

SOME ECOLOGICAL TRAITS AND RELATIONSHIPS OF THESE TRAITS WITH WOOD ANATOMY IN *QUERCUS PONTICA* C. KOCH

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Abstract

The ecological traits and relationships of these traits with wood anatomy of *Quercus pontica* C. Koch were examined. Despite some minor differences in wood anatomy *Q. pontica* is entirely within the range of wood anatomical variation of *Quercus*. For instance, *Q. pontica* has ring porous or semi-ring porous xylem anatomy like other oaks. There were no striking differences between the diameter of earlywood and latewood vessels and relatively low number of multiseriate rays were observed as compared to the other oak species in *Q. pontica* and the other prominent feature is multiseriate rays were not so wide and so long as compared to the other oak species. In addition to this, significant differences were found between full-leaf expansion and senescence in terms of N and P concentrations. Despite some differences proportional and absolute resorption were usually within the ranges reported for the other deciduous species.

Introduction

Quercus L., comprises of 531 tree and shrub species distributed among contrasting phytoclimates in the Northern Hemisphere, from temperate and subtropical deciduous forests to Mediterranean evergreen woodlands. Thus, they occupy habitats of widely varying moisture-supply capacity (Corcuera *et al.*, 2002).

Quercus pontica C. Koch is a deciduous tall shrub, low to medium height c. 3-5 m, with lax habit; young shoots glabrous, reddish-brown; buds ovoid, pubescent, scales with dark margins (Fig. 1). Leaves mostly at ends of branches, elliptic to broadly elliptic, 10-26 (-30) x 5-13 (-15) cm, \pm regularly serrate with 20-30 acute teeth, acute at apex, cuneate below; primary veins to c. 30, parallel, prominent; intercalary veins absent; upper surface glabrous, dark green, lower surface paler with scattered hairs on veins; petiole 1-2 cm. Fruits clustered on short stout peduncles at ends of branches. Cupule hemispherical, 15-20 mm diameter, brownish; scales triangular-ovate, acuminate with adpressed pits, pubescent; acorn $\frac{3}{4}$ exserted and belonging to the section of white Oak (Davis, 1982). Sapwood and heartwood differentiated, heartwood a little darker than sapwood.

Q. pontica is an Euxine element and a relict species, varying little in its characters and quite distinct among all the other Turkish oaks on account of the very large, regularly serrate leaves with numerous prominent parallel veins (Quézel *et al.*, 1980). This species is distributed in a restricted area as compared to the other oak species and occurs in the A8 square in Turkey according to the grid system of Davis (1982).



Fig. 1. General feature of *Q. pontica*.

The allocation of nutrients especially nitrogen within a tree have profound impacts on the physiology, growth and distribution of tree species. Tissue nitrogen concentration and allocation greatly influence the ecophysiology of species. Foliar nitrogen concentration is correlated with photosynthetic rates (Reich *et al.*, 1995; Martin *et al.*, 1998). Foliar nutrient content is widely recognized as an effective measure of the nutritional status of plants because leaves are the primary sites of physiological activity including photosynthesis, respiration, transpiration, gas exchange and nutrient storage (Orgeas *et al.*, 2002).

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 behaviour leads to a tight circulation in the ecosystem (Vitousek 1982). One of the most important methods to measure nutrient use efficiency in plants is to determine foliar resorption, the process of nutrient translocation from the leaves into storage tissues during senescence (Killingbeck & Costigan 1988).

The main objective of this study is to examine the relationships with wood anatomy and ecological traits of *Q. pontica* because wood anatomy has played a key role in ecological and habitat shifts within the genera and families (Carlquist 2003). In addition to this, foliar nitrogen, phosphorus and carbon concentrations were determined during full-leaf expansion and senescence and foliar resorption of *Q. pontica* was also investigated to compare proportional and absolute resorption with the other deciduous and evergreen species.

Materials and Methods

Study area and collection of samples for anatomical and ecological studies: This study was carried out around Trabzon (Hemşin pasture) and Rize (Cimil pasture) cities in which pure *Q. pontica* stands were found. These two cities are situated in the northeastern part of Turkey (Fig. 2).

