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Original article

Foliar N and P resorption and nutrient levels along an elevational gradient in *Juniperus oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Ball

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Abstract – *Juniperus oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Ball occurs in the Mediterranean region, on the southern part of Turkey and has been widely used in landscape planning and stabilization of coastal dunes. In this study foliar N and P resorption and foliar N, P and K concentrations (on a leaf mass basis) were investigated in *J. oxycedrus* subsp. *macrocarpa*. Foliar N, P, and K concentrations and absolute and proportional N and P resorption rates along the topographic position were not changed significantly. Significant correlations were found between absolute and proportional P resorption rates and soil moisture status. However, there were no significant correlation between absolute and proportional N resorption rates and soil moisture status. Foliar N and proportional N resorption were significantly correlated although absolute N resorption was not significantly correlated with foliar N. However, foliar P was significantly correlated both absolute and proportional P resorption.

***Juniperus oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Ball / absolute N and P resorption / proportional N and P resorption / Cupressaceae / soil moisture status**

Résumé – **Résorption foliaire de N, P et niveaux de nutrition chez *Juniperus oxycedrus* L. ssp. *macrocarpa* (Sibth. & Sm.) Ball le long d'un gradient altitudinal.** *Juniperus oxycedrus* L. ssp. *macrocarpa* (Sibth. & Sm.) se rencontre en région méditerranéenne dans le Sud de la Turquie. Il a été largement utilisé pour la stabilisation de dunes côtières et pour l'urbanisation. Dans ce travail, on a étudié chez cette espèce la résorption foliaire de N et P et les concentrations foliaires en N, P et K. Les concentrations foliaires en N, P et K et les taux de résorption (valeurs absolues et relatives) ne varient pas de façon significative avec la position topographique. Des corrélations significatives ont été trouvées entres les valeurs de résorption de P et l'humidité des sols. Cependant, il n'y a pas de corrélation significative entre les taux de résorption de N (valeurs absolues et relatives) et l'humidité des sols. La concentration foliaire en N et la résorption foliaire en N (valeurs relatives) étaient corrélées significativement bien que la résorption de N en valeurs absolues n'était pas corrélée avec la concentration foliaire en N. Pourtant les concentrations foliaires en P étaient significativement corrélées avec les résorptions de P (valeurs absolues et relatives).

***Juniperus oxycedrus* L. ssp. *macrocarpa* (Sibth. & Sm.) Ball / résorption de N et P / humidité du sol / Cupressacée**

1. INTRODUCTION

Concentrations of nutrients in mature leaves can indicate the nutritional status of a plant. For this reason, foliar analysis is a classic tool for diagnosing nutrient efficiencies and has long been applied to forests. Forest trees, shrubs and herbs retranslocate sizeable proportions of the nutrient content of leaves before leaf abscission. Retranslocation increases the control of the individual plant over the nutrient resources and it has acquired and allows the plant to reutilize them [30, 43]. One of the most important method to measure of nutrient use efficiency in plants is to determine foliar resorption, the process of nutrient translocation from the leaves into storage tissues during senescence [24, 27]. Oleksyn et al. [33] concluded that intraspecific genetic differences exist in foliage nutrient concentrations among diverse populations and as a result of interactions between temperature, litter quality and its mineralization, a tendency toward higher foliage concentrations of macronutrients can be an adaptive feature enhancing plants metabolic activity in their native habitats. Foliar resorption, can potentially supply the major part of the amounts needed in production of new foliage in the following year and such a conservative behavior leads to a tight circulation in the ecosystem [46].

It has been reported that individuals growing in less fertile sites may use nutrients more efficiently than those growing in

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more fertile sites. However, some stress factors such as low soil moisture may reduce resorption, especially of nitrogen. Several studies examining foliar nutrient resorption among temperate deciduous stands support these hypotheses for nitrogen and phosphorus [8, 19, 31].

