JOURNAL OF FOREST SCIENCE, *62*, 2016 (10): 485–491

doi: 10.17221/56/2016-JFS

Physiological responses of seedlings of different *Quercus castaneifolia* C.A. Mey. provenances to heterogeneous light environments

F. Babaei[1], S.G. Jalali[1], H. Sohrabi[1], A. Shirvany[2]

[1]*Department of Forestry, Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, Nour, Iran*

[2]*Department of Forestry and Forest Economics, Faculty of Natural Resources, University of Tehran, Karaj, Iran*

ABSTRACT: In this study, five biochemical traits obtained for seedlings of five different provenances of *Quercus castaneifolia* C.A. Meyer were used to evaluate the available light environment using instantaneous electronic readings as a standard. Experimental design was executed under controlled conditions at six different irradiance levels (10, 20, 30, 50, 60, and 70% of full light). Results show that among total chlorophyll (Chl_{mass}), chlorophyll a to b ratio (Chl_a:Chl_b), N, chlorophyll to N ratio (Chl:N), and peroxidase (POD) quantitative activity, the latter provides the highest realistic correlation with available irradiance. Ranking irradiance treatments on a Chl_{mass} basis, Chl:N ratio, and Chl_a:Chl_b ratio do not consistently distinguish different irradiance levels either within or between provenances, while the ranking produced by POD was an accurate reflection of the degree of irradiance within the shade houses, especially at 10–30%.

Keywords: peroxidase quantitative activity; Hyrcanian forest; chlorophyll content

In natural conditions, the light filtered through the forest canopy is known as one of the most important and heterogeneous physical factors (Théry 2001) that influence plant physiology, morphology, and reproductive capacity. Light measurements are relatively difficult to perform in the forest because of the variable nature of stratified canopy (Dale, Causton 1992) and the high spatial and temporal variability of light (Théry 2001). Generally, plants have the ability to alter their morphological and physiological traits to maximize fitness according to the light environment (Poorter et al. 2000). They often change leaf properties and biomass allocation patterns in accordance with available light (Sugiura, Tateno 2011). Leaves react most sensitively to environmental factors such as soil moisture, nutrients, and irradiance (Roche et al. 2004; Sugiura, Tateno 2011); subsequently, the causal relationships between leaf traits and various environmental factors can be recognized.

Ideally, some characteristics of plant morphological and physiological leaf traits could be used as a measure of available light (Dale, Causton 1992; Poorter 1999; Rozendaal et al. 2006; Xu et al. 2008; Sugiura, Tateno 2011). Several parameters such as: (*i*) total chlorophyll expressed on a leaf area basis, (*ii*) a leaf dry weight basis, (*iii*) specific leaf area, (*iv*) ratio of chlorophyll a to chlorophyll b (Chl_a:Chl_b) were used in bioassays for measurements of the light environment in different studies (Dale, Causton 1992; Beneragama, Goto 2010; Sugiura, Tateno 2011). Dale and Causton (1992) suggested the ratio of Chl_a:Chl_b as a realistic bioassay for the light environment particularly for single species studies, because it is physiologically flexible, least influenced by external factors (e.g. water availability and soil magnesium status), and varies predictably with light. There is also evidence of genetic control over the Chl_a:Chl_b ratio (Dale, Causton 1992).

Isoenzyme markers, especially peroxidase, are common methods for the study of plant genetic diversity. They also serve as indicators of environmental heterogeneity (Bogdanović et al. 2007;

Petrokas, Stanys 2008; Clarke et al. 2009). Unfavourable conditions such as high irradiance intensities and temperature can cause an increase in the production of reactive oxygen species (ROS) such as $^1O_2$ and H_2O_2 in plant tissue during photosynthesis and other reactions of cellular metabolism (Asada 1994). An increase in peroxidase activity is considered a protective system composed of antioxidants (Zolfaghari et al. 2010). Despite several different applications of peroxidase, to the best of our knowledge, the use of peroxidase in a trait for a light gradient has received no attention to date.

