

EFFECT OF CANOPY GAPS ON THE CONDITIONS FOR NATURAL REGENERATION IN MOUNTAINOUS BEECH FORESTS OF NORTHERN IRAN

Nazanin Hamrang^{1*}, Hassan Pourbabaei¹, Mehrdad Nikooy¹,
and David Pothier²

¹Department of Forestry, Natural Resources Faculty, University of Guilan, Somehsara, P. O. Box 1144, Guilan, Iran. *E-mail: nazninhamrang@yahoo.com

²Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, QC, G1V 0A6, Canada.

Received: 15 February 2015

Accepted: 11 November 2015

Abstract

This study investigates the effect of canopy gaps created by single-tree selection cutting on regeneration density and diversity in Oriental beech (*Fagus orientalis* Lipsky) forests of Northern Iran. Five gaps within each of three different size classes (small (100–200 m²), medium (200–300 m²), and large (300–400 m²)), together with 15 control areas located in the undisturbed forest surrounding each gap were randomly selected. Abundance of tree regeneration was measured in 4-m² quadrates established within each gap and control area. The percent cover of herbaceous species and litter depth was also quantified. Shannon diversity, Smith-Wilson evenness and Margalef richness indices were then computed for each quadrate. Results indicated that percent cover of herbaceous species increased significantly with increasing gap size while the opposite was observed for litter depth. Species richness and Shannon diversity index values were higher in gaps than in control areas, but significant differences were only detected between medium size gaps and control areas. With the exception of large gaps, regeneration density was higher in gaps than in control areas. These results indicate that natural tree regeneration in beech forests of Northern Iran tends to be maximized at intermediate levels of canopy gap size, which also correspond to intermediate levels of litter depth and percent cover of herbaceous species.

Key words: artificial gap, beech forests, herb-layer diversity, Hyrcanian region, regeneration.

Introduction

Forests are dynamic systems subjected to continuous changes (Stanciou and O'Hara 2005) induced by natural (e.g. fire or flood) or anthropogenic (e.g. harvesting) disturbances. These disturbances may markedly affect forest ecosystems (Legout et al. 2009) through, for example, the periodic formation of canopy gaps of different sizes that can produce differ-

ent mosaic patterns at the forest scale (Yamamoto et al. 2011). In turn, these gaps generally promote the establishment and development of tree seedlings that are important for forest sustainability and that can lead to significant changes in forest composition, structure and functions (Millington et al. 2012).

The effects of canopy gaps on tree regeneration have been studied by many authors (Denslow 1995, Mountford et al.

2006, d'Oliveira 2009, Sefidi et al. 2011, Diaci et al. 2012, Schwartz et al. 2013, Mallik et al. 2014). Several studies indicated that gaps can be a key factor in regeneration establishment and further seedling growth of many plant species (Runkle 1982, Sapkota et al. 2009, Muscolo et al. 2010, Schliemann and Bockheim 2011). For example, the density and diversity of woody plant regeneration were higher in gaps created by partial harvesting than in an adjacent undisturbed boreal forest stand (Mallik et al. 2014). Indeed, canopy gaps can cause changes in light, soil moisture, nutrient availability, litter depth and other factors that affect tree regeneration and long-term forest structure and composition (van Dam 2001, Dupuy and Chazdon 2008). In other words, canopy gaps can increase resource availability for plant regeneration and provide various niches for the establishment of tree species of different life traits, which can help maintain tree density and diversity (Nascimento et al. 2012).

On the other hand, canopy gaps were sometimes reported to have little influence on seedling establishment and growth (D'Oliveira and Ribas 2011) because many species, particularly shade-tolerant species, could be established before gap formation (Nagel et al. 2010). These contrasting results could be explained by differences in studied regions (Runkle 1985) as well as in gap features such as size, shape (Li et al. 2005), age (Clinton et al. 1994) and orientation (Duguid et al. 2013). In particular, gap size was reported to play an important role for the establishment, survival and growth of different tree species (Denslow 1987).