Whittaker [47] showed that nutrients vary with topographic position within a forest. Because of this, the examination of nutrient dynamics along interstand topographic gradients may be used to examine hypotheses relating fertility to nutrient content [18].

Juniperus oxycedrus L. subsp. *macrocarpa* (Sibth. & Sm.) Ball is a coniferous plant belonging to *Cupressaceae*. It is distinguished from related subspecies *Juniperus oxycedrus* L. subsp. *oxycedrus* with its longer and hard textured leaves and bigger cones [5]. This subspecies is rare in Turkey as compared to other coniferous species. It is also distributed in the Mediterranean region from Spain to Greece and in north-west Africa outside Turkey [12]. It is a shrub like plant and 2–3 m. in height, however it can be reached up to 6–7 m and female flowers have a quite decorative feature. So that it can be used widely in landscape planning [6]. It can also be used for stabilizing of sand dunes due to its dense root system and very resistant to salt spray. *J. oxycedrus* subsp. *macrocarpa* should be protected because this subspecies is very rarely occured in Turkey and the other Mediterranean countries. Except the study area the individuals of this subspecies are rather scattered [12].

In this study nitrogen (N), phosphorus (P) and potassium (K) concentrations (g/kg) in mature and fresh-litter leaves and absolute and proportional N and P resorption leaves of *J. oxycedrus* subsp. *macrocarpa* along a topographic position were investigated. This subspecies was chosen because it was occured along the entire topographic gradient. This study has two main objectives: (a) to investigate whether absolute and proportional foliar N and P and soil parameters were changed along the topographic position and, (b) to examine the factors which effective on absolute and proportional foliar N and P resorption.

2. MATERIALS AND METHODS

2.1. The study area and the collection of samples

J. oxycedrus subsp. *macrocarpa* specimens were collected from Tavşanburnu locality near the Didim town (Aydin; 37° E , 28° N) which is situated on the southwest part of Turkey. The canopy individuals were 15 years of age and had no obvious sign of damage [12]. In this area the individuals of this subspecies are very widespread. Mean annual temperature in the study area is 17.6 °C. Mean annual precipitation is 1001.7 mm. Maximum temperature for the hottest month; July (M) is 33.8 °C and minimum temperature for the coldest month; January (m) is 4.8 °C. Pluviometric quotient (Q) is 73. Mean annual relative humidity and relative humidity in summer are 62% and 51%, respectively. According to these data Central Mediterranean climate is seen in the study area by the method of Emberger [15]. The study area is located at C1 square based on the grid systeme of Davis [16].

20 × 20 m plots was sampled along topographic position from 10 to 200 m (10, 50, 150 and 200 m) from the sea level. Plots were selected to have closed tree canopies on southwest facing slopes. From each topographic position five *J. oxycedrus* subsp. *macrocarpa* individuals (≥ 4.5 m tall) were randomly selected and flagged. Individuals were selected ≥ 3 m from the stems of neighboring canopy trees to avoid potential microsite variation [11]. The coniferous species experiences strong increases in the nitrogen concentrations per needle in the successive growing seasons, hence the proportion of the total concentration reached during the needles's first months of life is considerably smaller [19], since five fresh leaves from throughout the midcrown per individual were taken to avoid effects of crown position in mature (mid-growing season) leaves (at the first half of August 1998). Freshly abscissed litter (five leaves) was also collected under each individual at the first half of May.

From each topographic position five soil samples were taken at a depth of 35 cm with a soil corer. Each sample from each topographic position was a composite of five subsamples collected at random beneath the plant specimens. The samples were brought to the laboratory in polyethylene bags. Soil samples were air-dried and sieved to pass through a 2 mm mesh prior to analysis. Because soil parameters changed very little during both sampling period soil samples belonging to both sampling period were pooled.

