

AVAILABILITY AND UPTAKE OF PHOSPHORUS IN SOILS OF FOREST ECOSYSTEMS

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Abstract

The aim of this work was to assess the availability and uptake of phosphorus in the soils of four forest ecosystems in Greece, i.e. a maquis, a deciduous oak, a beech and a fir forest. The highest concentrations of total P were observed in FH (mixture of F and H) horizons (914 to 1269 mg·kg⁻¹). In the mineral layers (up to 80 cm depth), the range was 439 to 850 mg·kg⁻¹. The percentages of the available P with regard to the total P were very low. In the FH horizons, they ranged from 2.4 % in the fir plot to 6.5 % in the beech plot. In the mineral layers, all percentages were less than 1.0 % in all forest types. The concentrations of available P were significantly and positively affected by the contents of soil organic C, total nitrogen and the clay percentage. Negative and significant relations were observed for the ratios P/C, P/N and the percentage of sand, whereas the content of total P did not affect the availability of P significantly. The P uptake by trees was based on the calculation of the above ground litterfall. It was found that, at least for the fir plot, the amounts of available P in soils up to the depth of 20 cm were not enough to cover the tree needs. It is hypothesized that the extra P needed is acquired by the dissolution of secondary minerals by root exudates.

Key words: extraction, litterfall, phosphorus, soil, tree uptake.

Introduction

For many forests of the world, growth and nutrient cycling are limited by phosphorus. There is increasing evidence that it is immobilized in the first stages of organic matter decomposition to a greater extent than nitrogen (Attiwill and Adams 1993). Lang et al. (2016) hypothesized that at sites rich in mineral-bound P, plant

and microbial communities use it from primary minerals and hence there is not a tight P cycle. In contrast, a tight cycle is crucial at sites poor in mineral bound P. A tight nutrient cycle exploits even the minute concentrations. The concentration of P in soil solution is very low. It ranges from 0.001 mg·L⁻¹ in very infertile soils to 1 mg·L⁻¹ in heavily fertilized soils (Belyazid and Belyazid 2012). The bulk of soil P is

immobilized in the organic and inorganic soil fractions. The distribution sinks and their competitiveness are topics of fundamental importance for the understanding the cycling of P in a forest environment (Attiwill and Adams 1993). Currently, there is evidence that anthropogenic environmental changes affect P nutrition by disrupting its cycling (Jonard et al. 2014). The authors suggested that excessive N deposition brought about reduced root and mycorrhizae growth, which resulted in reduced P uptake. In addition, higher tree growth due to increased CO₂ in the atmosphere require higher P uptake.

The total P content in forest soils is not a good predictor of tree nutritional status. Very often, a significant correlation with the foliar P content, in different tree species cannot be found (Ilg et al. 2009). It is inferred that most soil P is unavailable or not directly plant available. Other approaches employ the quantification of a number of different P fractions in mineral soils (Hedley et al. 1982). It is very often that researchers use only one extractant to assess available P. Different extractants correlate with distinct pools of P in soils and the extractability of a given pool is affected by soil properties (Wuenschere et al. 2015).

It was decided to use the Olsen phosphorus (OP) to assess the available P in soils. This method uses sodium bicarbonate (NaHCO₃) to extract plant available P. Originally it was developed for calcareous soils where P complexes with Ca. In the OP extraction, calcium carbonate (CaCO₃) is formed and in this way, the activity of Ca in the solution decreases as CaCO₃ precipitates. At the same time, the

dissolution of Ca phosphate is promoted. Furthermore, the high pH (8.5) of the extractant enhances phosphate desorption from Al and Fe oxides (Wuenschere et al. 2015). Later the OP was found to apply with success to acid soils as well (Tchuen-teu 1994, Bair and Davenport 2012). Do et al. (2007) argued that when this method is applied to acid soils the threshold for P deficiency should increase.

The aim of this work was to assess the total and available P in soils of four forest ecosystems in Greece and identify the dependence of the available P on soil physical and chemical parameters. In addition, the uptake of P was assessed taking into account parameters of the net primary production such as the fluxes of above ground litterfall of the forests. The calculated uptake needs for P was compared with the amounts of available P in soils to check the sufficiency of the soil P pools for the tree nutrition with this element. As mentioned above, the tree nutrition with regard to P has deteriorated and in this respect, this work will contribute to the understanding of P uptake.