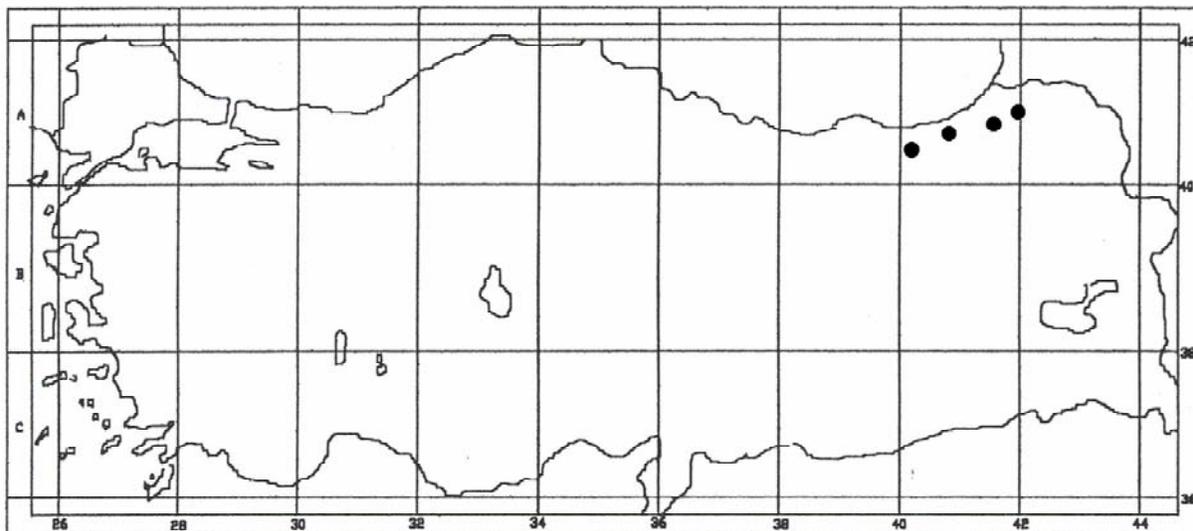


Fig. 2. The distribution of *Q. pontica* in Turkey.

Five 20x20 m plots was sampled. Plots were in homogeneous stands of vegetation on northwest facing slopes. Individuals of *Q. pontica* were selected ≥ 3 m. from the stems of neighboring canopy trees to avoid potential microsite variation, and they were also flagged (Boerner 1984; Kost & Boerner 1985; Boerner & Koslowsky 1989; Minoletti & Boerner 1994). Sampled leaves were fully developed and free of diseases and insect damage.

The height of all *Q. pontica* individuals and GBH (circumference at breast height) was measured. The number and the width of annual rings were recorded and for anatomical purposes, 1.5 x 1.5 x 1.5 cm blocks from the wood were removed and they were boiled. After that, transverse, radial and tangential slides were made. Material was softened in Ethylene diamine, followed by sectioning on a rotary microtome with a modified paraffine method (Carlquist 1982). Macerations were made by using Schulze method (nitric acid: potassium chlorate). Slides were stained with safranin O and FCF (Fast Green).

The terms are in accordance with the IAWA Committee on Nomenclature (Anon., 1964) and the qualitative and quantitative techniques were done according to Normand (1972) and Bozkurt (1992).

Since sun and shade leaves may differ in foliar nutrient concentrations, only outer sun leaves were collected (Grubb 1977). Deciduous forest species usually reached to full leaf expansion phase during early to mid-summer (Díaz & Cabido, 1997). Five fresh leaves from throughout the crown of individual plants were taken during full leaf expansion (July 1998). Five brown, dry and fully senesced leaves were also collected at the second half of October. Leaves of the studied species were harvested from the canopy with a pole pruner.

Methods of chemical analysis: Leaf samples were dried at 70° C until constant weight, grounded 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 Kjeltac Auto 1030 Analyser (Tecator, Sweden) after digesting the samples in concentrated H₂SO₄ with a Se catalyst. P was determined by the stannous chloride method by using a Jenway spectrophotometer. Carbon (%) content was determined by using a LECO SC-144 DR model C-S determinator (Allen *et al.*, 1986; Bayraklı, 1987).

Nutrient concentrations in mature leaves were expressed on a leaf mass basis (mg/g). Absolute resorption was calculated as the difference between N and P concentrations of leaves at the time of full leaf expansion and that of N and P concentrations of senesced leaves. 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 (De Mars & Boerner 1997; Hevia *et al.*, 1999).

