soil levels impacts tree P nutritional status. This influence was initially supported by detecting a strong significant relationship between readily soil extractable P, using simple PEMs, and the analysis of P content in tree foliage.

Accordingly, among several soil variables (PEMs, CEC, TP, SOC, and soil pH), the citric acid soil test is the best predictor of tree P nutrition. The citric acid indicator was also a reliable predictor of P stored in Norway spruce crown biomasses, of the rate of tree P uptake, and of site productivity. Multiple regression analyses revealed highly significant relationships between stocks of P extracted, using citric acid and P in metabolic active organs (e.g. needles and bark). Since the standard determination of tree P nutrition via foliage samples is costly, and P content in foliage fluctuates over time, a standardized bark analysis as a supplementary method could contribute to determining tree P nutrition more accurately. Moreover, stem-bark integrates over several years, and therefore, would be suitable for gaining a long-term overview of tree nutritional status.

We found that P nutrition of Norway spruce and European beech trees are governed by the stocks of available P in topsoil (0-40 cm of mineral soils), which is likely linked to the soil fertility, supported by mycorrhiza, the high accumulation of microorganisms, and maximum distribution of fine roots in this soil level. Hence, the values of plant-available P in topsoil play a very important role in tree P nutrition and govern site growth. Furthermore, selecting P stocks of PEMs as a first indicator using statistical modeling to predict the P in aboveground biomass organs indicates that the P nutritional status of adult trees in mature sites is likely limited to the quantity of P in the topsoil. Accordingly, for tree species with deeper reaching rooting systems, the inclusion of deeper soil layers (down to 80 cm) may be necessary for further investigations. As a consequence, for the next national soil survey, the citric acid soil test will be a promising tool for evaluating the plant-available amount of P in forest soils. This also raises important questions about the necessity of evaluating the plant-available P using other more expensive, more complicated, and more time-consuming methods.

Employing the results of the citric acid method, we detected no significant correlation between the stocks of plant-available P in soil and P internal cycling within the tree (via P re-translocation between needles of Norway spruce). After an intensive tree sampling, we found that the greatest variation in the concentration of P between first and second year needles is derived from an increase in needle weight. Therefore, P reuse between organs does not significantly influence P nutrition of Norway spruce trees. Hence, topsoil P fertility should still be the main index for vitality and optimal growth of Norway spruce trees in mature forests. Finally, the P cycle is relatively closed in forest ecosystems and present as interaction between P in the biomass and P in soil. For this reason, the aggregation of depth levels and pH-stratification in soils usually improved the quality of the regression models to predict tree P nutrition. Nevertheless, additional to PEMs results, the information about the background of site parent material should be also considered when evaluating plant-available P for soil and tree health. Hence, we recommend using information on stand history.

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XIII. PUBLICATION REPRINTS

The next pages show reprints of the three publications used in this thesis, which in throughout of manuscript were called as Appendices A, B, and C.

(A) page 67

(B) page 78

(C) page 90

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