Therefore, in this study, we evaluated physiological acclimation responses of *Quercus castaneifolia* C.A. Meyer, chestnut oak leaves, to a light gradient under controlled conditions along a precipitation gradient in the Hyrcanian vegetation zone in northern Iran. Chestnut oak is one of the most valuable species in Hyrcanian forests that is endemic in the Caucasus and this vegetation zone (Akhani et al. 2010). This species is a light-demanding deciduous tree distributed either in pure (4.6% of Hyrcanian forests) or mixed (1.9%) populations with hornbeam (*Carpinus betulus* Linnaeus) from the coastal plains to the highlands along the southern shore of the Caspian Sea from west to east (Sabeti 1994). Although there are examples of interspecific or inter-site comparisons of leaf morphological and physiological acclimation responses to light (Poorter 1999; Bloor, Grubb 2004; Gratani et al. 2006; Rozendaal et al. 2006), there are few multi-site studies. In the present study, we attempt to answer: (*i*) how leaves differ in their traits in different light levels, (*ii*) whether chestnut oak seedling acclimation responses to light vary in different provenances, (*iii*) which trait yields the best provenance and irradiance level separation.

MATERIAL AND METHODS

Characteristics of collected provenances. There are different precipitation regimes in the western and eastern parts of the Hyrcanian forest vegetation zone. Precipitation decreases gradually from west to east (Domoers et al. 1998). Annual rainfall in this region ranges from 2,045 mm in the west to 213 mm in the east, from (49.08°E, 37.58°N) to (55.7°E, 37.9°N), respectively, with high rainfall occurring in early autumn. The dry season ($P < 2T$, P – precipitation, T – temperature) is either very short or completely non-existent, especially in the western parts of the Hyrcanian forest. The large amount of rainfall over the south-central and south-western parts of the Caspian Sea and the lower amount of precipitation in the eastern parts result in a precipitation gradient in the region (Akhani et al. 2010).

To conduct this study, seed samples were collected from five provenances of chestnut oak from west to east of the Hyrcanian forests. The general characteristics of the studied sites are shown in Table 1.

Experiments were carried out in a greenhouse at the Faculty of Natural Resources and Marine Sciences of Tarbiat Modares University, located within the Hyrcanian forests (36°34'54"N, 52°02'32"E) in Mazandaran province (northern Iran). The climate is considered humid (Domoers et al. 1998). The area receives an average of 1,200 mm of precipitation per year in the form of rain at the lower and snow at the higher elevations with an average temperature of 17°C.

Light regime treatment. To study the growth response of chestnut oak seedlings to the light regime, six different irradiance levels, i.e. 10, 20, 30, 50, 60, and 70% of full light, were considered. The inside of the greenhouse was divided into six parts (shade houses). Each part was approximately 3.5 m long, 1.5 m wide and 2.2 m high. The six specified irradiance levels were created by covering the shade house walls with layers of neutral plastic which transferred 70% of full light, and the roofs with an increasing number of layers of neutral plastic. Each extra layer intercepted 10% of the incoming irradiance, creating six irradiance levels from 10 to 70% of full daylight irradiance. Each irradiance level contained 150 oak seedlings from five provenances (30 seedlings for each provenance were placed randomly in the treatment), plus 40 cm buffer at each of the north and south ends to avoid marginal effects. Photosynthetically active radiation measurements were done in the shade-houses base on comparisons of treatment vs. open sky instantaneous readings made at seedling height with a quantum sensor (LI-COR, Lincoln, USA) (Bloor, Grubb 2004). Every five seconds, a data logger sampled the measurements of a quantum sensor placed in the shade house, and from this data one-minute averages were produced. At each shade house, five measurements were taken (Table 2).

Growth treatment. Chestnut oak acorns were collected from about 10 to 15 mature healthy trees located in five provenances and were sown in plastic pots (15 × 10 cm) filled with a mixture of one-third of forest top soil and two-thirds of river sand in the autumn of 2011. The source of the forest soil was the oak forest region near the study site. The forest soil was used to provide a substrate with the natural composition of macro- and micronutrients, and the river sand provided for adequate drainage,

Table 1. Characteristics of the studied ecotypes (Domoers et al. 1998; Akhani et al. 2010; Pilembera – western provenance, Kelardasht, Lajim – central provenances, Kordkûy, Loveh – eastern provenances)

Province	Provenance	Altitude (m a.s.l.)	Coordinates	Temperature* (°C)	Precipitation* (mm)	Seed mean weight (g)
Guilan	Pilembera	650	37°34'25"N 49°01'40"E	15.1	2,045	5.41
Mazandaran	Kelardasht	1,000	36°35'52"N 51°05'30"E	16.4	1,293	8.00
	Lajim	800	36°18'22"N 53°05'48"E	18.0	703	7.25
Golestan	Kordkûy	800	36°43'27"N 54°07'21"E	17.8	601	7.41
	Loveh	800	37°21'11"N 55°39'44"E	17.8	488	7.41

*annual mean

which allowed daily watering. After germination in the spring, from late March to early April 2012, seedlings were positioned at a 10% irradiance level. Seedlings were set under light regime treatments by 1 May 2012. Seedlings were moved gradually to higher irradiance levels to avoid bleaching or wilting in response to the transfer, and they were watered twice weekly. Average transfer time was two to three weeks (15–20 days).