Chapin & Kedrowski (1983) indicated leaching was much less important than resorption in removing nutrients from senescing leaves. So potential N and P losses due to leaching were not measured. Leaching experiments indicated that less than 1 % of the autumnal reductions of N and P could have been due to leaching of foliage by precipitation (Killingbeck 1986; Killingbeck & Costigan 1988).

Taxonomic nomenclature followed that of Davis (1982) and Brummitt & Powell (1992).

Statistical analyses: One-way ANOVA test was performed whether or not N (mg/g), P (mg/g) and C (%) concentrations change with respect to leaf growth stage by using SPSS 10.0 version (Schaeffer & Anderson 1989; Anon., 1999). Dependent and independent variables were N, P and C concentrations and leaf growth stages, respectively.

Results

Anatomical traits: Detailed wood anatomical traits belonging to vessels, imperforate tracheary elements, vasicentric tracheids, axial parenchyma and rays of *Q. pontica* were given by Yilmaz *et al.* (2008).

The mean F/V ratio (ratio of length of libriform fibres to length of vessel elements) ranged from 2.03 to 2.23 in *Q. pontica*. In addition to this, *Q. pontica* had the highest number of apotracheal parenchyma in mm² as compared to other oak species. One of the most prominent features with respect to wood anatomy is high number of uniseriate rays (99.9%). The number of multiseriate rays (including biseriate rays) were lower as compared to uniseriate rays (Yilmaz *et al.*, 2008).

Ecological traits: Full-leaf expansion leaf P concentration in *Q. pontica* associated with values observed in the literature for broadleaf deciduous trees varied between 0.4 to 1.0 P (mg/g). However, full leaf expansion N concentration in *Q. pontica* was a bit higher than that of the values reported for other broadleaf deciduous trees, and varied between 10 to 16 N (mg/g). There were significant differences between full-leaf expansion and senescence in terms of N, P and C concentrations (Table 1).

Absolute and proportional foliar resorption are shown in Table 2. In addition to this, significant correlations were observed between foliar N and P concentrations and absolute and proportional resorption during both full-leaf expansion and senescence except for foliar N concentration and absolute N resorption during senescence (Table 3). Proportional N resorption values were usually lower than that of the other deciduous species. However proportional P resorption values were usually higher than that of the other deciduous species (Table 4).

Table 1. N (mg/g), P (mg/g) and C (%) concentrations during full-leaf expansion and senescence in *Q. pontica*.

| Nutrient | Growth period | | F-value |
|----------|---------------------|--------------|----------|
| | Full-leaf expansion | Senescence | |
| N (mg/g) | 24.90 ± 0.12 | 13.78 ± 0.15 | 30.071** |
| P (mg/g) | 0.57 ± 0.05 | 0.18 ± 0.02 | 44.559** |
| C (%) | 38.63 ± 1.02 | 35.84 ± 1.09 | 20.595** |

**p<0.01

Table 2. Absolute (mg/g) and proportional (%) resorption (± standard errors) in *Q. pontica*.

| Parameter | Mean (± standard error) |
|---------------------------|-------------------------|
| Absolute N resorption | 12.11 ± 2.25 |
| Proportional N resorption | 48.61 ± 8.78 |
| Absolute P resorption | 0.38 ± 0.06 |
| Proportional P resorption | 66.86 ± 6.72 |

Table 3. Pearson correlation coefficients between foliar N and P concentrations and absolute and proportional resorption rates.

| Parameter | Correlation Coefficient | Significance |
|---|-------------------------|--------------|
| Foliar N in mature leaves-absolute N resorption | -0.842 | ** |
| Foliar N in mature leaves-proportional N resorption | 0.645 | ** |
| Foliar P in mature leaves-absolute P resorption | -0.557 | ** |
| Foliar P in mature leaves-proportional P resorption | 0.952 | ** |
| Foliar N in senescence leaves-absolute N resorption | -0.188 | NS |
| Foliar N in senescence leaves-proportional N resorption | 0.777 | ** |
| Foliar P in senescence leaves-absolute P resorption | 0.659 | ** |
| Foliar P in senescence leaves-proportional P resorption | 0.953 | ** |

NS: Not significant ** p<0.01

Discussion

Despite some minor differences in wood anatomy, *Q. pontica* is entirely within the range of wood anatomical variation of *Quercus*. For instance, *Q. pontica* has ring porous or semi-ring porous xylem anatomy like other oaks. Ring-porous xylem anatomy allows rapid sap movement in large diameter, early-wood vessels when soil water plentiful and slower, but sustained, water movement in narrower late-wood vessels which are more resistant to cavitation, during drought (Abrams, 1990; Corcuera *et al.*, 2004). Similarly Yilmaz *et al.* (2008) found significant correlations between soil variables and wood anatomical traits in *Q. pontica*.