In many beech forests of Northern Iran, canopy gaps of different sizes, directly or indirectly created by human activities, are the dominant source of regeneration in *F.*

orientalis forests in northern Iran (Sagheb-Talebi et al. 2005, Sefidi et al. 2011). These authors reported that canopy gaps are generally well regenerated due to their particular environmental conditions. Northern Iranian forests, which are also known as Hyrcanian forests, have been established since over 1 million years and are considered one of the oldest forest ecosystems of the world. In the past, these forests covered 5 million ha but today, overexploitation reduced this area to about 1.8 million ha of which only 1.2 million ha are considered high quality commercial forests. This highlights not only the importance of protecting Northern Iranian forests, but also the necessity to help establish tree regeneration by creating canopy gaps through the application of selection cutting systems (Marvie-Mohadjer 2011).

To promote sustainability of these forests and pursue efficient forest harvesting, it is important to document the effects of canopy gaps on tree regeneration establishment. Therefore, the main objectives of this study are: 1) to determine the effects of canopy gaps created by selection cutting on tree regeneration density; 2) to compare tree species diversity between gaps of different sizes and adjacent forest areas; and 3) to explore the role of the percent cover of herbaceous species and leaf litter depth on the density and diversity of tree regeneration in different size gaps and forest areas.

Material and Methods

Study area

This study was conducted in an 82-ha forest area of Asalem region in the west of

Guilan province in Northern Iran. This area is located between latitudes 37°32'38" N and 37°35'56" N and longitudes 48°42'27" E and 48°47'55" E. The north aspect dominates the landscape whereas elevation varies from 900 to 2000 m a.s.l. According to the nearest meteorological station (Pylambara), mean annual temperature and precipitation are 15 °C and 1440 mm, respectively. Based on Domarten classification, the regional climate is considered very humid. Common forest soils are slightly acidic with a pH varying from 5.2 to 5.9. Types of parent material include tuff, shill and calcareous with minor traces of basalt and schist. The general soil type is forest brown (Dystric-Eutric Cambisols), with a texture from medium to slightly heavy and a maximum depth of 80 cm. This uneven-aged forest is of natural origin and is dominated by Oriental beech (*Fagus orientalis*). Dominant height is 32 m while mean stand density is 308 trees per hectare with many individuals observed in diameter classes 25 to 35 cm. The forest composition is completed by other deciduous broadleaved species, mainly Cappadocian maple (*Acer cappadocicum* Gled.), Common hornbeam (*Carpinus betulus* L.), Wild service tree (*Sorbus torminalis* (L.) Crantz), Wych elm (*Ulmus glabra* Huds.), Caucasian alder (*Alnus subcordata* C.A.Mey.), and Wild cherry (*Cerasus avium* (L.) Moench) (Anonymous 2003).

Treatments and data collection

Canopy gaps in the studied forest were created by single-tree selection system applied in 2006 while all measurements were conducted during July 2013. Canopy gaps were all located on a northern aspect with a slope varying from 30 to 35 %. At the beginning of the study, 35 artificial gaps were identified according to the pres-

ence of cut tree stumps. Because most of these gaps were elliptically shaped, gap area was estimated using Runkle's ellipsoid method (Runkle 1982):

$$A = \frac{\pi \cdot L \cdot W}{4},$$

where A is the gap area, L is the ellipse length (long diameter), and W is the ellipse width (short diameter). After determining the area, gaps were divided into three categories: small (100–200 m²), medium (200–300 m²), and large (300–400 m²) (Table 1). Then, five gaps were randomly selected in each category for a total of 15 gaps (Berg and Van Lear 2004).

Table 1. Characteristics of gaps created by single-tree selection system (Berg and Van Lear 2004).

Gaps	Area, m ²	Number of identified gaps	Number of selected gaps
Small	100–200	17	5
Medium	200–300	8	5
Large	300–400	10	5

To compare regeneration density and diversity observed in canopy gaps with those observed under closed canopy, control areas were identified in the undisturbed forest surrounding each gap. These control areas were selected to have topographical characteristics similar to those of adjacent gaps and were located at least 15 m from gap edges (Wang and Liu 2011). Control areas were as numerous as gaps, i.e. 5 control areas for each size class, for a total of 15 control areas. To determine the regeneration density (number of tree seedlings/m²) within each gap, 2×2 m quadrates were systematically established 1 m apart along the two diameters of the ellipsoidal

gaps (Brockway and Outcalt 1998). Their number established in each gap thus depended on the gap size and varied from 8 to 15. The establishment of quadrates in control areas followed exactly that of the corresponding gaps and their number thus also varied from 8 to 15 in each control area. Within each of these 4-m² quadrates, the number of tree seedlings shorter than 130 cm was determined (Abrari Vajari et al. 2011) as well the percent cover of herbaceous species using Domin's criterion (Mueller and Ellenberg 1989). In addition, the litter thickness was measured with a ruler in the center of each quadrate.

