

Foliar resorption and chlorophyll content in leaves of *Cistus creticus* L. (Cistaceae) along an elevational gradient in Turkey

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Foliar nitrogen and phosphorus dynamics, leaf resorption efficiency, proficiency, changing of chlorophyll a/b proportions in leaves of *Cistus creticus* L. (Cistaceae) along an elevational gradient (sea level-30 m, middle-670 m, high-880 m) were investigated. Statistically significant differences were found in foliar nitrogen and phosphorus content in terms of growth periods, while no significant differences were found according to elevations. Nitrogen and phosphorus resorption efficiency and proficiency values were high as compared to the other evergreen species. *Cistus creticus* effectively used nitrogen and phosphorus. No statistically significant differences were found among elevations in terms of specific leaf area. However, statistically significant differences were found in terms of growth periods. There were significant differences in chlorophyll a/b proportion according to both growth periods and elevations. Besides, the chlorophyll a/b proportion increased along senescence period.

Key Words: Leaf, nitrogen, phosphorus, resorption, chlorophyll, *Cistus creticus*, elevation

Introduction

The *Cistaceae* family includes 8 genera with 175 species distributed in the temperate zone of the northern hemisphere, especially in Mediterranean climates. Five *Cistus* L. species are found in Turkey (DAVIS 1965). *Cistus creticus* is an evergreen shrub and distributed all along the coastal belt of the Turkish Mediterranean phytogeographical region, as well as in some enclaves along the Black Sea coast. These species adorn habitats with their purple flowers from late March till June, extending from sea level up to an altitude of 1000 m (DAVIS 1965, BASLAR et al. 2001). The leaves of these species exude a fragrant, sticky gum called ladanum used in perfumery and folk medicine (BAYTOP 1994). *C. creticus* is one of the pioneer plants of secondary succession and it succeeds pine after fire. Therefore, sites where ladanum communities are distributed are evidence of the existence of pine forest communities before a fire in the environs (TURKMEN and DUZENLI 2005).

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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 (MAYOR and RODA 1992). But leaf nutrient concentrations vary with species, age of the tissue, climate, soil and other factors (SCHLESINGER 1997, TEKLAY 2004). Forest trees, shrubs and herbs retranslocate sizeable proportions of the nutrient content of leaves before leaf abscission (MAYOR and RODA 1992). One of the most important methods 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 (KILLINGBECK 1988, LUKEN 1988). In particular, seasonal changes in leaf nutrients occur in response to resorption or retranslocation before senescence (CHAPIN 1980). The rate of nutrient resorption from senescing leaves may also vary with the availability of nutrients for resorption. The duration of retention of leaf nutrients in a plant is largely a function of leaf resorption (ESCUADERO et al. 1992). Especially, N and P are largely withdrawn from senescing leaves before abscission, and used for new growth or stored in vegetative tissue until the next growing season (VAN HEERWAARDEN et al. 2003). This process plays an important role in nutrient conversation (CHAPIN 1980). Obviously, species and seasonal pattern of nutrients strongly influence nutrient resorption (TEKLAY 2004, AERTS 1996, CHAPIN and KEDROWSKI 1983, KILLINGBECK 1996).

It has been reported that individuals growing in less fertile sites may use nutrients more efficiently than those growing in 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 N and P (BOERNER 1984, ESCUADERO et al. 1992, MINOLETTI and BOERNER 1994). The nutrients resorbed from the trees during senescence are directly available for further plant growth, which makes a species less dependent on current nutrient uptake. Nutrients which are not resorbed, however, will be circulated through litterfall in the longer term. All of this has important implications for element cycling at the ecosystem level (AERTS and CHAPIN 2000, MARTÍÁEZ-SÁNCHEZ 2005).

Resorption can be expressed in two ways: as resorption efficiency and resorption proficiency. Resorption efficiency is most accurately calculated for any nutrient as area-specific mass in green leaves minus area-specific mass in senesced leaves divided by area-specific mass in green leaves, and the quantity multiplied by 100. A new measure of resorption was introduced by KILLINGBECK (1996) as resorption proficiency. Proficiency is simply the amount of a nutrient that remains in fully senesced leaves (KILLINGBECK 2004). From a biological perspective, an important advantage of measuring resorption as proficiency rather than efficiency is that proficiency is a more unequivocal measure of the degree to which selection has acted to minimize nutrient loss in ephemeral leaves (KILLINGBECK 2004).

The chlorophylls (Chl *a* and Chl *b*) are the most important photosynthetic pigments, and thus virtually essential for the oxygenic conversion of light energy to the stored chemical energy that powers the biosphere. From an applied perspective, leaf pigmentation is important to both land managers and ecophysiologicalists (RICHARDSON et al. 2002, LIN et al. 2005). The amount of solar radiation absorbed by a leaf is largely a function of the concentrations of leaf photosynthetic pigments and, therefore, low concentrations of chlorophyll can directly limit photosynthetic potential and hence primary production (CURRAN et al. 1990, FILELLA et al. 1995) Much of the leaf nitrogen is incorporated in chlorophyll, so

quantifying chlorophyll content gives an indirect measure of nutrient status (FILELLA et al. 1995, MORAN et al. 2000). Pigmentation can be directly related to stress physiology, as concentrations of chlorophylls generally decrease under stress and during senescence (PENU-ELAS and FILELLA 1998). The relative concentrations of pigments are known to change with abiotic factors such as light, so quantifying these proportions can provide important information about relationship between plants and their environment. The seasonal changes of leaf ecophysiological and ecomorphological characters depend on both internal and external factors. Particularly, seasonal changes are informative for evergreens, because the leaf character of a plant changes according to age of plant, growth of leaf and vegetative reproductive phases (NUNEZ-OLIVERA et al. 1996).