Materials and Methods

Sites description

All sites from which the material was collected belong to the Intensive Monitoring Survey of the ICP Forests network (UN-ICP-Forests 2020). They represent important forest ecosystems in Greece and this was the reason they were selected. Information about the plots is given in Table 1.

Table 1. Characteristics of the areas.

Area	Altitude, m	Soil parent material	Soil type	Vegetation
Amfilohia	360	Flysch	Haplic Luvisol	Maquis species: <i>Quercus ilex</i> L., <i>Arbutus unedo</i> L., <i>Phillyrea latifolia</i> L.
Ossa Mountain	740	Mica schist	Dystric Cambisol	<i>Quercus frainetto</i> Ten.
Ossa Mountain	890	Mica schist	Haplic Alisol	<i>Fagus sylvatica</i> L.
Karpenisi	1170	Flysch	Humic Alisol	<i>Abies borisii-regis</i> Mafft.

Note: Soil types are presented in accordance with FAO-UNESCO (1988); the term 'maquis' is defined as a scrubland vegetation of the Mediterranean region composed primarily of leathery, broad-leaved evergreen shrubs or small trees (Encyclopedia Britannica 2020).

Soil samples collection and pretreatment

It was carried out by means of systematic sampling in the summer of 2007. Inside the plots, along three lines having a distance of 25 m from each other, six soil pits (5 m away from each other) were excavated. From each pit, the organic horizons litter (L) and the FH layers were collected with a metallic frame having an area of 15×15 cm. Actually the L and the FH horizons together form the forest floor. In other forests, especially in northern countries, the F and H horizons are distinguishable but not in the Mediterranean forests where decomposition is fast. Mineral soil layers were collected with a shovel from the depths 0–10 cm, 10–20 cm, 20–40 cm and 40–80 cm. Six samples (approximately 2 kg each) per horizon and soil depth were mixed to have three pooled samples per horizon and depth. The bulk density of the mineral soils was measured with a cylinder of known volume (129 cm³). The value was converted to bulk density of fine earth (<2 mm) after subtracting the volume of coarse material. The percentage of large stones was estimated visually in the field. All soil samples were transferred to the laboratory and were air-dried. Apart from the L layer, the other samples passed

through a 2 mm sieve. For the total analysis for P subsamples of all soil layers were pulverized in a ball mill and stored for analysis. All results were expressed in 105 °C dry weight of soil.

Litterfall collection and pretreatment

Ten littertraps (cylindrical plastic buckets), each having a collecting area of 0.242 m², were placed systematically along a straight line in all plots, approximately 0.50 m above ground at a distance of 10 m from each other. The litterfall sampling for the fir and beech plots covers the period 2009 to 2017, for the maquis plot the years 2013 to 2017 and for the oak plot the 2010 to 2019 period. Collection of litterfall was done monthly or longer periods, depending on the accessibility of the area due to snow and the sufficiency of the material for chemical analysis. At each collection, a composite sample was formed by pooling the content of the ten littertraps. Three fractions were formed: foliar, woody (twigs, bark debris) and the rest consisted of flowers, fruits, lichens, mosses, insect frass, pollen and whatever did not belong in the first two categories. The fractions were dried at 80 °C for 48 h and weighed. Each fraction was ground in a blade mill, passed through a 1.0-mm

screen (20 mesh) and stored for analysis. All results were expressed in 105 °C dry weight of litterfall material.

Physical and chemical analysis

Soil texture analysis

The texture analysis (in sieved soil) was carried out with the pipette method (Miller and Miller 1987).

Chemical analysis

The pH was measured electrometrically (pH meter ORION 410-A) by a glass electrode in water (1:5 soil weight per volume of water). The concentrations of total N and organic C in soils were measured with a CN analyzer (Farina et al. 1991) (model Vario MAX, Elementar Company). For the determination of total P in ground litterfall and the L horizon subsamples were digested in a 2:1 mixture of nitric and perchloric acids ($\text{HNO}_3/\text{HClO}_4$) (Zasoski and Bureau 1977). Available P was extracted with a NaHCO_3 solution (Olsen and Sommers 1982). Total P in litterfall, soil L horizon and available P were determined with the ammonium molybdate method in a UV spectrophotometer (Varian-Cary model). Total P in soils (apart from the L horizon) was measured by means of the Energy Dispersive X-Ray Fluorescence (ED-XRF) method (Vanhoof et al. 2004) (XEROS model of the TURBOQUANT Company).

