

Biomass allocation of chestnut oak (*Quercus castaneifolia* C.A. Mey) seedlings: effects of provenance and light gradient

F. BABAEI SUSTANI¹, S.G. JALALI¹, H. SOHRABI¹, A. SHIRVANI²

¹Department of Forestry, Tarbiat Modares University, Nour, Mazandaran, Iran

²Department of Forestry, Tehran University, Karaj, Iran

ABSTRACT: Patterns of biomass allocation were determined for seedlings of five provenances of *Quercus castaneifolia* from west to east of the Hyrcanian forest along a rainfall gradient. Experimental design was executed under controlled conditions at seven different light levels (10, 20, 30, 40, 50, 60, 70 and 100% full light). We quantified the biomass allocation patterns to leaves, stems and roots. For all provenances total mass increased with irradiance at low light levels, reaching an optimum at an intermediate level but decreasing at a high irradiance level. As results show, in drier provenances and at high light levels, the seedlings invest more biomass into root mass to facilitate water uptake and to alter their leaf size to prevent overheating. In contrast, at wetter provenances and low light levels, towards increased light interception, more biomass is allocated proportionally to leaves and the stems but, accordingly, less to roots. The leaf to root ratio (L/R) was negatively correlated with light, with high correlation at wetter provenances compared to drier ones. In contrast, the relationship between the root to shoot (R/Sh) ratio and light was positively correlated with light, but it was weak at drier provenances and became gradually stronger at wetter ones. Such relationships indicated that chestnut oak seedling growth strategies are different along a rainfall gradient to irradiance levels. Despite similar growth conditions in the greenhouse, different growth strategies may be the result of genetic adaptation to the ecological conditions, especially when precipitation regimes prevail in the native habitat.

Keywords: leaf to root ratio; Hyrcanian forest; adaptation; environmental factor

Plants have the ability to modify their phenotype to maximize fitness according to the environmental conditions. For example, they often change leaf properties and biomass allocation pattern in accordance with light (POORTER 1999), water supply (MARKESTEIJN, POORTER 2009) and nutrient conditions (HERMANS et al. 2006). The term of biomass allocation which is the relative amount of biomass present in the various organs, is not fixed but may vary over time, across environmental conditions and among species. A quantitative understanding of biomass allocation patterns helps us to understand plant ecology and evolution, and have many uses in silviculture practice and implementation (POORTER et al. 2012). These patterns and the extent to what they vary among environmental conditions affect and set limits on

biomass production and utilization (REICH 2002). In general, many environmental factors affect the biomass allocation such as light and water availability (CHATURVEDI, RAGHUBANSHI 2012). Unfortunately, the knowledge of the physiological basis underlying the variation in biomass allocation is poor. Many researchers have worked with the subject, and suggested the balanced growth hypothesis. This hypothesis postulates that plants allocate more biomass to the organs capturing the most limiting resources, such as light, water and nutrients (SUGIURA, TATENO 2011). Water and light availability is often negatively correlated across environmental gradients. When water availability increases along rainfall or topographical gradients, primary production increases, vegetation becomes denser and light availability thus

decreases. Drought-tolerant species allocate more biomass to their root system to enhance water uptake, thus limiting biomass allocation to the shoot system, and ultimately their capacity to forage for light (REICH et al. 1998; POORTER 1999; MARKESTEIJN, POORTER 2009). In contrast, in low light, towards increased light interception, more biomass is allocated proportionally to leaves (POORTER 1999) and the stem, but less to roots (REICH et al. 1998; POORTER 1999). In high light, the radiation load increases and the plants invest more biomass in root mass to facilitate water uptake (POORTER 1999). Subsequently, plants growing in low-light environments generally have higher L/R than those growing in high-light environments regardless of functional groups (KITAJIMA 1994; SACK, GRUBB 2002). However, this hypothesis is only an intuitive explanation and cannot propose a quantitative estimation of the leaf to root ratio (L/R). Meanwhile, it is well established that leaf and root functions are highly interrelated, subsequently, producing excessive leaves may decrease the growth rate due to decreased root functions, such as nutrient uptake capacity (OSONE, TATENO 2003). This leads to an idea that there will be equilibrium between leaves and roots for optimal biomass allocation that maximizes the whole plant growth rate (SUGIURA, TATENO 2011).