The present study addresses three main objectives : (1) the seasonal variation of N and P contents, efficiency and proficiency, and (2) to find whether N and P resorption efficiency and proficiency is changed along an elevational gradient or not, (3) determining chl a/b in leaves of the evergreen *C. creticus* L. along an elevational gradient.

Material and methods

Study area

This study was conducted in natural *Cystus creticus* populations at Samsun (41°17' N; 36°20' E) and Amasya (40° 39' N; 35°51' E) counties in 2004–2006. Samsun and Amasya are situated on the north, Black Sea region of Turkey (A6 square based on the grid system of Davis) (Fig. 1). Mean annual temperature and precipitation in Samsun (30 m a.s.l. 670 m a.s.l.) and Amasya (880 m) are 12.16 °C, 65.7 mm and 13.37 °C, 450.3 mm, respectively

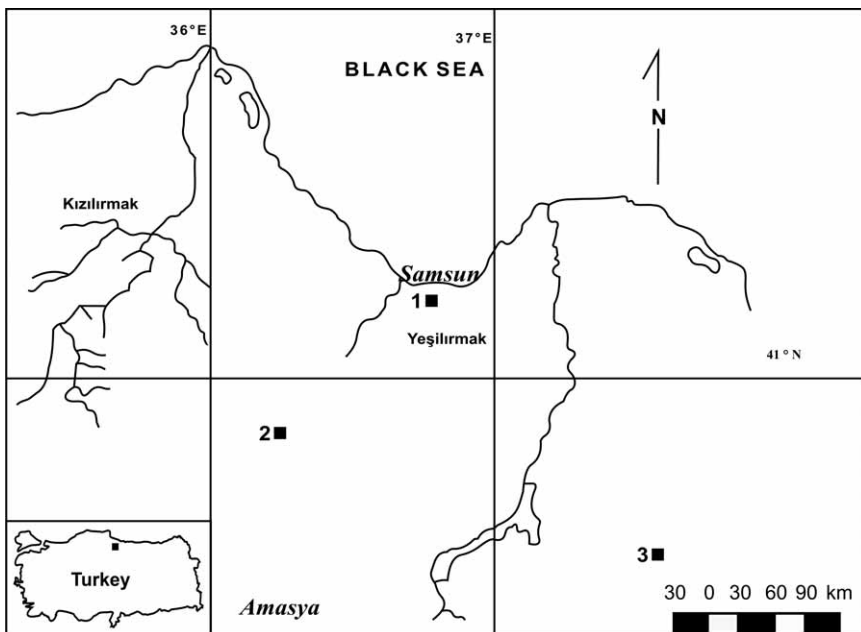


Fig. 1. The map of study area. 1 – Kurupelit (30 m), 2 – Kavak (670 m), 3 – Yenice (880 m).

(Tab. 1). A western Mediterranean type precipitation regime is present in Samsun. A western Black Sea region 2nd type oceanic precipitation regime is seen in Amasya (AKMAN 1990).

Cistus creticus occurs on loamy and strongly alkaline soils (Tab. 1).

Tab. 1. General characters of the study areas. (See Fig.1)

| Locality | Mean annual temperature (°C) | Mean annual precipitation (mm) | Soil Texture | pH | Composition of the study area |
|----------|------------------------------|--------------------------------|--------------|------|--|
| Samsun | 12.16 | 65.70 | Loamy | 8.35 | <i>Pinus pinea</i> dominates, <i>Quercus ilex</i> , <i>Cistus salviifolius</i> . |
| Amasya | 13.37 | 45.03 | Loamy | 8.20 | <i>Pinus pinea</i> dominates, <i>Cistus salviifolius</i> . |

Sampling

Plant samples were collected from along an elevational gradient from 30 to 880 m. Five (25 m × 25 m) plots were chosen in homogeneous places at altitudes of 30 m a.s.l., 670 m a.s.l. and 880 m a.s.l. in homogeneous places. In each plot, at least five individuals were randomly selected and flagged. Individuals were selected ≥2.5 m from the stems of neighboring canopy trees to avoid potential microsite variation (BOERNER and KOSLOWSKY 1989). Leaf samples from throughout the midcrown per individual were taken to avoid effects of crown position of the canopy and subcanopy species and consisted of leaves with no evidence of insect attack.