According to the “limited growth hypothesis” for ring or semi-ring porous wood has led to a decrease in the intensity of vegetative growth, which was accompanied by reduced levels of growth regulators. The latter was followed by an increase in sensitivity of the cambium to relatively low levels of internal stimulators. Therefore, extremely low hormonal levels can influence the anatomy of the xylem in a ring-porous tree and causes limited xylem production (Aloni *et al.*, 1997).

Table 4. Proportional (%) N and P foliar resorption for some deciduous and evergreen species.

| Species | Leaf habit | N | P | Locality | Source |
|------------------------------|------------|-------|-------|---------------------|-----------------------------|
| <i>Quercus pontica</i> | Deciduous | 48.6 | 66.8 | Northeastern Turkey | Present study |
| <i>Quercus ilicifolia</i> | Deciduous | 70.0 | 59.1 | Rhode Island | Killingbeck & Costigan 1988 |
| <i>Q. rubra</i> | Deciduous | 70.0 | 55.0 | Southern Québec | Côte <i>et al.</i> , 2002 |
| <i>Viburnum cotinifolium</i> | Deciduous | 55.7 | 48.5 | India | Ralhan & Singh 1987 |
| <i>Fagus sylvatica</i> | Deciduous | 72.0 | 70.0 | Sweden | Staaf 1982 |
| <i>F. grandifolia</i> | Deciduous | 62.0 | 77.0 | Southern Québec | Côte <i>et al.</i> , 2002 |
| <i>F. orientalis</i> | Deciduous | 73.4 | 72.9 | Northeastern Turkey | Kutbay <i>et al.</i> , 2003 |
| <i>Acer saccharum</i> | Deciduous | 66.0 | 78.0 | Southern Québec | Côte <i>et al.</i> , 2002 |
| <i>Fraxinus americana</i> | Deciduous | 59.0 | 54.0 | Southern Québec | Côte <i>et al.</i> , 2002 |
| <i>Populus grandidentata</i> | Deciduous | 68.0 | 60.0 | Southern Québec | Côte <i>et al.</i> , 2002 |
| <i>Corylus avellana</i> | Deciduous | 39.6 | 14.0 | Poland | Zimka & Stachurski 1992 |
| <i>Lonicera maackii</i> | Deciduous | 33.6 | 40.2 | Ohio | De Mars & Boerner 1997 |
| <i>Vaccinium vacillans</i> | Deciduous | 25.7 | 29.1 | Rhode Island | Killingbeck & Costigan 1988 |
| <i>V. arctostaphylos</i> | Deciduous | 28.52 | 51.75 | Northeastern Turkey | Kutbay <i>et al.</i> , 2003 |
| <i>Nothofagus pumilio</i> | Deciduous | 62.7 | 43.8 | Central Chile | Hevia <i>et al.</i> , 1999 |
| <i>Rh. luteum</i> | Deciduous | 55.8 | 79.71 | Northeastern Turkey | Kutbay <i>et al.</i> , 2003 |
| <i>D. pontica</i> | Evergreen | 51.14 | 57.37 | Northeastern Turkey | Kutbay <i>et al.</i> , 2003 |
| <i>Quercus ilex</i> | Evergreen | 33.0 | 43.0 | Spain | Mayor & Rodà 1992 |

Earlywood vessels have a bit larger than that of latewood vessels and they do not constitute to a continuous ring. Earlywood and latewood vessels constitute to radial and oblique serials towards the end of annual rings. Perforation plates are simple. Vessel-ray pits with reduced borders or apparently simple, rounded or angular or horizontal to vertical and tyloses in vessels are present, thinwalled like other *Quercus* species. Rays both broad and narrow. Broad rays are very evident on both the tangential and cross sections and appear as a very conspicuous fleck on the radial surface like other *Quercus* species. Porosity patterns with weakly expressed earlywood pore zones occur in many Mediterranean species. Ray width and height vary widely within the genus and also within individual species and even individual plants (Carlquist, 2003).