Leaf sampling. To examine the functional responses to irradiance, we measured five traits (Chl_{mass}, Chl:N, peroxidase (POD) quantitative activity, Chl_a:Chl_b, N_{mass}) as a function of the light regime (Fig. 1). Leaf sampling (about 30 g) was carried out from 23 to 25 August 2012 on three randomly selected individuals of each provenance from each shade house when the sampled seedlings had been set under light regime treatments for about four months. First, three replicate subsamples of 0.1 g leaf fresh weight were removed and stored at 4°C. This material was used to determine chlorophyll content spectrophotometrically after extraction with dimethylformamide (Porra et al. 1989; Oguchi et al. 2003). Chl (a and b) concentrations were calculated according to Porra et al. (1989).

To estimate N content, leaves were oven-dried at 70°C for at least 48 h and then weighed (Poorter 1999) and N_{mass} was determined using the Kjeldahl methodology.

Table 2. Rank order of the treatments based on comparisons of treatment vs. open sky instantaneous readings made at noon at seedling height with a quantum sensor (LI-COR, Lincoln, USA)

Irradiance treatment (%)	PAR (% of full daylight ± SE)
70	70.40* ± 2.29
60	57.19 ± 2.21
50	49.12 ± 2.39
30	31.17 ± 3.42
20	19.62 ± 3.23
10	11.02 ± 0.56

*mean of 5 replicates ± SE, PAR – photosynthetically active radiation, SE – standard error

The fresh leaf material for POD study was placed separately into individual bags, conserved in a portable refrigerator and later stored at 4°C until extraction. For enzyme extraction, leaf tissue was crushed separately using a mortar and a pestle, and the enzyme was extracted using extraction buffer: 1 g of leaf of each tree separately was ground with 3 ml of extraction buffer [2 g ascorbic acid, 3.8 g borax (decahydrate), 50 g polyethylene glycol, 1.2 g tris-hydrochloride, 2 g ethylenediaminetetraacetic acid disodium salt dihydrate, 3.6 g NaCl] and refrigerated at 4°C for 24 h. Peroxidase activity was determined spectrophotometrically at 530 nm with 0.2 ml of 0.01M acetate buffer A and B (1:1), 0.4 ml 3% H_2O_2, 0.2 ml 0.01M benzidine as the reagent solution (Korori 1989).

Statistical analysis. All traits were ln-transformed prior to analysis to increase normality and homoscedasticity. The traits of leaves from the six irradiance treatments were compared using a two-way ANOVA with provenances and irradiance levels as fixed factors. Mean values of traits were compared using Tukey's test to examine differences between treatments. The amount of variation explained by provenances, irradiance, and interaction was calculated as the sum of squares of the effect in proportion to the total sum of squares of the model equivalent to R^2 (Quero et al. 2006). All statistical analyses were done using the SPSS statistic package (Version 19, 2010).

Least significant range (LSR) at $P = 0.05$ was calculated by Eq. 1:

$$\text{Tukey}_{\alpha} = q_{\alpha,\, t,\, df(E)} \times (\sqrt{\text{MSE}}/n) \qquad (1)$$

where:

q – values obtained from Tukey's table,
α – 0.05 or 0.01,
t – degree of freedom factor + 1,
$df(E)$ – degree of freedom error,
MSE – mean square error,
n – number of treatments.

RESULTS

Variation in leaf trait responses as a result of light gradient, provenances and their interaction

As Fig. 1 shows, all investigated traits showed a decreasing trend to irradiance except Chl_a:Chl_b. The Chl:N ratio showed no special trend to light.

Peroxidase showed a decreasing response to irradiance with the largest changes at the lowest irradiance levels (10–30%), and levelling-off at intermediate and high irradiance levels (50–70%). As LSR shows, the POD also distinguishes provenances better than the other traits, especially at low irradiance levels (Fig. 1).