Chemical analyses

Leaf samples were dried at 60 °C until constant weight, ground, and sieved and digested in a mixture of nitric and perchloric acids with the exception of samples for nitrogen (N) analysis. Nitrogen was determined by the micro Kjeldahl method with a Kjeltac Auto 1030 Analyser (Tecator, Sweden) after the samples were digested in concentrated H₂SO₄ with a selenium catalyst. Phosphorus (P) was determined with the stannous chloride method with the use of a Jenway spectrophotometer (ALLEN et al. 1986). Concentrations of chlorophyll a and b were determined according to standard methods (ODABAS 1981).

Leaf samples were scanned and leaf area was calculated with the use of a SPSS 10.0 for Windows (ANONYMOUS 1999).

Specific leaf area (SLA) was calculated according to (CORNELISSEN et al. 1997, KUTBAY 2001):

$$SLA = \Sigma LA \text{ (cm}^2\text{)} / \Sigma LDW \text{ (}\mu\text{g)}$$

$$N \text{ contents} = \Sigma LDW \text{ (}\mu\text{g)} \times \text{crude N concentration} / SLA = \mu\text{g cm}^{-2}$$

$$P \text{ contents} = \Sigma LDW \text{ (}\mu\text{g)} \times \text{crude P concentration} / SLA = \mu\text{g dm}^{-2}$$

LA – Leaf area (cm²)

LDW – Leaf dry weight (μg)

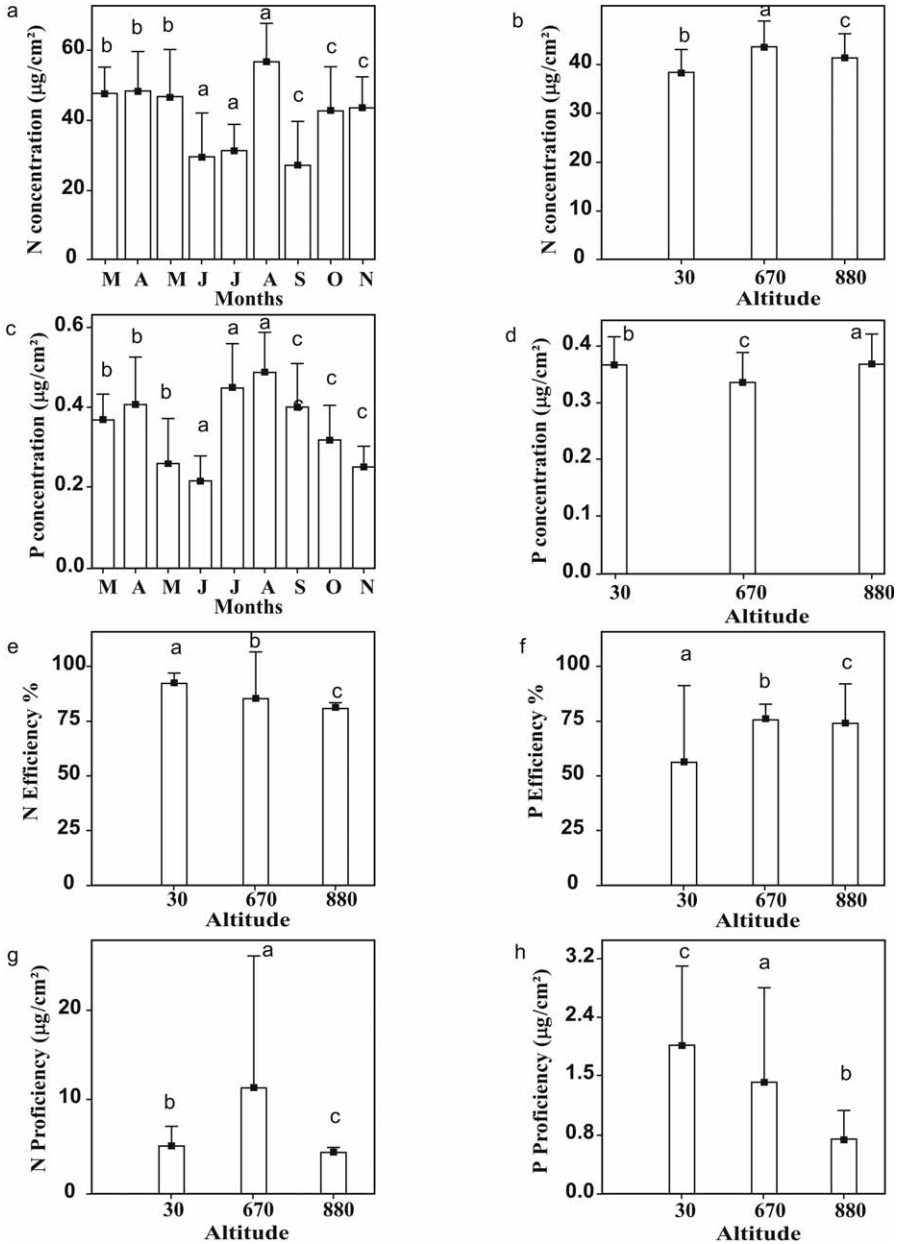


Fig. 2. Concentration of N and P ($\mu\text{g}/\text{cm}^2$), percentage of N resorption efficiency (NRE), P resorption efficiency (PRE), N resorption proficiency (NRP) and P resorption proficiency (PRP). Seasonal N concentrations (a), N concentrations along the elevational gradient (b), seasonal P concentrations (c), P concentrations along the elevational gradient (d), NRE (%) along the elevational gradient (e), PRE (%) along the elevational gradient (f), NRP concentration along the elevational gradient, PRP concentration along the elevational gradient (g) (Standard errors are indicated. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test).