Rays were uniseriate or biseriate. Uniseriate rays were abundant. However, lower number of multiseriate rays were observed than the other oak species in *Q. pontica* and the other prominent feature is multiseriate rays were not so wide and so long as compared to the other oak species (Kasaplıgil, 1992; Yılmaz et al. 2008). Bordered pits were also observed between vessel and parenchyma like in other *Fagaceae* members. However, in oak species simple pits were present between vessel and parenchyma. In *Q. pontica* simple pits of paratracheal parenchyma were bigger than that of the simple pits of apotracheal parenchyma and they were elliptical. Intervessel pits are round and alternate (Yılmaz et al., 2008). Vasicentric tracheids are surround vessels and best known in *Quercus* species like in *Q. pontica*, although they occur in many other dicotyledons (Carlquist, 2001).

The mean F/V ratio (ratio of length of libriform fibres to length of vessel elements) was found to be ranged from 2.03 to 2.23 in *Q. pontica*. In dicotyledons, in general the mean vessel element length and fibre length figures would give an F/V ratio of 2.03 and F/V ratio of *Q. pontica* was within the ranges reported for most dicotyledons (Carlquist, 2003).

There were significant differences between full-leaf expansion and senescence in terms of N and P concentrations. In general, macroelements especially nitrogen concentration in leaves is strongly correlated with photosynthetic capacity and it has been known that photosynthetic capacity was decreased during senescence and remobilization of mineral nutrients (except calcium and manganese) from leaves to woody parts (Feller & Fischer 1994; Marschner 1995). Orgeas et al., (2002) stated temporal variation which is regulated by leaf ageing processes was much more important in mineral nutrition than spatial variation which is regulated mainly by disturbance. Significant differences were also observed in some other deciduous species eg., canopy and subcanopy species in a *Fagus orientalis* Lipsky forest and a *Quercus cerris* L. var. *cerris* forest (Kutbay & Kılınc 1994; Kutbay et al., 2003). Full leaf expansion N concentration in *Q. pontica* was a bit higher than that of the values reported for other broadleaf deciduous trees (Schulze et al., 1994) and similar to the other oak species like *Q. alba*, *Q. prinus*, *Q. rubra* (Martin et al., 1998). Species with high foliar nitrogen concentrations may possess a competitive advantage. Nitrogen concentration has also been correlated with respiration like photosynthetic capacity in many plant species and tissues, suggesting that high levels of nitrogen during the growing season may lead to high photosynthate production and as a result of this low cellular maintenance respiration, thereby allowing an organism to maximize carbon gain (Martin et al., 1998).

C concentrations and proportional N resorption of *Q. pontica* were somewhat lower than those values reported for other deciduous forest species. However, proportional P resorption was usually higher than the other *Quercus* species and P resorption in *Q.*

pontica was more efficient than the other *Quercus* species. *Quercus* species obtain the bulk of their total carbon assimilation during a few weeks in late spring and early summer. A rapid deployment of the leaf biomass in *Quercus* species can therefore have a very high influence on total carbon gain for the whole of the year, since it allows these species to deploy their photosynthetic capability during the most favourable stages of the growth season. The only way of guaranteeing that the leaves begin to photosynthesize early in the favourable season is to maintain a strong relative growth rate, which may also be a good defense against the abundant herbivorous insects at this time of year (Albert & Pescoller-Tiefenthaler, 1992; Kutbay *et al.*, 2003; Mediavilla & Escudero, 2003).

Although, Aerts (1996) pointed out that relations between leaf nutrient status and leaf nutrient resorption were very weak, Hevia *et al.*, (1999) showed that such a relationship does exist, at least for N. The observation of significant correlations between foliar N and P concentrations and absolute and proportional resorption during both full-leaf expansion and senescence except for foliar N concentration and absolute N resorption during senescence indicated that there were some relations between leaf nutrient status and leaf nutrient resorption in *Q. pontica*. Côté *et al.*, (2002) also found some relations between leaf nutrient status and leaf nutrient resorption. Future research should be done for more precise explanation of leaf nutrient status and leaf nutrient resorption in deciduous and evergreen species.