Data handling and statistical analysis

The amounts of P (available) in soils were calculated taking into account the P concentrations, bulk density and the masses of soil per layer after subtracting the estimated volume of rocks. The litterfall flux-

es were calculated by multiplying the P concentrations of each fraction by its dry weight. The annual total litterfall fluxes of P were found by summing up the annual litterfall fluxes of all fractions.

For the soil properties the average values of the three replicates were calculated and the coefficients of variations as the percentages of the standard deviations over the means. The same procedure was followed for the annual fluxes of P in total litterfall but the replicates here were the yearly fluxes. Table 4 contains the amounts ($\text{kg}\cdot\text{ha}^{-1}$) of available P in the various soil layers. This data was used to assess the available P for the take up.

The statistical dependence of available P was examined for a variety of soil parameters in the mineral soil layers by means of the Principal Component Analysis (PCA). The predictors chosen were pH, clay and sand, total P, N, C and the ratios C/N, P/C and P/N. The dependence of P on pH and soil texture is well known (Brady 1984). The other variables represent elements and ratios, which in the authors' opinion may affect available P. Nutrient ratios, have often been used to assess tree nutrition (Michopoulos 2013; Tessier and Raynal 2003). The replicates in space of the soils collected were also included in the PCA calculations. PCA technique is very useful when the number of the initial correlated variables is large (Zitko 1994).

Results

The percentages of available P, with regard to total P, calculated from Table 2 ranged from 2.4 % in the fir plot to 6.48 % in the beech plot with regard to the FH layer. In the mineral layers, all percentages were below one. It is worth noting

Table 2. Soil properties in the four forest sites.

Layer	pH	Clay, %	Sand, %	C, %	Total N, g·kg ⁻¹	Total P, mg·kg ⁻¹	Available P, mg·kg ⁻¹
Maquis							
L				49.4 (2.8)	11.2 (8.5)	351 (17)	
FH	6.6 (3.7)			26.0 (7.1)	13.6 (8.2)	914 (4.3)	35.6 (14)
0–10 cm	6.26 (2.0)	23.6 (6.2)	20.3 (8.9)	5.0 (14)	3.03 (13)	565 (2.6)	3.17 (40)
10–20 cm	6.18 (6.6)	24.2 (14)	21.6 (15)	2.73 (17)	1.89 (14)	481 (0.8)	1.04 (44)
20–40 cm	6.12 (2.3)	26.0 (19)	21.2 (22)	1.44 (17)	1.15 (14)	441 (5.4)	0.59 (65)
40–80 cm	6.53 (5.7)	29.3 (15)	20.1 (22)	0.86 (14)	0.83 (11)	439 (9.4)	0.73 (7.0)
Oak							
L				45.9 (3.1)	12.6 (5.8)	634 (4.3)	
FH	6.19 (1.6)			20.1 (9.5)	9.62 (10)	924 (6.4)	45.8 (7.7)
0–10 cm	5.35 (0.7)	16.2 (3.8)	38.9 (3.6)	3.46 (14)	1.98 (15)	680 (2.1)	4.43 (0.39)
10–20 cm	5.45 (1.5)	16.6 (2.3)	36.4 (5.2)	20.9 (16)	1.23 (19)	624 (6.6)	1.21 (1.1)
20–40 cm	5.43 (1.2)	16.1 (2.5)	34.5 (8.2)	1.18 (3.7)	0.725 (3.9)	643 (3.6)	0.082 (98)
40–80 cm	5.42 (0.7)	13.6 (4.2)	46.6 (3.2)	0.57 (17)	0.378 (13)	632 (2.8)	0.043 (53)
Beech							
L				47.3 (0.6)	14.3 (4.2)	685 (7.0)	
FH	5.75 (4.9)			26.9 (3.5)	13.6 (1.1)	956 (2.5)	62.0 (0.03)
0–10 cm	4.83 (2.4)	20.0 (5.5)	26.4 (10)	4.32 (4.5)	2.09 (8.2)	633 (2.7)	4.39 (25)
10–20 cm	5.08 (2.1)	21.8 (2.1)	22.8 (0.8)	2.95 (8.7)	1.54 (11)	630 (8.9)	1.32 (17)
20–40 cm	5.24 (0.6)	21.5 (0.3)	21.3 (4.2)	2.09 (12)	1.20 (8.6)	661 (4.8)	1.27 (33)
40–80 cm	5.27 (1.1)	15 (4.1)	30.4 (6.6)	0.908 (3.2)	0.582 (2.2)	585 (11)	3.35 (118)
Fir							
L				50.8 (0.7)	12.3 (9.3)	881 (12)	
FH	6.48 (0.2)			23.0 (14)	12.2 (13)	1269 (5.6)	30.5 (6.0)
0–10 cm	6.07 (2.0)	27.2 (2.0)	29.5 (1.2)	5.12 (20)	3.31 (16)	850 (3.1)	5.26 (28)
10–20 cm	5.77 (3.1)	31.2 (2.1)	24.7 (8.1)	3.36 (10)	2.45 (9.4)	825 (3.0)	2.68 (14)
20–40 cm	5.54 (1.2)	33.0 (6.7)	21.0 (6.0)	2.75 (3.5)	2.12 (4.4)	818 (1.5)	2.90 (38)
40–80 cm	5.32 (1.5)	34.9 (14)	23.2 (11)	1.53 (19)	1.35 (15)	731 (4.9)	6.60 (37)