Resorption efficiency was calculated as the percentage of N, P and recovered from senescing leaves (ORGEAS et al. 2002, REJMANKOVA 2005):

$$[(\text{Nutrient in live leaves} - \text{Nutrient in senescent leaves}) / \text{Nutrient in live leaves}] \times 100$$

Statistical analyses

One and two-way analysis of variance (ANOVA) tests and multivariate General Linear Models procedure were carried out with the use of the programme SPSS 10.0. The dependent and independent variables were foliar nutrient concentrations and foliar resorption and, growth period and localities, respectively. Tukey's HSD test was used to rank means following analysis of variance with the use of SPSS 10.0. Pearson correlation coefficients were also calculated with SPSS 10.0 version (ANONYMOUS 1999).

Results

Nitrogen and phosphorus dynamics and specific leaf area

Nitrogen and phosphorus concentrations of *C. creticus* changed according to months and altitudes (Figs. 2a, 2b, 2c, 2d). There were statistically significant differences in terms of N and Specific Leaf Area (SLA) ($P < 0.01$) but there were no significant differences in P concentration (Tabs. 2, 3). The highest N concentration was observed in August ($55.5 \mu\text{g cm}^{-2}$). In the beginning of senescence (September), the N concentration of leaves decreased ($25.3 \mu\text{g cm}^{-2}$). The highest P concentration was observed in August ($0.49 \mu\text{g cm}^{-2}$) while the lowest P concentration was found in June and November ($0.21 \mu\text{g cm}^{-2}$, $0.25 \mu\text{g cm}^{-2}$) while the flower were in bloom (Figs. 2a, 2b, 2c, 2d).

Tab. 2. The comparison of the monthly changes in N, P, specific leaf area (SLA) and leaf mass area (LMA) in *C. creticus* by using one-way ANOVA.

| Parameter | | Sum of Square | df | Mean square | F | Sig. |
|-----------|----------------|---------------|-----|-------------|-------|----------|
| N | Between Groups | 8100.518 | 8 | 1012.565 | 8.307 | 0.000** |
| | Within Groups | 18648.795 | 153 | 121.888 | | |
| | Total | 26749.313 | 161 | | | |
| P | Between Groups | 0.756 | 8 | 9.448E-02 | 1.784 | 0.084 NS |
| | Within Groups | 8.103 | 153 | 5.296E-02 | | |
| | Total | 8.858 | 161 | | | |
| SLA | Between Groups | 0.747 | 8 | 9.338E-02 | 6.961 | 0.01** |
| | Within Groups | 0.966 | 72 | 1.342E-02 | | |
| | Total | 1.713 | 80 | | | |
| LMA | Between Groups | 59.338 | 8 | 7.417 | 6.535 | 0.01** |
| | Within Groups | 81.725 | 72 | 1.135 | | |
| | Total | 141.063 | 80 | | | |

* $P < 0.05$ ** $P < 0.01$ NS: Not Significant

Tab. 3. The comparison of the monthly changes in N, P and specific leaf area (SLA) in *C. creticus* by using Tukey's HSD test.

| Months | N | P | SLA |
|------------|----------|---------|----------|
| March | 4.76bc | 0.20 ab | 0.34 bcd |
| April | 7.16bc | 0.66 a | 0.38 abc |
| May | 15.03bc | 0.92 a | 0.38 abc |
| June1 | 6.78ab | 0.18 ab | 0.38 abc |
| July | 28.00a | 0.24 ab | 0.33 bcd |
| August | 15.93bc | 0.14 ab | 0.26 cd |
| September | 10.39 bc | 0.26 ab | 0.19 d |
| October | 9.80 bc | 0.26 ab | 0.44 ab |
| November | 3.94 c | 0.22 ab | 0.54 a |
| F-value | 8.307 | 1.784 | 6.961 |
| Std. Error | 0.368 | 0.767 | 0.546 |

*P< 0.05 **P< 0.01

Nitrogen and phosphorus concentrations of *C. creticus* changed with respect to study period and along the elevation gradient. N concentration was higher in July ($28 \mu\text{g cm}^{-2}$) and at 670 m ($44 \mu\text{g cm}^{-2}$) (Figs. 2a, 2b). The lowest N concentration was found in September ($25.3 \mu\text{g cm}^{-2}$) and at 30 m ($38 \mu\text{g cm}^{-2}$). The highest P concentration ($37.5 \mu\text{g cm}^{-2}$) was determined at 880 m, while the lowest P concentration ($34 \mu\text{g cm}^{-2}$) was found at 670 m (Figs. 2c, 2d). In the present study, it was found that mature leaf nutrients was higher than in senescent leaf. There were significant differences during the study period ($p < 0.01^{**}$), whereas there were no significant differences along the elevational gradient (Tabs. 2, 4).