2.2. Methods of chemical analysis

Leaf samples were dried at 70 °C until constant weight, ground, and sieved and digested in a mixture of nitric and perchloric acids with the exception of samples for N analysis. Nitrogen was determined by the micro Kjeldahl method with a Kjeltec Auto 1030 Analyser (Tecator, Sweden) after digesting the samples in concentrated H_2SO_4 with a selenium catalyst. P was determined with stannous chloride method by using a Jenway spectrophotometer. K was determined by Petracourt PFP-7 flame photometer [3]. Very similar N indices of retranslocation were obtained using either leaf area or percentage content as the basis for calculation in different Mediterranean evergreens [37, 39]. So nutrient concentrations in mature leaves were expressed on a leaf mass basis (g/kg). Absolute resorption was calculated as the difference between the concentration of mature leaves and fresh litter foliar concentration. Proportional resorption was found by dividing the absolute resorption by the nutrient concentration in mature leaves. The proportional resorption is thus the proportion of nutrient concentration in a mature leaf that is removed from the leaf before it is shed [32, 34, 35, 40, 42]. Resorption estimation was not derived for K because it is easily leached from senescing leaves [44]. Leaching experiments indicated that less than 1 g/kg of the autumnal reductions of N and P could have been due to leaching of foliage by precipitation [24]. Chapin and Kedrowski [14] indicated that leaching was much less important than retranslocation in removing nutrients from senescing leaves. So that potential N and P losses due to leaching was not measured.

Soil texture was determined by the Bouyoucus hydrometer method. pH values were measured in deionized water (1:1). Soil nitrogen (g/kg) was determined by the micro Kjeldahl method. Soil phosphorus (g/kg) was determined spectrophotometrically following the extraction by ammonium acetate. Soil potassium (g/kg) was determined by using a Petracourt PFP-7 flame photometer after nitric acid wet digestion. Organic matter (g/kg) concentration was determined by Walkley-Black method [7]. For the determination of soil moisture (cm^3 H_2O/100 cm^3 soil) about 250–300 g samples were placed in soil pins, weighed fresh, dried at 105 °C for 48 h, then weighed dry and then soil moisture was calculated on a volume basis [9]. The results of soil analysis were explained according to Bayraklý [7].

One and two-way analysis of variance (ANOVA) tests and Pearson correlation coefficients were carried out by using MINITAB [4, 38]. Tukey's honestly significant difference (HSD) test was used to rank means following analysis of variance.

Table I. Foliar nutrient concentrations in mature leaves (g/kg). Standard errors are given in parenthesis.

Nutrient	Valley °	Slope°°	Slope°°°	Upland°°°°	F-value	Probability	Significance
N	10.8 (1.78)	9.8 (0.81)	6.4 (0.56)	8.2 (0.81)	3.079	0.090	NS
P	0.16 (0.04)	0.15 (0.06)	0.13 (0.07)	0.28 (0.002)	1.515	0.283	NS
K	0.40 (0.06)	0.26 (0.02)	0.23 (0.04)	0.26 (0.003)	3.198	0.084	NS

°10 m, °°50 m, °°°150 m, °°°°200 m.
NS: not significant.

Table II. Fresh litter foliar nutrient concentrations (g/kg). Standard errors are given in parenthesis.

Nutrient	Valley °	Slope°°	Slope°°°	Upland°°°°	F-value	Probability	Significance
N	7.38 (2.16)	7.01 (1.95)	2.96 (0.006)	4.98 (1.98)	1.334	0.330	NS
P	0.004 (0.006)	0.004 (0.006)	0.004 (0.02)	0.006 (0.006)	1.242	0.357	NS
K	0.005 (0.002)	0.51 (0.21)	0.48 (0.13)	0.27 (0.05)	2.810	0.108	NS

°10 m, °°50 m, °°°150 m, °°°°200 m.
NS: not significant.

Table III. The differences between mature and fresh leaf litter foliar nutrient concentrations.