Note: in parentheses are the coefficients of variation.

that the fir plot had the lowest percentage of available P in the FH horizon and the highest percentages in the mineral soils in all plots.

The variability, expressed by the coefficients of variation, of soil properties are showed in Table 2. The available P showed the highest one especially in deeper soil horizons.

The results of Figure 1 depicting the PCA axes and the vectors of the parameters are combined with Table 3. The component 1 represents the horizontal

axis of Figure 1, whereas the component 2 the vertical one. The first principal component is the linear combination of x-variables that has maximum variance (among all linear combinations). It accounts for as much variation in the data as possible. The second principal component is the linear combination of x-variables that accounts for as much of the remaining variation as possible, with the constraint that the correlation between the first and second component is 0 (Zar 1999).

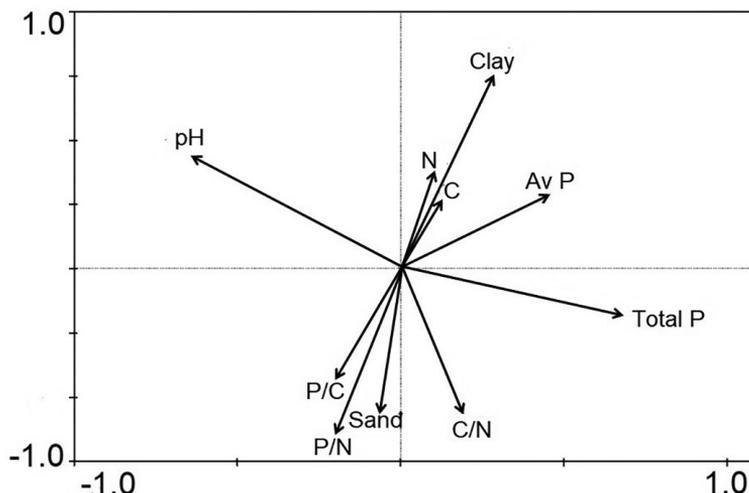


Fig. 1. PCA ordination diagram for the relation of available P with the soil properties.

Table 3. Component matrix with the relations of the available P and soil parameters derived from the PCA.

Indicator	Component	
	1	2
Available P, mg·kg ⁻¹	0.632	0.295
Total P, mg·kg ⁻¹	0.325	0.452
pH	0.245	-0.742
C, %	0.846	0.403
N, g·kg ⁻¹	0.909	0.184
C/N	0.065	0.866
Clay, %	0.607	-0.589
Sand, %	-0.617	0.550
P/C	-0.889	-0.110
P/N	-0.920	0.096

As the available P had the highest value there (0.632 in the component 1), the component 1 was chosen to check the results of the PCA. Values around 0.600 or higher are considered satisfactory as they explain at least 40 % of the variability of the parameters (Comrey 1962). Therefore, from Table 3 the parameters having a satisfactory and positive relationship with the available P are the organic C, total N and the clay percentage. Negative relationships were observed for the sand

percentage, the ratios P/C and P/N.

In comparison with the three other plots, the maquis plot had the lowest amounts of available P (Table 4) in the deepest mineral layers due to the high percentage of rocks. This fact shows the importance of calculating the rock percentages even only visually when there is need to express the nutrients in amounts per area in soils. It must be also pointed out that the amounts of available P are based on the concentrations of the OP. Other extractants (water, 0.01 M CaCl₂, Mechlich, etc.) would have given different amounts of available P. In any case, it is a reliable indication for P concentrations and the same conclusion should be drawn for the calculated amounts of P in soils.