Tab. 4. The comparison of the elevation gradient in N, P, specific leaf area (SLA) and leaf mass area (LMA) in *C. creticus* by using one-way ANOVA.

| Parameter | | Sum of Square | df | Mean square | F | Sig. |
|-----------|----------------|---------------|-----|-------------|-------|---------|
| N | Between Groups | 441.810 | 2 | 220.905 | 1.320 | 0.270NS |
| | Within Groups | 26601.618 | 159 | 167.306 | | |
| | Total | 27043.428 | 161 | | | |
| P | Between Groups | 0.318 | 1 | 0.318 | 5.661 | 0.020NS |
| | Within Groups | 4.442 | 79 | 0.056 | | |
| | Total | 4.760 | 80 | | | |
| SLA | Between Groups | 0.035 | 1 | 0.035 | 1.486 | 0.226NS |
| | Within Groups | 1.844 | 79 | 0.023 | | |
| | Total | 1.878 | 80 | | | |
| LMA | Between Groups | 0.502 | 1 | 0.502 | 0.282 | 0.597NS |
| | Within Groups | 140.561 | 79 | 1.779 | | |
| | Total | 141.063 | 80 | | | |

*P< 0.05 **P< 0.01 NS: Not Significant

Significant correlations were found among N, P and N/P ($p < 0.01^{**}$, $p < 0.05^{*}$) (Tab. 5). Strong positive correlations were reported between green-leaf N concentration and N/P and N contents, respectively for *C. creticus*. However, significant differences were found along the elevational gradient and during the growth period in respect to the N/P ratio. Negative correlations were found between green-leaf P concentrations and the N/P ratio (Tab. 5). N/P ratios of *C. creticus* were > 16 at only at 30 m, but < 14 at 670 and 880 m, respectively. Except for March, June and July the N/P ratio was < 14 during the study period (Tab. 6).

Nitrogen and phosphorus resorption efficiency and resorption proficiency

The highest N resorption efficiency (85.60) was found at 30 m, while the lowest N resorption efficiency value (80.36) was found at 880 m (Fig. 2e). The highest and lowest N resorption proficiency (11.18, 4.85) were found at 670 and 30 m, respectively (Figs. 2g). However, the highest P resorption efficiency (78) was found at 670 m while the lowest P resorption efficiency value (53.48) was found at 30 m (Figs. 2f). The highest and lowest P resorption proficiency (1.95, 0.79) were found at 30 and 880 m, respectively (Fig. 2h).

Chlorophylls (Chl a, Chl b, Chl a + b, Chl a/b)

It was found that chlorophyll content of *C. creticus* changed both seasonally and along the elevational gradient (Tab. 7, Figs. 3a, b, c, d). In *C. creticus*, the highest chl a content was found in October ($38 \mu\text{g cm}^{-2}$) and at 880 m ($28 \mu\text{g cm}^{-2}$), while the lowest chl a content was found in November ($13 \mu\text{g cm}^{-2}$) and at 670 m ($17 \mu\text{g cm}^{-2}$) (Figs. 3a, b).

The highest chl b content of *C. creticus* was observed in June ($70 \mu\text{g cm}^{-2}$) and at 880 m ($9.7 \mu\text{g cm}^{-2}$) while the lowest chl b was found in August ($17.5 \mu\text{g cm}^{-2}$) and at the 670 m ($8.2 \mu\text{g cm}^{-2}$) (Figs. 3c, d). Chl a and chl b values exhibited significant changes seasonally and along the elevational gradient. chl a + b content was higher in June ($73 \mu\text{g cm}^{-2}$) and at 670 m ($37 \mu\text{g cm}^{-2}$) (Figs. 3e, f), while the lowest chl a/b content was found in July ($0.49 \mu\text{g cm}^{-2}$) and at 880 m ($1.08 \mu\text{g cm}^{-2}$), respectively (Figs. 3g, h).

Seasonal chl a, chl b, chl a + b and chl a/b of *C. creticus* are compared in table 8 and 9, using one way anova and Tukey's HSD. According to statistical analysis there were significant differences in terms of seasonal variation ($p < 0.01^{**}$, $p < 0.05^{*}$) but no significant differences along the elevational gradient (Tabs. 8, 9).

Tab. 5. Pearson correlations among N, P content and N/P in *C. creticus* ($^{**}p < 0.01$; $^{*}p < 0.05$)

| | N | P | N/P |
|-----|--------|----------|----------|
| N | 1.000 | 0.059 | 0.199* |
| P | 0.059 | 1.000 | -0.289** |
| N/P | 0.199* | -0.289** | 1.000 |

Tab. 6. N/P ratio in *C. creticus* along the elevational gradient

| | N/P | |
|----------|-----------|--------------|
| Locality | 30m | 18.89 > 16 |
| | 670m | 13.65 < 14 |
| | 880m | 10.07 < 14 |
| Months | March | 18.47 > 16 |
| | April | 13.72 < 14 |
| | May | 15.92 < 14 |
| | June | 16.51 > 16 |
| | July | 20.34 > 16 |
| | August | 12.16 < 14 |
| | September | 9.73 < 14 |
| | October | 5.15 < 14 |
| | November | 2.87 < 14 |