In this study, we measured the biomass allocation in seedlings of five provenances of *Quercus castaneifolia* C.A. May (chestnut oak) from west to east of Hyrcanian forest along a rainfall gradient. Hyrcanian forest is characterized by various ecological conditions from 400 to 2,200 mm precipitation, zero to 5,671 m elevation and different vegetation landscape from conifers to broad-leaves. Chestnut oak is one of the economically important species which are widely distributed in the Hyrcanian vegetation zone. Unfortunately, the knowledge of the chestnut oak responses to environmental factors is poor. Light is one of the controllable physical factors in a forest that can directly affect many silvicultural operations, seedling growth and reproduction (THÉRY 2001). Yet, none of the studies to date has documented the effects of the irradiance gradient on the chestnut oak seedling growth strategy. Meanwhile, the ability of plants to adapt themselves to biotic and abiotic stresses can be achieved either through the phenotypic plasticity of individuals or by a high genotypic variability of populations (CALLAWAY et al. 2003). Hence, there may be different responses to irradiance among different provenances due to genetic variation [genetic variation among chest-

nut oak populations is reported (unpublished data)]. In this study we concerned to discuss the biomass allocation strategy in a light and rainfall gradient. The experiment was carried out in controlled conditions at seven different light levels. We hope that the findings will help in planning applications of nature-based management of Caucasian oak forests.

MATERIAL AND METHODS

Characteristics of collected provenances. There are different rainfall regimes in the western and eastern parts of the Hyrcanian Forest vegetation zone. Topographic change from west to east causes a decrease in annual precipitation, an increase in dry season length and greater interannual rainfall variability for the Hyrcanian forests (DOMROES 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 through the early autumn. There is a very short duration or absence of a dry season, especially in the western parts of the Hyrcanian forest. The high rainfall over the central and western parts of the south Caspian Sea and the reduction of rainfall in the eastern parts provide a rainfall gradient in the region (AKHANI et al. 2010). Five provenances of chestnut oak along this rainfall gradient from west to east of the Hyrcanian forests were collected in the form of seed to investigate biomass allocation strategies of chestnut oak seedlings to a rainfall gradient. The general characteristics of the studied sites are elucidated in Table 1.

Light treatments. To study the biomass allocation responses to a light regime, eight different irradiance levels of irradiance, i.e. 10, 20, 30, 40, 50, 60, 70 and 100%, were considered. To create conditions to achieve our purpose, the inside of the greenhouse was divided into seven parts (as shade houses). Each part was approximately 3.5 m long by 1.5 m wide and 2.20 high. Then, the seven specified irradiance levels were created by covering the walls of the shade houses by layers of neutral plastic, which transfers 70% of full light, and covering the roofs with an increasing number of layers of neutral shade netting. Each extra layer intercepted 10% of incoming irradiance, which created seven irradiance levels including 10 to 70% irradiance. Seedlings grown in the openness area received 100% irradiance level. Each irradiance level contained 150 oak seedlings from five prov-

Table 1. Characteristics of studied sites

Province	Provenances	Altitude (m)	Coordinates	Temperature* (°C)	Rainfall* (mm)	Number of seeds (kg)
Guilan	Pilembera	650	37°34'25"N 49°1'40"E	15.1	2,045	185
Mazandaran	Kelardasht	1,000	36°35'52"N 51°5'30"E	16.4	1,293	125
	Lajim	800	36°18'22"N 53°5'48"E	18	703	138
Golestan	Kordkoy	800	36°43'27"N 54°7'21"E	17.8	601	135
	Loveh	800	37°21'11"N 55°39'44"E	17.8	488	135

*annual mean

enances (30 seedlings for each provenance were placed randomly in the treatment), plus 40 cm buffer at each of the northern and southern ends to avoid marginal effects. Photosynthetically active radiation (PAR) measurements were done in the shade houses based on comparisons of treatment vs open-sky instantaneous readings made at seedling height with a quantum sensor: Li-Cor, Lincoln, USA (BLOOR, GRUBB 2004). In this way 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. Photosynthetically active radiation (PAR) measurements were estimated in the shade houses based on comparisons of treatment vs. open sky (Table 2).