In our study, the irradiance level was the most important determinant of the variation in leaf traits, as indicated by the high *F*-values (Table 3). Peroxidase and N_{mass} were significantly influenced by provenance, and there was a high interaction between factors for POD and N_{mass} (Table 3). The variation in leaf traits due to irradiance intensity (average $R^2 = 0.30$) was much larger than the variation due to provenances (average $R^2 = 0.03$) or the interaction between provenances and irradiance levels ($R^2 = 0.23$) (Table 3).

DISCUSSION

Leaf physiological trait responses to light gradient

The results show that most of the traits are influenced by the light environment (Fig. 1, Table 3) indicating the importance of the irradiance effects

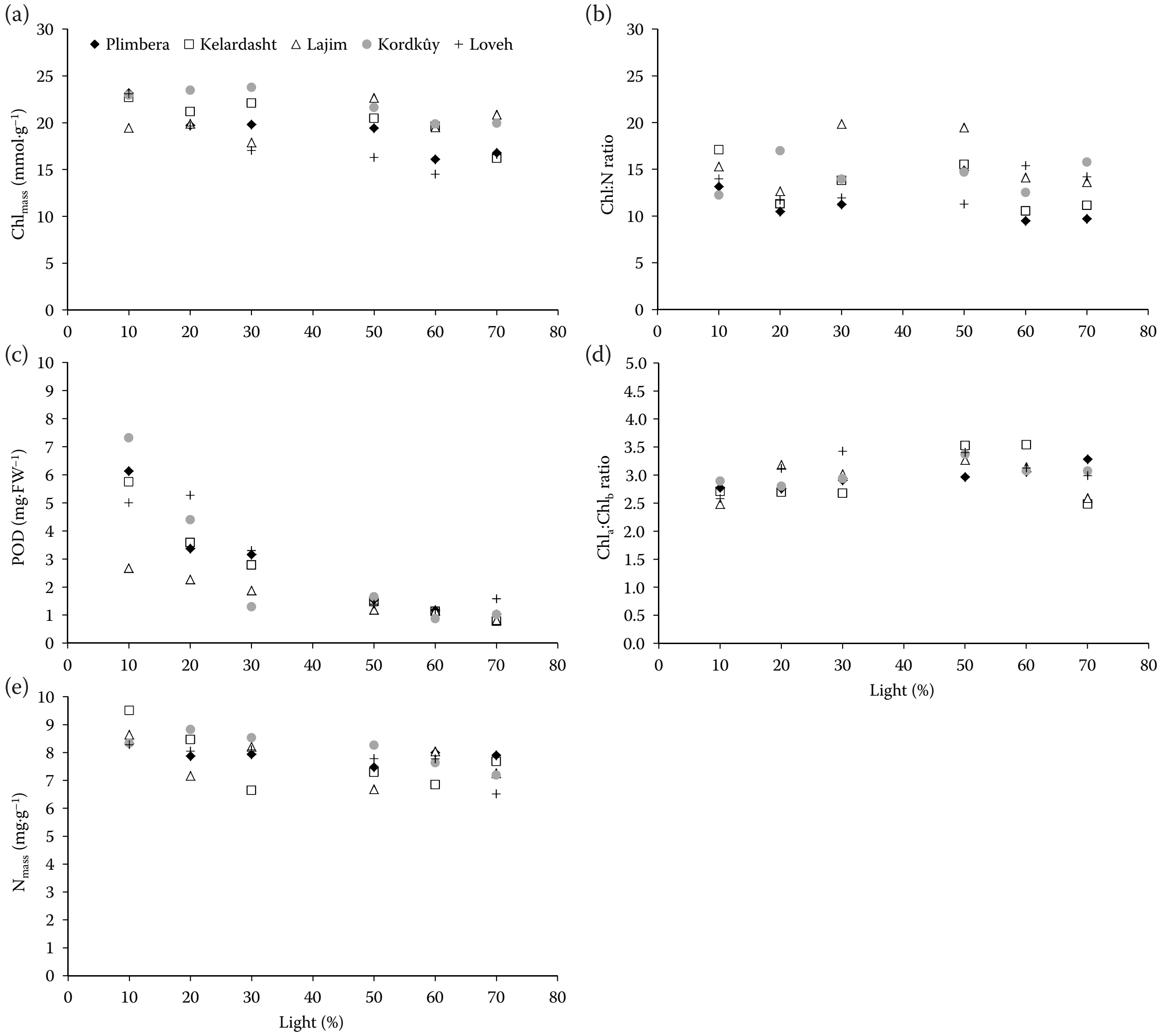

Fig. 1. Light intensity dependence for the five provenances: Plimbera, Kelardasht, Lajim, Kordkûy, Loveh, showing five variables: total chlorophyll – Chl_{mass} (a), Chl:N ratio (b), peroxidase (POD) quantitative activity (c), Chl_a:Chl_b ratio (d), N_{mass} (e). Least significant range is at $P = 0.05$