Tab. 7. The comparison of the monthly changes in Chl a, Chl b, Chl a+b, Chl a/b in *C. creticus* by using one-way ANOVA.

| Parameter | | Sum of Square | df | Mean square | F | Sig. |
|-----------|----------------|---------------|----|-------------|--------|---------|
| Chl a | Between Groups | 1478.563 | 5 | 295.713 | 10.528 | 0.000** |
| | Within Groups | 1348.237 | 48 | 28.088 | | |
| | Total | 2826.800 | 53 | | | |
| Chl b | Between Groups | 21111.373 | 5 | 4222.275 | 64.882 | 0.000** |
| | Within Groups | 3123.641 | 48 | 65.076 | | |
| | Total | 24235.015 | 53 | | | |
| Chl a+ b | Between Groups | 15462.828 | 5 | 3092.566 | 21.764 | 0.000** |
| | Within Groups | 4262.787 | 30 | 142.093 | | |
| | Total | 19725.615 | 35 | | | |
| Chl a/b | Between Groups | 13.720 | 5 | 2.744 | 6.029 | 0.001* |
| | Within Groups | 13.653 | 30 | 0.455 | | |
| | Total | 27.373 | 35 | | | |

*P< 0.05 **P< 0.01 NS: Not Significant

Tab. 8. The comparison of the monthly changes in Chl a, Chl b, Chl a+b, Chl a/b in *C. creticus* by using Tukey's HSD test.

| Months | Chl a | Chl b | Chl a+b | Chl a/b |
|------------|---------|---------|---------|---------|
| June | 23.40 a | 45.57 a | 70.07 a | 0.65 b |
| July | 23.53 a | 55.00 a | 62.26 a | 0.47 b |
| August | 12.90 b | 7.00 b | 21.20 b | 1.89 a |
| September | 11.16 b | 4.63 b | 21.49 b | 2.15 a |
| October | 15.51 b | 11.79 b | 26.06 b | 1.71 ab |
| November | 11.16 b | 13.35 b | 21.64 b | 1.60 ab |
| F-value | 10.528 | 64.882 | 21.764 | 6.029 |
| Std. Error | 2.49 | 3.80 | 6.88 | 0.38 |

*P< 0.05 **P< 0.01

Discussion

It has been found that foliar nutrient contents of deciduous species in the early growing season are high. These values are stable from mid-growing season to the beginning of senescence, but low in the beginning of abscission. Similar results were reported for some evergreen species. However, foliar nutrient concentrations for some evergreen species increase in the abscission phases (KUTBAY and KILINÇ 1994, HEVIA et al. 1999). In deciduous species the most mature phases of leaf are mid-summer (DIAZ and CABIDO 1997). However, in evergreen species fully-expanded leaves are found in the middle of spring but this phase may change according to climatic factors (HEVIA et al., 1999). There were notable seasonal

Tab. 9. The comparison of the elevation gradient in Chl a, Chl b, Chl a+b, Chl a/b in *C. creticus* by using one-way ANOVA.

| Parameter | | Sum of Square | df | Mean square | F | Sig. |
|-----------|----------------|---------------|----|-------------|-------|----------|
| Chl a | Between Groups | 398.7 | 5 | 199.3 | 4.187 | 0.201 NS |
| | Within Groups | 2428.1 | 48 | 47.6 | | |
| | Total | 2826.8 | 53 | | | |
| Chl b | Between Groups | 890.5 | 2 | 445.3 | 0.973 | 0.385 NS |
| | Within Groups | 23344.5 | 51 | 457.7 | | |
| | Total | 24235.0 | 53 | | | |
| Chl a+ b | Between Groups | 609.1 | 2 | 304.5 | 0.526 | 0.596 NS |
| | Within Groups | 19116.5 | 33 | 579 | | |
| | Total | 19725.6 | 35 | | | |
| Chl a/b | Between Groups | 0.2 | 2 | 0.1 | 0.137 | 0.873 NS |
| | Within Groups | 27.1 | 33 | 0.8 | | |
| | Total | 27.4 | 35 | | | |

* $P < 0.05$ ** $P < 0.01$ NS: Not Significant

variations in N and P concentrations in *C. creticus*. The N and P dynamics of *C. creticus* are a bit different from similar species (i.e. *Cistus laurifolius*) and N concentration peaked in July, while P concentration peaked in August. In other words, a summer peak was observed in both N and P concentrations. Peak concentrations of N and P of similar species in Mediterranean region were May and March for N and P, respectively, on an area basis and this may be due to differences in phenological patterns. However, the overall pattern for P concentrations was quite similar to that of *C. laurifolius* (MILLA et al. 2004). Foliar N and P concentrations in the present study were low in the early growing season as compared to the mid-growing season. Although P concentrations declined, N concentrations increased in the senescence period (Figs. 2a, c).

HOBBIE and GOUGH (2002) stated that species with short leaf lifespans (deciduous trees, sedges, and forbs) have higher foliar nutrient concentrations than evergreen species. However, N and P resorption efficiency values in the present study were found to be higher than that of other evergreen species (Fig. 2e). A longer leaf life span is regarded as a mechanism for conserving nutrients since it reduces the loss of minerals during leaf abscission (LIMA et al. 2006).