The method is accurate under very homogeneous light conditions (BEAUDET et al. 2004; DELAGRANGE et al. 2004; COGLIASTRO et al. 2006) and is useful as an objective scale against which the four bioassays can be examined.

Table 2. Rank order of the treatment based on comparisons of treatment vs. open sky instantaneous readings made at noon at seedlings height with a quantum sensor

Treatment (%)	PAR (%) full daylight \pm SE
100	100.00* \pm 0.00
70	70.40 \pm 2.29
60	57.19 \pm 2.21
50	49.12 \pm 2.39
30	31.17 \pm 3.42
20	19.62 \pm 3.23
10	11.02 \pm 0.56

PAR – photosynthetically active radiation, *mean of 5 replicates

The experiment was carried out in the greenhouse at the Faculty of Natural Resource and Marine Science of Tarbiat Modares University, located in a part of the Hyrcanian forests (36°34'54"N, 52°2'32"E) in Mazandaran province in the north of Iran. The climate is considered as humid. The area receives an average of 1,200 mm of rainfall per year, in the form of rain at the lower and snow at the higher elevations, with an average temperature of 17°C.

Growth treatment. Chestnut oak seeds were collected from mature trees located in five provenances, and were sown in plastic pots (15 × 10 cm) filled with one third of forest top soil and two thirds of river sand, in the autumn of 2011. After germination in the spring, in late March to early April of 2012, they were positioned at a 10% irradiance level. Seedlings were set up under light regime treatments by 20 June 2012. Moving the seedlings to higher irradiance levels was carried out gradually to avoid bleaching or wilting in response to the transfer, and they were left to grow, watered twice weekly. The mean times for moving the seedling to higher irradiance levels were two to three weeks.

Once the seedlings were acclimated to their present light environment, sampling was carried out from 21 to 23 November on three randomly selected individuals of each provenance from each shade house. After harvesting, the seedlings were divided into leaves, stem and roots. The leaf area (LA) for three seedlings was determined for all leaves along the stem with a portable laser leaf area meter (CI-202, CID, Inc., Vancouver, WA). For estimating the seedling dry weight, the seedling parts were oven-dried for at least 48 h at 70°C and weighed (POORTER 1999). All measured seedlings had no signs of stem breakage or resprouting. From the primary data the leaf mass area was derived (LMA; leaf mass/leaf area, g·cm⁻²).

Statistical analysis. A comparison of the mean values of variables was done by Tukey's test to examine differences between provenances and treatments. All variables were transformed to natural logarithms before analyses (POORTER 1999). Statistical analyses were done using SPSS 19 STATISTICA (SPSS, Chicago, USA).

RESULTS

As results showed, the highest biomass was attained at an intermediate light (20–60%) and rainfall gradient (1,300–600 mm, including central provenances: Kelardasht, Lajim and Kordkûy) (Fig. 1). Most of the biomass is allocated to root > stem > leaf, respectively (Table 3). The root biomass increased at 50–60% of full light and Loveh (driest site) and Kelardasht showed the highest root biomass compared to other sites. In contrast, leaf and stem biomass decreased with light and central provenances showed the highest amount of leaf and stem allocation (Table 3).

The L/R ratio was negatively correlated with light. At wet provenances (Pilembera, Kelardasht, Lajim) the variation in L/R was strongly correlated with light (coefficient of determination R^2 : Pl = 0.76, Kl = 0.76, Lj = 0.82), but at dry provenances (Kordkûy and Loveh) this relation gradually disappeared (R^2 : Kr = 0.17, Lo = 0.31). The relationship between root to shoot (R/Sh) ratio and light was also weak at dry provenances (R^2 : Kr = 0.56, Lo = 0.25) and became gradually stronger at wet provenances (R^2 : Pl = 0.83, Kl = 0.94, Lj = 0.55) (Fig. 2).