References

- Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.*, 7: 227-238.
- Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? *J. Ecol.*, 84: 597-608.
- Albert, R. and G. Pescoller-Tiefenthaler. 1992. Nutrient content and ionic pattern in beech (*Fagus sylvatica* L.) from natural stands in Eastern Austria and ecological implications. *Vegetatio*, 101: 81-95.
- Allen, S.E., H.M. Grimshaw, J.A. Parkinson, C. Quarmby and J.D. Roberts. 1986. Chemical Analysis: In: *Methods in Plant Ecology*. (Eds.): S. Chapman. 1: 411-466, Blackwell Scientific Publications, Oxford.
- Aloni, R., J.D. Alexander and M.T. Tyree. 1997. Natural and experimentally altered hydraulic architecture of branch junctions in *Acer saccharum* Marsh. and *Quercus velutina* Lam. trees. *Trees.*, 11: 255-264.
- Anonymous. 1964. The IAWA, Committee on Nomenclature. Multilingual glossary of terms used in wood anatomy. *Verlagsbuchanstalt Konkordia*, Winterthur.
- Anonymous. 1999. SPSS 10.0 for Windows. *SPSS Incorporation*. New York.
- Bayraklı, F. 1987. Plant and soil analysis. *University of Ondokuz Mayıs Publications*, Samsun.
- Boerner, R.E.J. 1984. Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to nutrient fertility. *J. Appl. Ecol.*, 21: 1029-1040.
- Boerner, R.E.J. and S.D. Koslowsky. 1989. Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest. *Soil Biol. Biochem.*, 21: 795-801.
- Bozkurt, Y. 1992. Wood Anatomy *Faculty of Forestry Publications*, İstanbul.
- Brummitt, R.K. and C.E. Powell. 1992. Authors of Plant Names. *Royal Botanic Gardens*, Kew.
- Carlquist, S. 1982. The use of thylene diamine in softening hard plant structures for paraffin sectioning. *Stain Tech.*, 57: 311-317.
- Carlquist, S. 2001. *Comparative wood anatomy*. Springer Verlag Publications, Heidelberg.
- Carlquist, S. 2003. Wood anatomy of woody Polygonaceae: analysis of a family with exceptional wood diversity. *Bot. J. Linn. Soc.*, 141: 1-19.