Nutrient	F-value	Probability	Significance
N	8.064	0.010	**
P	20.450	0.002	**
K	11.112	0.003	**

** $P < 0.01$.

3. RESULTS

N foliar concentrations in mature leaves ranged from 5.38–14.00 (g/kg). Fresh litter N concentrations ranged from 2.90–10.10 (g/kg). Mature and fresh litter P foliar concentrations ranged from 0.09–0.30 and 0.02–0.07 (g/kg), respectively. For K foliar concentrations the values were ranged from 0.23–0.53 and 0.03–0.32 (g/kg), respectively (Tabs. I and II).

Nutrient concentrations were significantly decreased in fresh litter leaf samples (Tab. III).

Statistical assesment of proportional and absolute resorption rates showed that foliar N and P proportional and absolute resorption rates did not change significantly along topographic positions (Tabs. IV and V).

The soils under *J. oxycedrus* subsp. *macrocarpa* were clay-loam with 378.4 g/kg clay content. Soil N concentrations were high (Tab. VI). However, soil K concentrations were low to medium levels. Soil P concentrations were low especially in valley positions, however these values increased in slope positions. *J. oxycedrus* subsp. *macrocarpa* occur on neutral soils with respect to pH values. Organic matter values were low in valley positions. However, there was a sharp increase at 50 m. After that organic matter concentrations were decreased, however slope and upper positions are still rich in organic matter.

Table IV. Proportional resorption rates (%) along the topographic position. Standard errors are given in parenthesis.

Nutrient	Valley	Slope	Slope	Upland	F-value	Probability	Significance
N (%)	34.7 (13.32)	31.4 (16.05)	53.0 (3.49)	41.9 (18.11)	3.481	0.709	NS
P (%)	70.8 (4.16)	54.1 (19.38)	63.8 (7.34)	77.4 (0.95)	1.024	0.432	NS

NS: not significant.

Table V. Absolute resorption rates (g/kg) along the topographic position. Standard errors are given in parenthesis.

Nutrient	Valley	Slope	Slope	Upland	F-value	Probability	Significance
N	3.3 (0.91)	2.8 (1.24)	3.4 (0.49)	3.2 (1.40)	0.063	0.978	NS
P	0.11 (0.03)	0.10 (0.06)	0.009 (0.06)	0.2 (0.01)	1.405	0.310	NS

NS: not significant.

Table VI. Mean values for soil paremeters along the topographic position and the comparison of soil parameters by one-way ANOVA test. Standard errors are given in parenthesis. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test.

Soil parameter	Valley	Slope	Slope	Upland	F-value	Probability	Significance
N (g/kg)	0.26 (0.05)a	0.63 (0.02)b	0.51 (0.01)b	0.29 (0.01)a	41.010	0.001	**
P (g/kg)	0.008 (0.33×10^{-3})a	0.007 (0.001)a	0.012 (0.03)a	0.020 (0.003)b	12.088	0.001	**
K (g/kg)	0.004 (1.00×10^{-3})a	0.51 (0.21)a	0.48 (0.13)a	0.27 (0.05)a	6.354	0.008	**
pH	7.33 (0.04)a	7.40 (0.08)a	7.33 (0.11)a	7.46 (0.04)a	12.499	0.001	**
Organic matter (g/kg)	0.99 (0.67)a	9.80 (4.94)a	2.59 (0.04)a	4.11 (0.74)a	26.724	0.000	**
Moisture cm^3 $H_2O/100\ cm^3$ soil	47 (3.66)a	88 (11.33)b	62 (3.66)a	88 (6.41)a	9.180	0.002	**

** $P < 0.01$.

Table VII. Pearson correlation coefficients between foliar N and P concentrations and absolute and proportional resorption rates and resorption rates and soil moisture.

Parameter	Correlation coefficient	Significance
Foliar N in mature leaves-absolute N resorption	–0.252	NS
Foliar N in mature leaves-proportional N resorption	–0.634	**
Foliar P in mature leaves-absolute P resorption	0.737	**
Foliar P in mature leaves-proportional P resorption	0.993	**
Absolute N resorption-Soil moisture	0.389	NS
Proportional N resorption-Soil moisture	0.260	NS
Absolute P resorption-Soil moisture	–0.652	**
Proportional P resorption-Soil moisture	–0.506	**

NS: not significant. ** $P < 0.01$.