As Fig. 3 shows, LA decreases with light in a linear form. In contrast, an increase in light irradiance causes an increase in leaf mass area (LMA) in all provenances, and the response is nonlinear.

DISCUSSION

The influence of light on the seedling biomass allocation demonstrates that seedlings attain their maximal growth rate in intermediate light condi-

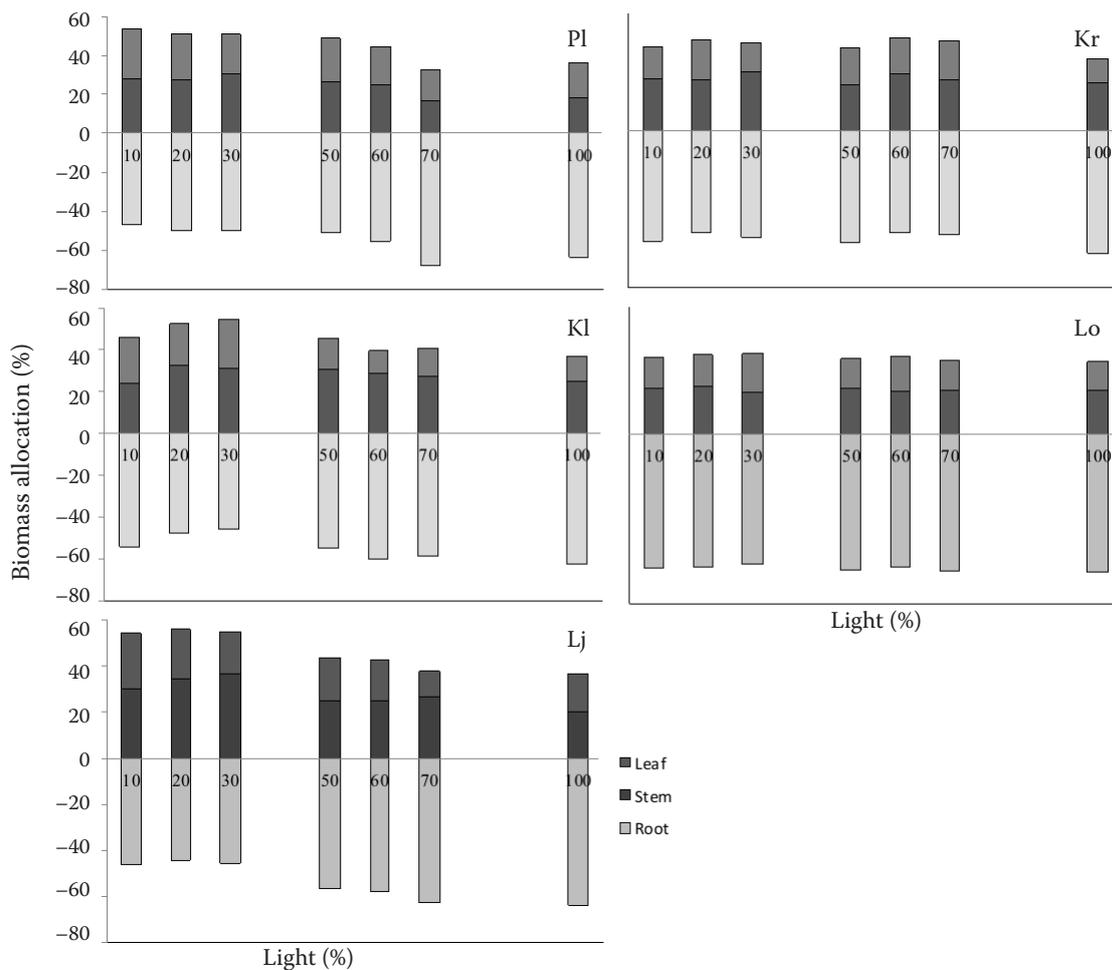


Fig 1. Biomass allocation to leaf, stem and root in five provenances at seven different light levels, Pl – Pilembera, Kl – Kelardasht, Lj – Lajim, Kr – Kordkûy, Lo – Loveh

Table 3. Mean value of leaf, stem and root biomass for the five provenances and light treatment