The greater the resorption efficiency, the more nitrogen is reused by the plant (CORTE et al. 2009). N resorption efficiency was higher at 30 m in *C. creticus* and decreased along the elevational gradient. However, P resorption efficiency was higher at 670 m. *C. creticus* individuals effectively used nitrogen at low elevations, whilst phosphorus was effectively used at high elevations. It has been hypothesized that N and P resorption efficiency usually decreased as nutrient concentrations in green leaves increased (RATNAM et al. 2008). N and P resorption efficiency usually and green leaf N and P concentrations in *C. creticus* leaves supported that hypothesis.

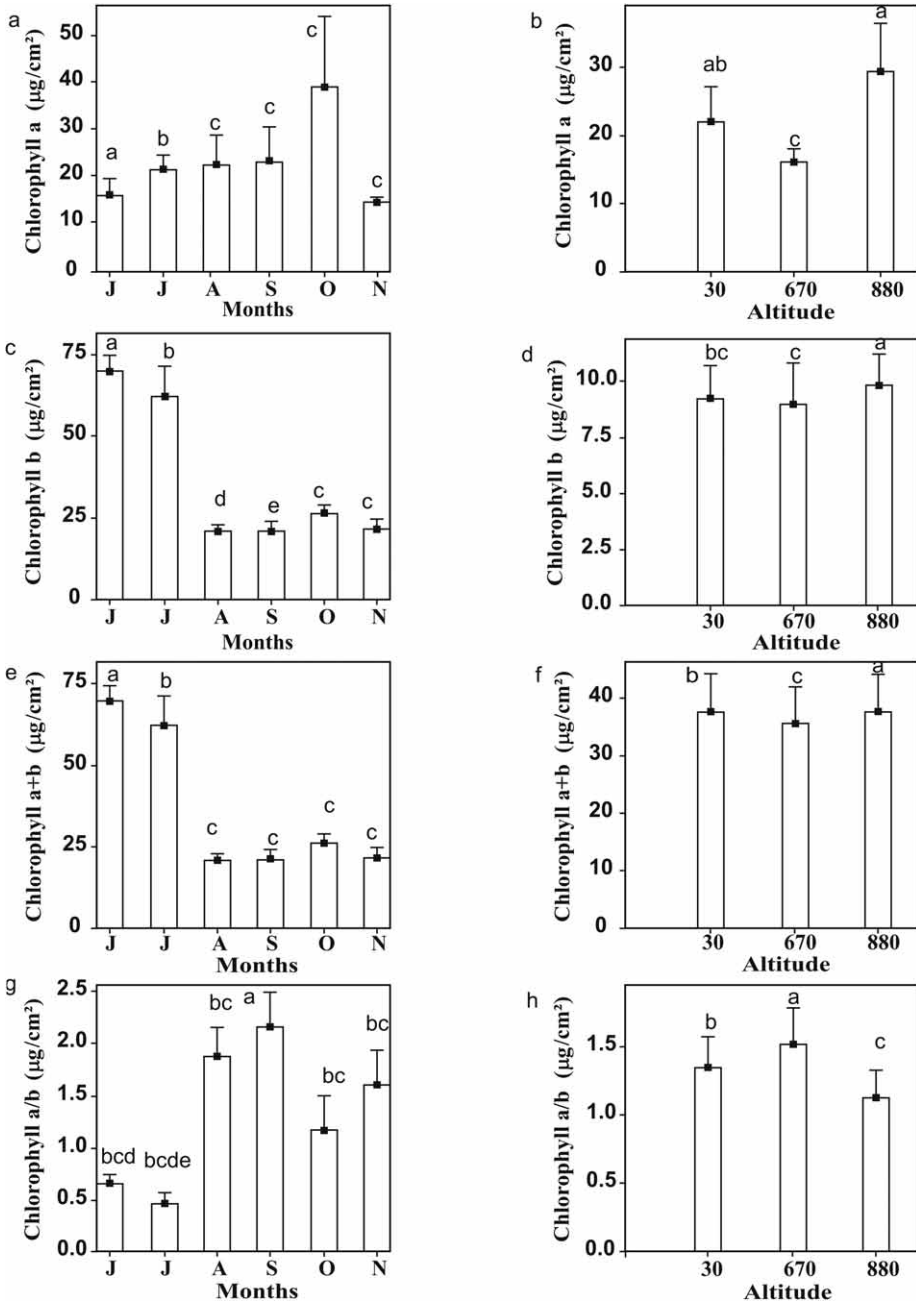


Fig. 3. Pigment content ($\mu\text{g cm}^{-2}$). Seasonal chlorophyll *a* content (a), along the elevational gradient (b), seasonal chlorophyll *b* content (c), chlorophyll *b* content along the elevational gradient (d), seasonal chlorophyll *a+b* content (e), chlorophyll *a+b* content along the elevational gradient (f), seasonal chlorophyll *a/b* content, chlorophyll *a/b* content along the elevational gradient (Standard errors are indicated. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test).