Table 3. Two-way ANOVA with light ($n = 7$) and provenances ($n = 5$) as fixed factors. Total R^2 of the model are indicated. An equivalent for R^2 was calculated as the sum of squares of the effect in proportion to the total sum of squares

Variable	Provenances			Light			Interaction			Total R^2
	F-value	P-value	R^2	F-value	P-value	R^2	F-value	P-value	R^2	
POD quantitative activity	10.39	***	0.04	60.64	***	0.36	5.92	***	0.14	0.54
Chl_{mass}	0.81	NS	0.02	5.75	***	0.23	1.25	NS	0.2	0.45
Chl_a:Chl_b	0.06	NS	0.01	8.1	***	0.31	1.3	NS	0.2	0.52
N_{mass}	1.87	*	0.07	4.24	**	0.39	2.21	*	0.3	0.75
Chl:N	0.92	NS	0.03	4.47	***	0.25	1.44	NS	0.32	0.6

POD – peroxidase, Chl – chlorophyll, $P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, NS – not significant

on traits related to the variation in leaf characteristics. The light environment varies spatially and temporally (Bloor, Grubb 2004; Rozendaal et al. 2006) and the ability to respond to such changes in resource availability may be critical to seedling growth success. From many studies, leaves are known as organs very sensitive to the environmental light conditions and as responding to it (Poorter 1999; Bloor, Grubb 2004; Delagrange et al. 2004; Rozendaal et al. 2006; Xu et al. 2008). The observed responses can be assigned to the adaptive ability of oak seedlings to cope with light as a heterogeneous environmental factor. As Fig. 1 shows, there is a decreasing trend with irradiance for Chl_{mass}, and an increasing trend for the Chl_a:Chl_b ratio. In low irradiance, light is considered a limiting resource. So the efficiency of light capture was enhanced through an increase in chlorophyll content on a mass basis (Hikosaka, Terashima 1995; Poorter, Evans 1998; Rozendaal et al. 2006; Valladares, Niinemets 2008), and decreases in N content on a mass basis and Chl_a:Chl_b ratio (Gratani et al. 2006; Valladares, Niinemets 2008). It has also been well established that photosynthetic pigments, mostly chlorophyll a and b, tend to increase when irradiance decreases to facilitate light harvesting. When there is little light available, plants produce more chlorophyll b than chlorophyll a to increase its photosynthetic ability. This is necessary because chlorophyll a molecules capture a limited wavelength, so accessory pigments like chlorophyll b are needed to aid in the capture of a wider range of light. Then, there is a higher ratio of chlorophyll b to chlorophyll a. This is adaptive, as increasing chlorophyll b increases the range of wavelengths absorbed by the shade chloroplasts.

We expected that POD quantitative activity would increase at 10–30 and 70% irradiance, but the results show a different trend (Fig. 1). Peroxidase quantitative activity was high at low irradiance levels (10–30%) and reached its lowest values at intermediate and high irradiance levels (30–70%). An increase in peroxidase activity was considered an early response to different stresses and may provide cells with resistance against the formation of H_2O_2, which is formed when plants are exposed to stress factors (Zolfaghari et al. 2010). Various abiotic stresses such as excess light (Hansen et al. 2002), drought, salt stress and CO_2 limiting conditions enhance the production of ROS in chloroplasts (Gill, Tuteja 2010). The production of ROS is also an unavoidable consequence of aerobic respiration. As noted before, our experiment was carried out at controlled conditions. High temperature and water stress are two secondary effects of high irradiance intensities (James, Bell 2000) which intensify the stress effects and increase the POD quantitative activity. By considering the controlled conditions at the greenhouse, we can assume that only the effects of light gradient have been indicated in this experiment. The assumption could be presumable from the curve produced by POD which is an accurate reflection of the degree of irradiance within the shade houses, especially at 10–30% on the basis of both light meter reading and observation. Hence it seems that the POD responses to irradiance could be an indicator of light tolerance of chestnut oak seedlings.