	Leaf ^a	Stem ^a	Root ^a
Provenance			
Plimbera	1.27 ± 0.56 ^b	1.62 ± 0.83 ^b	3.49 ± 1.20 ^b
Kelardasht	1.81 ± 0.67 ^a	2.66 ± 0.85 ^a	5.38 ± 1.66 ^a
Kordkoy	1.46 ± 0.60 ^{ab}	2.29 ± 1.17 ^{ab}	4.66 ± 1.86 ^{ab}
Lajim	1.65 ± 0.80 ^{ab}	2.30 ± 0.83 ^{ab}	4.63 ± 1.68 ^{ab}
Loveh	1.25 ± 0.48 ^b	1.85 ± 0.80 ^b	5.51 ± 1.91 ^a
Exposure			
10	1.83 ± 0.69 ^a	2.36 ± 0.88 ^a	4.87 ± 1.70 ^{ab}
20	1.90 ± 0.90 ^a	2.57 ± 1.29 ^a	4.24 ± 1.36 ^{ab}
30	1.88 ± 0.81 ^a	2.62 ± 0.98 ^a	4.72 ± 1.25 ^{ab}
40	1.40 ± 0.60 ^{ab}	2.19 ± 1.13 ^a	4.56 ± 1.87 ^{ab}
50	1.53 ± 0.45 ^{ab}	2.36 ± 1.14 ^a	5.47 ± 2.04 ^a
60	1.68 ± 0.74 ^{ab}	2.38 ± 1.21 ^a	5.25 ± 1.92 ^a
70	0.96 ± 0.46 ^b	1.53 ± 0.74 ^b	3.84 ± 2.08 ^b
100	1.03 ± 0.49 ^b	1.62 ± 0.83 ^b	4.66 ± 1.80 ^{ab}

^avalues are means ± SD for five provenances, ^{a, b} significant at $P < 0.05$

tions in all provenances (Fig. 2). And the biomass investment showed a decreasing trend at 10% and 70–100% of full light. This could be explained by considering that chestnut oak is intermediate in shade tolerance (REBBECK et al. 2012). The

growth depression in low light may be a result of light limitation which caused producing excessive leaves to capture more light, which may decrease the growth rate due to decreased root functions, such as nutrient uptake capacity (SUGIURA, TATE-