Table 4. Amounts of available P in the soils.

Layer	Maquis	Oak	Beech	Fir
	kg·ha ⁻¹			
FH	1.05	0.08	0.27	2.43
0–10 cm	1.74	3.21	2.54	3.26
10–20 cm	1.12	1.15	1.17	2.28
20–40 cm	1.08	1.52	1.58	4.69
40–80 cm	0.54	1.50	3.49	10.8

In terms of absolute numbers, the concentrations of available P are considered satisfactory for the FH layers but not for the mineral when the thresholds for agricultural soils ($11 \text{ mg}\cdot\text{kg}^{-1}$) (Bai et al. 2013) are taken into account.

Table 5 shows the means and ranges of the aboveground total litterfall measured in the field, whereas Table 6 contains the means and ranges of the belowground litterfall calculated from literature.

Table 5. Annual fluxes of P in the total aboveground litterfall and coefficients of variation (CV).

Indicator	Maquis	Oak	Beech	Fir
Average, $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$	2.82	3.55	2.67	5.74
Range, $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$	1.88–4.25	2.36–4.81	1.60–4.04	3.67–8.71
CV, %	29	20	29	33

Table 6. Annual fluxes of P in the belowground litterfall (fine roots production) calculated from Table 5 and literature.

Indicator	Maquis	Oak	Beech	Fir
	$\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$			
Average	2.07	2.61	1.96	4.22
Range	1.38–3.12	1.73–3.54	1.18–2.97	2.70–6.40

Discussion

Magnitudes of total and available P in soils

The concentrations of total P in the FH horizons were found consistently higher than those in L layer and mineral soils. In comparison, Yanai (1992) found somewhat higher values for total P in the forest floor of the Hubbard Brook experimental forests (with the exception of fir, which had similar values), 70 years of age in USA. Schoenau et al. (1989) examined the forms of P in prairie and boreal forest in Canada. In native Chermozen they found similar concentrations of total P in the FH horizons of Luvisol and Gleysol but much lower concentrations in the FH of Chermozens. In the mineral horizons, the results were similar. In any case, the concentrations of total P in our work were within the range of $200\text{--}800 \text{ mg}\cdot\text{kg}^{-1}$ found in mineral soils (Cross and Schlesinger

1995) with the exception of the fir plot, which slightly exceeded the upper limit. This high concentration of total P in the soils of the fir plot should be ascribed to the relatively high contents of organic C and clay in comparison with the other three plots (Table 2). Other authors found considerably higher concentrations of total P in forest soils ($37\text{--}1773 \text{ mg}\cdot\text{kg}^{-1}$) in the top soil (0–15 cm) (Achat et al. 2009).

As mentioned in the results section, the percentages of available P with regard to total P calculated from Table 2 ranged from 2.4 % in the fir plot to 6.48 % in the beech plot with regard to the FH layer. In the mineral layers, all percentages were below one. Schoenau et al. (1989) found higher percentages of available P (extracted also with sodium bicarbonate) approximately 12 and 13 % in the FH horizons, whereas in the mineral soils the percentages values were above one. These high percentages in those cold climates should be attributed to slower de-

composition rates in comparison with the forest types in the Mediterranean zone.

The question that arises is about the high difference between the magnitudes of available, total P and the origin of the latter in mineral soils, which is appreciably high even in soil depth. According to Bowman and Cole (1978), NaHCO_3 solution can extract highly labile organics of low molecular weight containing P but not resistant organic P that is strongly associated with the mineral fraction. The resistant P also comprises inorganic P bonded to Al and Fe sesquioxides. As time passes, some labile P forms (including OP) can be included in soil minerals and thus increase the residual P fraction. Therefore, the high amounts of total P in the 20–40 cm and 40–80 cm of the plots can be either resistant organic or inorganic P. In future times, these fractions can replenish the labile P pools when the latter are exhausted by plant uptake (Smeck 1985).

The available P presents higher variability in deeper soil horizons than those of the total P. This might be due to the different mineralization rates of organic P in the soil. McGill and Cole (1981) argued that there is an independent mineralization process of organic P (apart from the one following the C mineralization) caused by enzymes released by plant roots. One might expect that this increased variability should have occurred in the rhizosphere zone and not so much in deeper soil layers. Maybe the hydrological path (which becomes more complicated in depth) of the root enzymes can affect the concentrations of available P in deeper horizons as well.