Although peroxidase is a light-activated enzyme, the results of this study surprisingly showed that its activity increased upon low irradiance treatment, whereas other studies showed that irradiance caused a sharp rise in the enzyme activity (Reddy et al. 1985). The result of the present study is supported by Begam and Vivekanandan (1990) that *Vigna unguiculata* (Linnaeus) Walpers showed an increase in POD quantitative activity upon low irradiance treatment. They discussed the results in relation to the age of leaves. In this study, leaf sampling was investigated when the sampled seedlings had been set under light regime treatments for about four months. It seems that POD quantitative activity increases in mature leaves, which is in agreement with Begam and Vivekanandan (1990) and Moustaka et al. (2015).

Prasad and Saradhi (2004) and Sofo et al. (2009) observed in their experiments that antioxidant enzymes decreased with an increase in the duration of exposure to intense light. Consequently, high light intensity may lead to an imbalance between antioxidant defence and the amount of active oxygen species, thus resulting in more severe stress in physiology and ecology of chestnut oak seedlings.

Overall, our results indicated that POD is physiologically flexible and varies with irradiance. The most appropriate rank, especially at 10–30% light, for the five different provenances, is also that of POD (Fig. 1) and POD could distinguish the irradiance levels better than other traits did (Fig. 1), both within and between provenances. Therefore, we suggest POD to study different provenances and their responses to environmental conditions, especially light.

Acknowledgement

We are grateful to S. Azizi and S. Gharemahmodli for their help with harvesting. B. Naseri is acknowledged for his help in collecting seeds and Dr. M. Matinizadeh for his help in laboratory. J.L. Quero and C. Puerta-Piñero are acknowledged for their help in improving the manuscript.

References

Akhani H., Djamali M., Ghorbanalizadeh A., Ramezani E. (2010): Plant biodiversity of Hyrcanian relict forests, N Iran: An overview of the flora, vegetation, paleoecology and conservation. Pakistan Journal of Botany, 42: 231–258.

Asada K. (1994): Production and action of active oxygen species in photosynthetic tissues. In: Foyer C., Mullineaux P. (eds): Photooxidative Stresses in Plants: Causes and Amelioration. Boca Raton, CRC Press, Inc.: 77–104.

Begam M.N., Vivekanandan M. (1990): Light activation of enzymes in relation to leaf age in *Vigna unguiculata* (L.) Walp. and *Zea mays* L. Proceedings: Plant Sciences, 100: 225–231.

Beneragama C.K., Goto K. (2010): Chlorophyll a:b ratio increases under low-light in "shade-tolerant" *Euglena gracilis*. Tropical Agricultural Research, 22: 12–25.

Bloor J.M.G., Grubb P.J. (2004): Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. Functional Ecology, 18: 337–348.

Bogdanović J., Milosavić N., Prodanović R., Dučić T., Radotić K. (2007): Variability of antioxidant enzyme activity and isoenzyme profile in needles of serbian spruce (*Piceaomorika* (Panc.) Purkinye). Biochemical Systematic Ecology, 35: 263–273.

Clarke J.B., Sargent D.J., Bošković R.I., Belaj A., Tobutt K.R. (2009): A cherry map from the inter-specific cross *Prunus avium* "Napoleon" × *P. nipponica* based on microsatellite, gene-specific and isoenzyme markers. Tree Genetics & Genomes, 5: 41–51.

Dale M.P., Causton D.R. (1992): Use of the chlorophyll a/b ratio as a bioassay for the light environment of a plant. Functional Ecology, 6: 190–196.

Delagrange S., Messier C., Lechowicz M.J., Dizengremel P. (2004): Physiological, morphological and allocational plasticity in understory deciduous trees: Importance of plant size and light availability. Tree Physiology, 24: 775–784.

Domoers M., Kaviani M., Schaefer D. (1998): An analysis of regional and intra-annual precipitation variability over Iran using multivariate statistical methods. Theoretical and Applied Climatology, 61: 151–159.

Gill S.S., Tuteja N. (2010): Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48: 909–930.

Gratani L., Covone F., Larcher W. (2006): Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. Trees, 20: 549–558.

Hansen U., Fiedler B., Rank B. (2002): Variation of pigment composition and antioxidative systems along the canopy light gradient in a mixed beech/oak forest: A comparative study on deciduous tree species differing in shade tolerance. Trees, 16: 354–364.