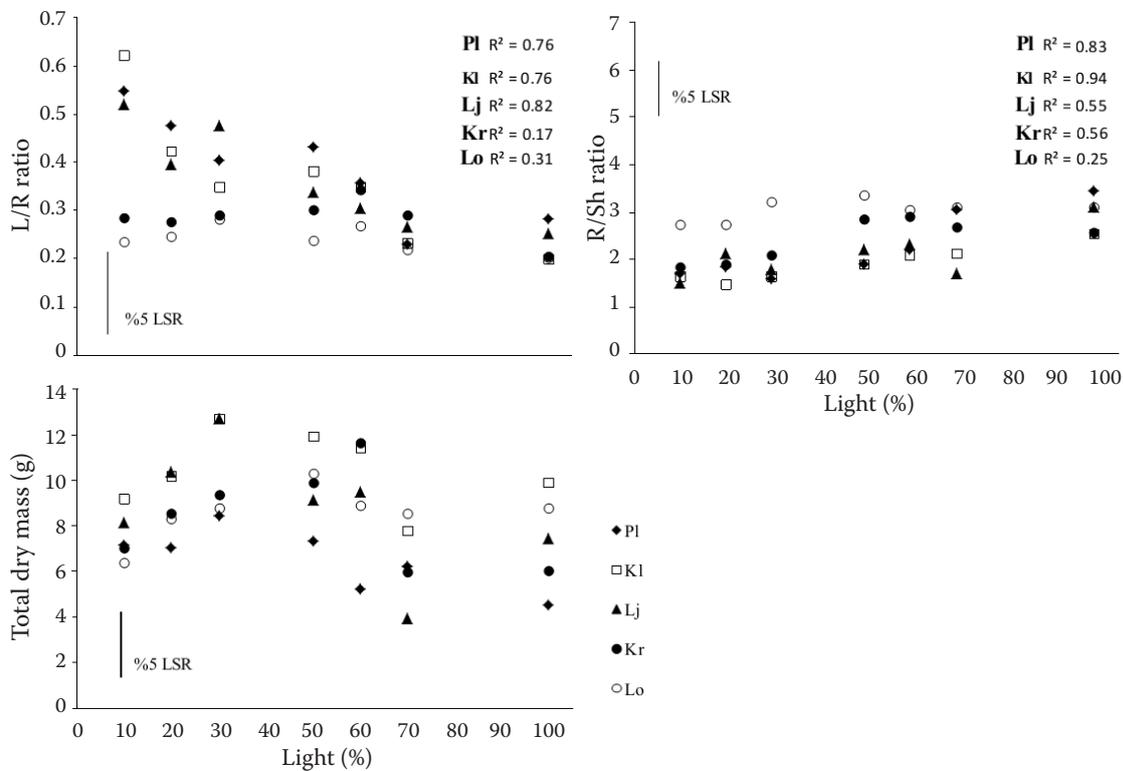


Fig 2. Relationship between the R/Sh and L/R ratio and total biomass for five provenances with light (Least Significant Range (LSR) is at $P = 0.05$, coefficients of determination are shown), Pl – Pilembera, Kl – Kelardasht, Lj – Lajim, Kr – Kordkûy, Lo – Loveh

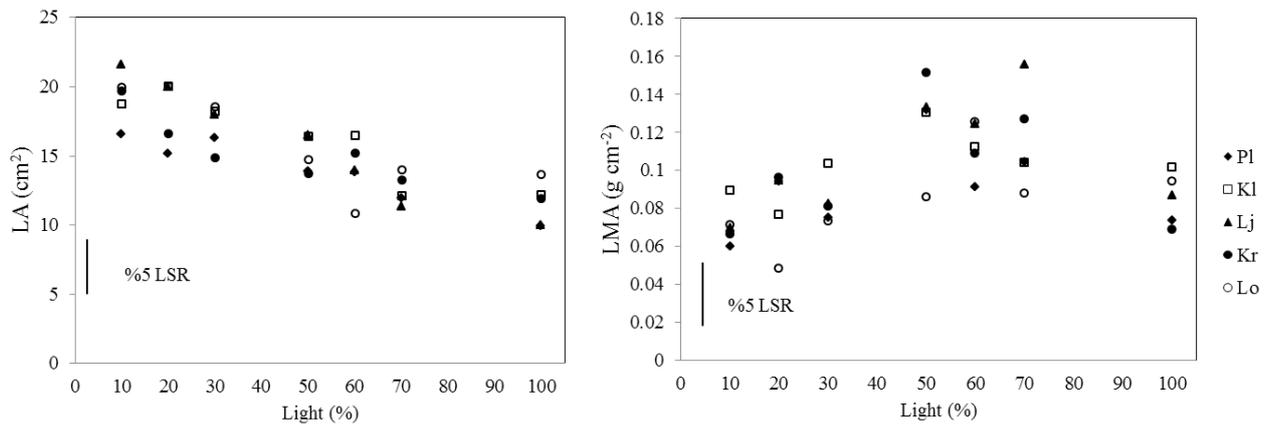


Fig 3. Leaf area (LA) and leaf mass (LMA) responses to light in five different provenances (Least Significant Range (LSR) is at $P = 0.05$), PI – Pilembera, KI – Kelardasht, Lj – Lajim, Kr – Kordkúy, Lo – Loveh

NO 2011). In contrast, in high irradiance conditions the seedling morphology is not flexible and there is little capacity in seedling morphology to acclimatize with high irradiance intensity. High irradiance causes irreversible damage to the photosynthetic system (YE, ZHAO 2010), stomatal closure (HAMERLYNCK, KNAPP 1996), less biomass allocation to the root for water uptake and strongly reduces the photosynthetic gain and the potential growth rate (REICH et al. 1998; POORTER 1999). Hence, chestnut oak shows an optimal response at intermediate irradiance levels. Similar results have been reported on many other species (POORTER 1999; PUERTA-PIÑERO et al. 2007; PÉREZ-RAMOS et al. 2010).