There were significant differences along the topographic position in respect to N, P, K and soil moisture (Tab. VI).

Significant correlations were found between foliar N and P concentrations and absolute and proportional resorption rates and resorption rates and soil moisture (Tab. VII).

4. DISCUSSION

It has been found that foliar N was not changed significantly among topographic positions. The lack of significant differences in foliar N among topographic positions may have resulted from carbon dilution effect or luxury consumption [18]. The lack of significant differences may also reflect the narrower intrastand fertility gradients among topographic positions due to narrow distribution of this subspecies [19].

N concentration values of *J. oxycedrus* subsp. *macrocarpa* are within the ranges reported for the other evergreen coniferous species (Tab. I) as reported by Schulze et al. [40].

Aerts [1] reported that mean nutrient proportional resorption rate was 47% for N and 50% for P in evergreen species. Proportional N resorption rates in the present study were consistently lower than in other studies except for the slope topographic positions (150 m). For example, Boerner [8] and Cote et al. [10] reported a range of 26.5–63.7 and 56–71% N resorption, respectively in deciduous forests. Chapin & Kedrowski [14] indicated that high concentrations of phenolics especially in evergreen leaves, as observed in low-productivity species growing at infertile sites may lead to precipitation of proteins before protein hydrolysis, which reduces nutrient resorption. Valley topographic positions in the study area were usually infertile and proportional N resorption rates in valley positions were low as compared to the other topographic positions (Tabs. IV and VI).

However, P resorption rates were usually within the ranges reported by Killingbeck and Costigan [24] for several species. Proportional P resorption in the present study was particularly high especially at valley and upland sites (Tab. IV) and exceeded the values reported by Aerts [1] and similar to Cote et al. [10]. However, proportional N resorption values at valley and upland sites were lower than that of the values reported by Aerts (1996) although proportional N resorption was within the average values (Tab. IV) reported by Aerts [1].

De Mars and Boerner [18] stated that both absolute and proportional P resorption were significantly greater in the valley topographic positions where soil P was lowest. However, in the present study, absolute and proportional P resorption was higher in the upland topographic positions (Tabs. IV and V).

It can be argued that individuals growing on nutrient-rich sites may have larger absolute and proportional retranslocation of foliar nutrients, since their mature leaves are likely to have higher concentrations of nutrients, of which a greater proportion are in hydrolyzable forms [30]. However, a consistent pattern was not found with respect to N and P resorption rates in the present study (Tabs. IV and V). Aerts [1] indicated that nutrient resorption was not very responsive to increased nutrient availability. The lack of significant differences in N resorption rates may simply result from the fact that foliar N levels were not significantly different among topographic positions [18]. N proportional resorption was greater in the slope and upper topographic positions (150–200 m) where soil moisture was higher in both sampling dates as indicated by del Arco et al. [17], Hocking [22] and Kost and Boerner [25] and this might reflect inefficient proportional N resorption by *J. oxycedrus* subsp. *macrocarpa* individuals in valley topographic positions (Tab. IV). There were significant correlations between absolute and proportional P resorption rates and soil moisture status (Tab. VII). However, there were no significant correlation between absolute and proportional N resorption rates and soil moisture status (Tab. VII) on the contrary to several studies [17, 21, 24]. However, soil moisture were significantly changed along the topographic position (Tab. VI).

There were no significant overall effects of topography on foliar N concentration, despite significant topographic differences in mean soil N availability (Tabs. I, II and VI). These results were contrast with the studies that have shown high foliar N in more fertile sites [10] and studies that have shown lower foliar N in nutrient poor sites [24, 27]. Foliar P and K concentrations were also not exhibited significant differences in respect to topographic positions according to the results of one-way ANOVA test (Tab. I). However, there were significant differences between N, P and K concentrations of mature and fresh litter leaves (Tab. III).