In some evergreen species, N resorption efficiency values were found to range from 25.7% – 75.1% (KILLINGBECK and COSTIGAN 1988, HEVIA et al. 1999, MEDIAVILLA and ESCUDERO 2003, ESCUDERO et al. 1992, KUTBAY et al. 2003, ÖZBUCAK et al. 2008). Woody evergreens show a higher resorption than deciduous species because mature evergreens have lower nutrient concentrations than deciduous leaves (KILLINGBECK 1996). In some deciduous species like *Quercus suber*, *Populus nigra* and *Frangula alnus* N resorption efficiency was found to be 47.9, 62.6 and 61.6, respectively (ESCUDERO et al. 1992). In the present study, N and P resorption efficiency values of evergreen *C. creticus* were found that are higher than those of other evergreen species (KILLINGBECK and COSTIGAN 1988, ESCUDERO et al. 1992). The N and P resorption processes are more efficient due to the higher N and P concentrations before senescence (MILLA et al. 2004).

Low N and P concentrations were found in some deciduous species at high elevations. However, it was found that N and P concentrations in evergreen species increased along an elevation gradient (HEVIA et al. 1999). Similar results were observed in the present study for the evergreen *C. creticus* (Figs. 2b, 2d). This may probably be due to the decrease of soil moisture along the elevational gradient (KUTBAY and OK 2003).

Resorption proficiency is considered a more stable indicator of the plant capacity to re-use nutrients than resorption efficiency (KILLINGBECK 1996, LIMA et al. 2006). According to KILLINGBECK (1996) N and P resorption proficiencies are high when they are below 50 g cm⁻² and 3 g cm⁻², respectively. Based on these threshold values N and P resorption proficiencies are biochemically complete in *C. creticus* (Figs. 2 g, h).

N/P ratios are more important than N and P concentrations in terms of mineral nutrition (GUSEWELL 2005). If N/P < 14, N-limitation is present. However, if N/P > 16, P-limitation is present (KOERSELMAN and MEULEMAN 1996). In present study, the N/P ratio of *C. creticus* was found to be below 14 at 30, 670 and 880 m, whilst the N/P ratio was found to be > 16 at 30 m (Tab. 6). As a result of this, P-limitation is present at low elevations, while the N-limitation is present at high elevations. N and P resorption efficiency in *C. creticus* were quite high as compared to the other evergreen species, which may probably be due to N- and P-limitation along the elevational gradient (Tab. 6).

Chlorophyll *a* is located only in the reaction centres of the photosystems, while Chl *b* is located both in the reaction centres and the light harvesting complexes (LIN et al. 2005). A change in the Chl *a/b* ratio reflects an adaptation mechanism to balance the amount of light captured by the leaf and its utilization for photochemical processes (LIN et al. 2005).

FILELLA and PEÑUELAS (1999) found that chlorophyll concentrations were not significantly changed along the elevational gradient. However, COVINGTON (1975) and RICHARDSON and BERLYN (2002) found chlorophyll concentrations changed significantly along the elevational gradient, which the present study confirms. These results are further evidence of the usefulness of reflectance measures for the rapid and noninvasive detection of plant stress (RICHARDSON and BERLYN 2002).

Chlorophyll *a* and *b* contents were curvilinear in style. Similar results were reported for the chlorophyll *a* and *b* contents in *Phyllostachys pubescens* (LIN et al. 2005). Chl *a*, *b* content and Chl *a+b* content of mature leaves was higher in summer than in autumn with respect to leaf growth phases ($P < 0.01$) (Figs. 3a, c, e). Chlorophyll *a* content was higher at 30 m and 880 m (Fig. 3b), while chlorophyll *b* was higher at 880 m (Fig. 3d). Chl *a+b* content

was similar in all the elevations (Figs. 3e, f). Chl *a/b* ratio of mature leaves was higher in autumn than summer with respect to leaf growth phases ($P < 0.01$) (Figs. 3g, h). In particular, Chl *b* content declined more than that of Chl *a* (Figs. 3a, b, c, d). Similar results were found in some studies (LIN et al. 2005). SCHEUMAN et al. (1999) observed that the Chl *a/b* ratio of barley seedling increased during senescence from 2.9 at day 0 to 5 at day 8, and suggested that either degradation of Chl *b* was faster than that of Chl *a* or that Chl *b* was transformed into Chl *a*. GOSSAUER and ENGEL (1996) proposed that the conversion of Chl *b* to Chl *a* should precede chlorophyll degradation in higher plants. LIN et al. (2005) reported a chlorophyll content decrease but a Chl *a/b* ratio increase during leaf senescence. In the present study the Chl *a/b* ratio increased in August, September and October (Fig. 3g). Chlorophyll a and b contents were decreased after senescence due to vulnerability to winter stress and the chl *a/b* ratio was compatible to the shade acclimation hypothesis, which indicates the increasing shade characteristics of leaves (ZELIOU et al. 2009).

The resorbed nitrogen may be used for the synthesis of chlorophyll a (JAIN and GADRE 2004). Leaf ecological and physiological traits are important factors to define plant photosynthetic rates. These traits also play an important role in determining the nutrient cycle.

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