It is also well established that in low irradiance, light is considered a limiting resource; so in order to enhance light capture, more biomass is allocated proportionally to leaves and stem, leading to higher LA. By increasing the area of a given unit of leaf biomass, the interception of light is increased under low-light conditions, while more photosynthetic biomass per unit leaf area enhances photosynthetic capacity in high light. Therefore, LMA increases with light. These results are in line with POORTER (1999) and FILA and SARTORATO (2011) studies.

Central provenances show the highest biomass, which may be a result of the best function of seedlings at an intermediate rainfall gradient. When water availability increases along the ecological gradient, vegetation becomes denser and light availability thus decreases. Since chestnut oak is considered as intermediate in shade tolerance in the seedling stage (REBBECK et al. 2012), a decrease in light availability causes a decrease in total biomass at wetter provenance (Pilembera). In contrast, at dry sites water is the most limiting resource for seedling growth and survival. Con-

sequently, seedlings of dry sites enhance water uptake through an increased biomass allocation to roots, which allows them to forage more efficiently in deeper soil layers, where more water is available, especially in the dry season (ENGELBRECHT et al. 2005). Since the leaf and root function is correlated, hence producing more roots at the sacrifice of leaf growth is a strategy in dry sites to facilitate water uptake to enhance the growth rate. But this strategy decreased leaf functions and subsequently, total biomass decreased. As noted above, we conclude that both western and eastern provenances are under stressed conditions, hence, the central provenances have the best function compared to others.

All seedlings were exposed to the same treatments in controlled conditions in a greenhouse, but our results show that the L/R ratio was highly correlated with light at wet provenances compared with the seedlings of dry ones. The relationship between R/Sh ratio and light also showed a similar trend. Leaf to root (L/R) and root to shoot (R/Sh) ratios as two major factors dictating plant growth rate and fitness could be helpful for understanding plant growth strategies in natural ecosystems, and refer to the balance between investment in light intercepting organs and that in water and nutrient organs. In general, plants growing in low-light environments have higher L/R and lower R/Sh than those growing in high-light environment regardless of functional groups. Biomass allocation of dry and moist provenances differed, which is in line with the balanced growth hypothesis which predicts that, under a given regime of stresses, plants maximize their surface area for the intake of the most limiting resource (MARKESTEIJN, POORTER 2009) such as water in dry sites and irradiance in wet sites. Such strategies allow seedlings to have the best function under stressed conditions. For chestnut oak

as a species with broad fundamental niches in Hyrcanian forests, variation in adaptive characteristics may be achieved by a combination of genotypic differentiation and phenotypic plasticity (CORDELL et al. 1998). Water shortage is a serious problem for the seedlings in dry sites. Hence, producing more roots at the sacrifice of leaf growth, under all light treatments, is an ecological adaptation in dry sites to facilitate water uptake. Consequently, the L/R and R/Sh ratio is weakly correlated with light in these sites. However, it seems that these differences are results of genetic adaptation to the ecological conditions (BOARDMAN 1977; JAMES, BELL 2000). Our results are in line with ASPELMEIER and LEUSCHNER (2006) and MEIER and LEUSCHNER (2008), who reported that the genotype had a strong influence on leaf, root and shoot morphogenesis, growth and the morphological responses to drought.

Such experiments help us to identify plant strategy along an environmental gradient and to plan applications of nature-based management of oak forests. According to the results, light is an important factor that influences chestnut oak seedling biomass allocation and L/R and R/Sh ratio at moist provenances. Whereas at dry sites water has the most important role in growth and biomass allocation. Foresters have traditionally been concerned with producing the maximum amount of wood per unit of land area and in the shortest time possible. They routinely deal with trees growing in plant communities and with factors affecting competition among the trees in a stand. Hence, the growth response to the light gradient among different provenances could be an interesting topic to reach foresters' goals.

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Corresponding author:

SAYAD GHOLAMALI JALALI, Tarbiat Modares University, Department of Forestry, Nour, Mazandaran, P.O.Box 14115-335, Iran; e-mail: jalali_g@modares.ac.ir