The differences between the present study and the other studies with respect to foliar resorption may probably due to the other studies were usually carried out with deciduous forest species. According to Chapin and Kedrowski [14] such differences may be due to the different strategy of evergreen and deciduous species in using of nutrients. For example, leaves rather than stems are the major site of overwinter storage in evergreen species [36].

It has been observed that mature and fresh litter foliar N, P and K concentrations were significantly different. Similar results were reported for some *Quercus* species [26, 28]. In general, macroelements especially nitrogen concentration in leaves is strongly correlated with photosynthetic capacity [36] and it has been known that photosynthetic capacity was decreased during senescence [20] and remobilization of mineral nutrients (except calcium and manganese) from leaves to woody parts [29]. However, there was a difference between evergreen and deciduous species in transferring of phosphorus. In evergreen species, the decline in P concentration was usually due to dilution of P during senescence rather than to P retranslocation from needles [14].

Chapin & Kedrowski [14] found a positive correlation between the N concentration of mature leaves and N resorption rate and they were suggested that leaf N concentration may partially control leaf N retranslocation, however P retranslocation was not controlled by leaf P concentration. Negative correlation coefficients were obtained with respect to absolute and proportional N concentrations and N concentration of mature leaves. For example, there was a significant and negative correlation between foliar N and proportional N resorption rate. However, there were no significant correlation between N absolute resorption rate and N concentration of mature leaves in the present study. The strong positive correlations were found between foliar P concentrations and absolute and proportional P resorption rates (Tab. VII). Several other authors were also arrived at conflicting conclusions, in both intraspecific [41, 45] and interspecific comparisons [14, 17, 32].

It has been reported that nutrient-poor sites usually show greater levels of nutrient retranslocation [13, 32, 46]. In addition to this, in nutrient-poor environments, species produce relatively small amounts of litter due to low productivity and long lifespans of the various tissues. This litter generally has low nutrient concentrations and high concentrations of secondary compounds such as lignin and phenolics. Thus, species from nutrient-poor environments produce litter that decomposes slowly and from which only low amounts of nutrients are released. The opposite holds for species from fertile environments. Owing to their high productivity and high tissue turnover rates, they produce relatively large amounts of litter. Moreover, this litter contains relatively high concentrations of mineral nutrients and low concentrations of secondary compounds. As a result, this litter decomposes relatively quickly and releases high amounts of nutrients. Thus, in nutrient-poor ecosystems the combination of low productivity (and thus low litter production) and low litter decomposability may lead to a low rate of ecosystem nutrient cycling [2]. Low fresh litter nutrient concentrations in the present study may be explained in this way. Soil P concentrations in valley positions were rather low in the present study although P concentrations can be high in upland positions and this may be caused high P resorption rates. However, soil N concentrations were high along the topographic position. Several studies were showed that the relationship between retranslocation and soil fertility was not observed in all cases [14, 17, 18, 23, 32] and nutrient resorption probably reflected topographic differences in moisture than in fertility. Thus, soil moisture was significantly changed along the topographic position in the present study (Tab. VI). Moreover, it was not known which factors control nutrient resorption from senescing tissues, how this is related to the dynamics of secondary compounds in senescing tissues, and how these processes are reflected in litter decomposition and nutrient release from litter [2].

It is possible to say that proportional P resorption was more efficient in *J. oxycedrus* subsp. *macrocarpa* as compared to the other evergreen species in the light of the data presented by Aerts [1]. However, proportional N resorption *J. oxycedrus* subsp. *macrocarpa* was not efficient as compared to the other evergreen species except for slope topographic positions (Tab. IV).

Several researches reached conflicting results with respect to the relationships between leaf nutrient status and resorption. Although, Aerts [1] pointed out that relations between leaf nutrient status and leaf nutrient resorption were very weak, Hevia et al. [21] showed such a relationship does exist, at least for N. So that future research should be done to more precise explanation of leaf nutrient status and leaf nutrient resorption in deciduous and evergreen species.

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