- Carlquist, S. 2003. Wood and stem anatomy of woody Amaranthaceae s.s.: ecology, systematics and the problems of defining rays in dicotyledons. *Bot. J. Linn. Soc.*, 143: 1-19.
- Chapin, F.S. and R.A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn resorption in evergreen and deciduous taiga trees. *Ecology*, 64: 376-391.
- Corcuera, L., J.J. Camarero and E. Gil-Pelegrín. 2002. Functional groups in *Quercus* species derived from the analysis of pressure-volume curves. *Trees*, 16: 465-472.
- Corcuera, L., J.J. Camarero and E. Gil-Pelegrín. 2004. Effects of a several drought on *Quercus ilex* radial growth and xylem anatomy. *Trees*, 18: 83-92.
- Côté, B., J.W. Fyles and H. Djalilvand. 2002. Increasing N and P resorption efficiency and proficiency in northern deciduous hardwoods with decreasing foliar N and P concentrations. *Ann. For. Sci.*, 59: 275-281.
- Davis, P.H. 1982. *Flora of Turkey and the East Aegean Islands*. Vol. 7. Edinburgh: *Edinburgh University Press*.
- De Mars, B.G. and R.E.J. Boerner. 1997. Foliar nutrient dynamics and resorption in naturalized *Lonicera maackii* (Caprifoliaceae) populations in Ohio, USA. *Amer. J. Bot.*, 84: 112-117.
- Díaz, S. and M. Cabido. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8: 463-474.
- Feller, U. and A. Fischer. 1994. Nitrogen metabolism in senescing leaves. *Crit. Rev. Pl. Sci.* 13: 241-273.
- Grubb, P.J. 1977. Control of forest growth and distribution on wet tropical mountains. *Ann. Rev. Ecol. Syst.* 8: 38-107.
- Hevia, F., M.L. Minoletti., K.L.M. Decker and R.E.J. Boerner. 1999. Foliar nitrogen and phosphorus dynamics of three Chilean *Nothofagus* (Fagaceae) species in relation to leaf lifespan. *Amer. J. Bot.*, 86: 447-455.
- Kasaplıgil, B. 1992. *Quercus* L. species in Turkey during present and past. - Turkish Ministry of Forestry Publications, İstanbul.
- Killingbeck, K.T. 1986. The terminological jungle revisited: making a case for use of the term resorption. *Oikos* 46: 263-264.
- Killingbeck, K.T. and S.A. Costigan. 1988. Nutrient resorption in a guild of understory shrub species: niche differentiation and resorption thresholds. *Oikos*, 53: 366-374.
- Kost, J.A. and Boerner R.E.J. 1985. Foliar nutrient dynamics and nutrient use efficiency in *Cornus florida* *Oecologia*, 66: 602-606.
- Kutbay, H.G. and M. Kılınç. 1994. Sclerophylly in *Quercus cerris* L. var. *cerris* and *Phillyrea latifolia* L., and edaphic relations of these species. *Vegetatio* 113: 93-97.
- Kutbay, H.G., E. Yalcın and A. Bilgin. 2003. Foliar N and P resorption and foliar nutrient concentrations in canopy and subcanopy of a *Fagus orientalis* Lipsky forest. *Belg. J. Bot.*, 136: 35-44.
- Marschner, H. 1995. Mineral nutrition of higher plants. *Academic Press Limited*, London.
- Martin, J.G., B.D. Kloeppel., T.L. Schaefer, D.L. Kimbler and S.G. McNulty. 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. *Can. J. For. Res.*, 28: 1648-1659.
- Mayor, X. and F. Rodà. 1992. Is primary production in holm oak forests nutrient limited? *Vegetatio*, 99: 209-217.
- Mediavilla, S. and A. Escudero. 2003. Relative growth rate of leaf biomass and leaf nitrogen content in several mediterranean woody species. *Pl. Ecol.*, 168: 321-332.
- Minoletti, M.L. and R.E.J. Boerner. 1994. Drought and site fertility effects on foliar nitrogen and phosphorus dynamics and nutrient resorption by the forest understory shrub *Viburnum acerifolium* L. *Amer. Mid. Nat.*, 131: 109-119.
- Normand, D. 1972. Manuel D'identification des Bois Commerciaux. *CTFT*, Paris.
- Orgeas, J. J.M. Ourcival and G. Bonin. 2002. Seasonal and spatial patterns of foliar nutrients in cork oak (*Quercus suber* L.) growing on siliceous soils in Provence (France) *Pl. Ecol.*, 164: 201-211.

- Quézel, P., M. Barbéro and Y. Akman. 1980. Contribution à l' étude de la végétation forestière d' Anatolie septentrionale. *Phytocoenologia*, 8: 365-519.
- Ralhan, P.K. and S.P. Singh. 1987. Dynamics of nutrients and leaf mass in central Himalayan forest trees and shrubs. *Ecology*, 68: 1974-1983.
- Reich, P.B., B.D. Kloeppel, D.S. Ellsworth and M.B. Walters. 1995. Difference photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia*, 104: 24-30.
- Schaefer, R.L. and R.B. Anderson. 1989. The student edition of MINITAB, User' s Manual. - *Addison Wesley Publishing Company*, New York.
- Schulze, E.D., F.M. Kelliher, C. Körner, J. Lloyd and R. Leuning. 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: A global scaling exercise. *Ann. Rev. Ecol. Syst.*, 25: 629-660.
- Staaf, H. 1982. Plant nutrient changes in beech leaves during senescence as influenced by site characteristics. *Oecol. Plant.*, 3: 161-170.
- Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. *Amer. Nat.*, 119: 553-572.
- Yilmaz M., B. Serdar, L. Altun and A. Usta. 2008. Relationships between environmental variables and wood anatomy of *Quercus pontica* C. Koch (Fagaceae). *Fres. Env. Bull.*, 17: 902-910.
- Zimka, J.R. and A. Stachurski. 1992. Intensity of resorption of macro- and micronutrients from ageing foliage of deciduous forest vegetation. *Ekol. Polsk.*, 40: 333-351.

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