Hikosaka K., Terashima I. (1995): A model of the acclimation of photosynthesis in the leaves of C3 plants to sun and shade with respect to nitrogen use. Plant, Cell & Environment, 18: 605–618.

James S.A., Bell D.T. (2000): Influence of light availability on leaf structure and growth of two *Eucalyptus globulus* ssp. *globulus* provenances. Tree Physiology, 20: 1007–1018.

Korori S.A.A. (1989): Gelelektrophoretische und spektralphotometrische Untersuchungen zum Einfluß der Temperatur auf Struktur und Aktivität der Amylase- und Peroxidaseisoenzyme verschiedener Baumarten. [Ph.D. Thesis.] Vienna, University of Natural Resources and Life Sciences: 105.

Moustaka J., Tanou G., Adamakis I.D., Eleftheriou E.P., Moustakas M. (2015): Leaf age-dependent photoprotective and antioxidative response mechanisms to paraquat-induced oxidative stress in *Arabidopsis thaliana*. International Journal of Molecular Sciences, 16: 13989–14006.

Oguchi R., Hikosaka K., Hirose T. (2003): Does the photosynthetic light-acclimation need change in leaf anatomy? Plant, Cell & Environment, 26: 505–512.

Petrokas R., Stanys V. (2008): Leaf peroxidase isozyme polymorphism of wild apple. Agronomy Research, 6: 531–541.

Poorter H., Evans J.R. (1998): Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia, 116: 26–37.

Poorter L. (1999): Growth response of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. Functional Ecology, 13: 396–410.

Poorter L., Kwant R., Hernandez R., Medina E., Werger M.J. (2000): Leaf optical properties in Venezuelan cloud forest trees. Tree Physiology, 20: 519–526.

Porra R.J., Thompson W.A., Kriedemann P.E. (1989): Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: Verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochimica et Biophysica Acta, 975: 384–394.

Prasad K.V.S.K., Saradhi P.P. (2004): Enhanced tolerance to photoinhibition in transgenic plants through targeting of glycinebetaine biosynthesis into the chloroplasts. Plant Science, 166: 1197–1212.

Quero J.L., Villarm R., Marañón T., Zamora R. (2006): Interactions of drought and shade effects on four Mediterranean *Quercus* species: Physiological and structural leaf responses. New Phytologist, 170: 819–834.

Reddy K.P., Subhani S.M., Khan P.A., Kumar K.B. (1985): Effect of light and benzyladenine on dark-treated growing rice (*Oryza sativa*) leaves II. Changes in peroxidase activity. Plant & Cell Physiology, 26: 987–994.

Roche P., Diaz-Burlinson N., Gachet S. (2004): Congruency analysis of species ranking based on leaf traits: Which traits are the more reliable? Plant Ecology, 174: 37–48.

Rozendaal D.M.A., Hurtado V.H., Poorter L. (2006): Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Functional Ecology, 20: 207–216.

Sabeti H. (1994): Forests, Trees and Shrubs of Iran. Yazd, Yazd University Press: 886.

Sofo A., Dichio B., Montanaro G., Xiloyannis C. (2009): Photosynthetic performance and light response of two olive cultivars under different water and light regimes. Photosynthetica, 47: 602–608.

Sugiura D., Tateno M. (2011): Optimal leaf-to-root ratio and leaf nitrogen content determined by light and nitrogen availabilities. PLoS ONE, 6: 1–9.

Théry M. (2001): Forest light and its influence on habitat selection. Ecology and Management, 153: 251–261.

Valladares F., Niinemets U. (2008): Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics, 39: 237–257.

Xu F., Guo W., Xu W., Wang R. (2008): Habitat effects on leaf morphological plasticity in *Quercus acutissima.* Acta Biologica Cracoviensia. Series Botanica, 50: 19–26.

Zolfaghari R., Hosseini S.M., Korori S.A.A. (2010): Relationship between peroxidase and catalase with metabolism and environmental factors in Beech (*Fagus orientalis* Lipsky) in three different elevations. International Journal of Environmental Sciences, 1: 243–252.

Received for publication May 22, 2016
Accepted after corrections September 14, 2016

Corresponding author:

Assoc. Prof. Seyed Gholamali Jalali, Tarbiat Modares University, Faculty of Natural Resources and Marine Sciences, Department of Forestry, Imam Khomeini Street, 46414-356 Nour, Iran; e-mail: jalali_g@modares.ac.ir