Factors affecting available P in soils

The PCA analysis showed that both organic C and total N (Table 3) affect the avail-

able P in soils (positively). This means that the release of P from organic matter depends on the C necessary for energy and N to cover the N needs of microorganisms. The negative effects of P/N and P/C emphasize the dependence of C and N. The positive dependence of available P on the clay percentage has to do with the mineralization of organic P but also with dissolution of secondary minerals containing P through root exudates. The PCA did not disclose a satisfactory relationship with the total P. Similarly, Liu et al. (2014) found a significant correlation of available P with organic C and total N but not with total P in a subtropical forest situated in southern China. It is also logical that the sand percentage had a significant negative effect. This soil fraction cannot withhold any P compound.

P uptake by forests

An indirect way to assess the P uptake by plants is by estimating the litterfall input to the forest floor. Trees have to take up all the P they lose in litterfall (Cole and Rapp 1981). The averages and the ranges of the above ground total litterfall fluxes for P are showed in Table 5. The values are close to those mentioned in literature. Yanai (1992) found $4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in a hardwood forest (Hubbard Brook), whereas Hansen et al. (2009) measured 2.1 to $3.3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of P in litterfall fluxes in five even-aged stands of Norway spruce, Sitka spruce, Douglas-fir, European beech and common oak at three different locations in Denmark.

The below ground litterfall has not been calculated in this work but it must be taken into account that the mycorrhizae fungi can account for 50 % of the annual throughput of biomass (Fogel 1980). In this work, we have not calculated the fine

root production and mortality. A rough estimate to apply could be that from An et al. (2017) who worked in variety of deciduous and conifer forests. They assessed the carbon flux of fine roots to be 25 % of the Net Primary Production, whereas that of the above ground litterfall was 34 %. Furthermore assuming that the P fluxes in fine roots tissues are approximately the same with the aboveground litterfall, then the numbers in Table 5, both means and ranges, should be multiplied by 25/34 to find the fluxes of fine roots. So a new Table 6 can be made from Table 5 containing the fine root production and mortality. Admittedly, that is an approximation, which helps nevertheless to make a rough picture of the P uptake needs. If we add the calculated P flux of the fine roots (Table 6) to the respective values in Table 5, the total litterfall above and below ground in the four forest types can be found. For example, for the fir forest one has to add the averages fluxes 5.74 and 4.22 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of tables 5 and 6, respectively to find the average total flux of P 9.96 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. The same calculations have to be made for the ranges. Of particular interest are the highest ranges of the new litterfall. They become 7.4, 8.4, 7.0, and 15.1 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for the maquis, oak, beech and fir forests, respectively. We calculated the highest range because we want to know the extreme situation needs. The values represent the highest needs for uptake. From these numbers the P inputs to the ecosystems should be subtracted. When considering them to a forest, one has to mention the deposition input which is low (0.05–1.7 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and the weathering input from apatite, also low (0.05 to 1 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) (Belyazid and Belyazid 2012). If from the above-mentioned numbers the total input (let us say 3 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) is subtracted, we have 4.4,

5.4, 4.0, and 12.1 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ needs for P uptake for the respective plots (for the highest range of litterfall). To check that the available P in soils suffices for these needs, we have to see the amounts of available P in soils in Table 4. Up to the depth of 20 cm the sums of amounts are 3.9, 4.4, 4.0 and 8.0 $\text{kg}\cdot\text{ha}^{-1}$. This depth was chosen because P uptake usually takes place in the surface soil layers. This was the case for the sugar maple stands in the Quebec Appalachians (Pare and Bernier 1989) and in stands for *Banksia* spp. in Australia (Grierson and Attiwill 1989). It appears that the fir stand (more than the others) cannot cover its needs for P uptake only from the available P in soil as determined by NaHCO_3 . These needs are probably met by P dissolved from soil minerals through the exudation of low molecular organic acids such as oxalic acids (Plassard and Dell 2010). This happens when the litterfall, both above and below ground, or in other words, when the net primary production is high and there is need to replenish the nutrients invested in it.

Conclusion

The release of P from the soil organic matter depends on the C necessary for energy and N to cover the N needs of microorganisms. It was also found that the clay percentage also affected positively the availability of P. The FH horizon is the most important soil layer to supply P to the forest trees as it contains the highest percentage of available P with regard to the total P amount. For the fir forest, the dissolution of minerals in the soils through roots exudates is also essential as the needs for uptake can exceed the amounts of available P in the surface soil layers

from which the P uptake usually takes place.

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