Data analysis

To calculate diversity, evenness, and richness of regeneration species in the gaps and control areas, the following indices were used:

- Shannon-Wiener diversity index,

$$H' = -\sum_{i=1}^S p_i \ln p_i,$$

- Smith-Wilson evenness index

$$E_{\text{var}} = \frac{2}{\pi \arctan \left\{ \frac{\sum_{i=1}^s \left(\log_e(n_i) - \frac{\sum_{j=1}^s \log_e(n_j) / s \right)^2}{s} \right\}}.$$

- Margalef's richness index

$$D_{\text{mg}} = \frac{S-1}{\ln N},$$

where: p_i is the relative frequency of the i^{th} species, n_i is the number of individuals of the i^{th} species, n_j is the number of individual of the j^{th} species, S is the total number of species (richness), and N is the total number of individuals. These indices were calculated using the Ecological Methodology software (Krebs 1999).

Kolmogorov-Smirnov test was used to evaluate the normality of data and Levene's test was used to investigate the homogeneity of variances. After securing data normality, paired t -tests were used to compare tree regeneration density and diversity between canopy gaps and control areas. Regression analyses were used to examine the relationships between gap area and both litter depth and percent cover of herbaceous species by giving a gap area of 0 m to each control area. All statistical analyses were performed using the SPSS 16.0 software.

Results

Effect of canopy gaps on tree regeneration density and diversity

Regeneration densities were higher in small and medium size canopy gaps compared to control areas, but no significant differences were found between them (Table 2).

Diversity and richness index values were greater in all size gaps compared to control areas. Shannon-Wiener (H') and Margalef (D_{mg})

Table 2. Mean (\pm SE) density of tree seedlings (N/m²) in gaps and corresponding control areas (CA).

Study areas	Density, N/m ²	p
Small gap	47 \pm 5.5	
CA	46 \pm 10.6	0.864 ^{ns}
Medium gap	122 \pm 25.7	
CA	93 \pm 24.7	0.227 ^{ns}
Large gap	83 \pm 18.7	
CA	143 \pm 49.9	0.417 ^{ns}

Note: ns is no significance.

index values were significantly higher in the medium size gaps than in the control areas ($\alpha < 0.5$), while Smith-Wilson evenness index was lower in gaps than in control areas even though differences were not significant (Table 3).

Effect of canopy gaps on percent cover of herbaceous species and litter depth

The percent cover of herbaceous species significantly increased with increasing gap size (Fig. 1a), while the opposite was observed for litter depth (Fig. 1b).

Regression analysis calculated between litter depth and tree seedling densities are presented in Figure 2. Within both canopy gaps and control areas, tree seedling density was negatively and significantly related to litter depth, with a steeper slope associated with control areas compared to canopy gaps (Fig. 2).

Discussion

In general, higher values of both Margalef's richness and Shannon diversity indices were observed in gaps of various sizes compared to control areas in accordance

Table 3. Mean (\pm SE) of diversity indices in gaps and corresponding control areas (CA).

Study areas	Diversity indices		
	H'	E_{var}	D_{mg}
Small gap	1.22 \pm 0.2	0.545 \pm 0.1	3.137 \pm 0.2
CA	1.2 \pm 0.1	0.719 \pm 0.1	2.926 \pm 0.3
Medium gap	1.28 \pm 0.1*	0.379 \pm 0.1	3.187 \pm 0.4*
CA	0.84 \pm 0.7*	0.745 \pm 0.05	1.967 \pm 0.2*
Large gap	1.49 \pm 0.09	0.588 \pm 0.1	3.365 \pm 0.4
CA	1.03 \pm 0.1	0.605 \pm 0.1	2.99 \pm 0.5

Note: * indicate a significant difference at $P < 0.05$ between gaps and control areas. H' – Shannon-Wiener diversity index; E_{var} – Smith-Wilson evenness index; D_{mg} – Margalef's richness index.

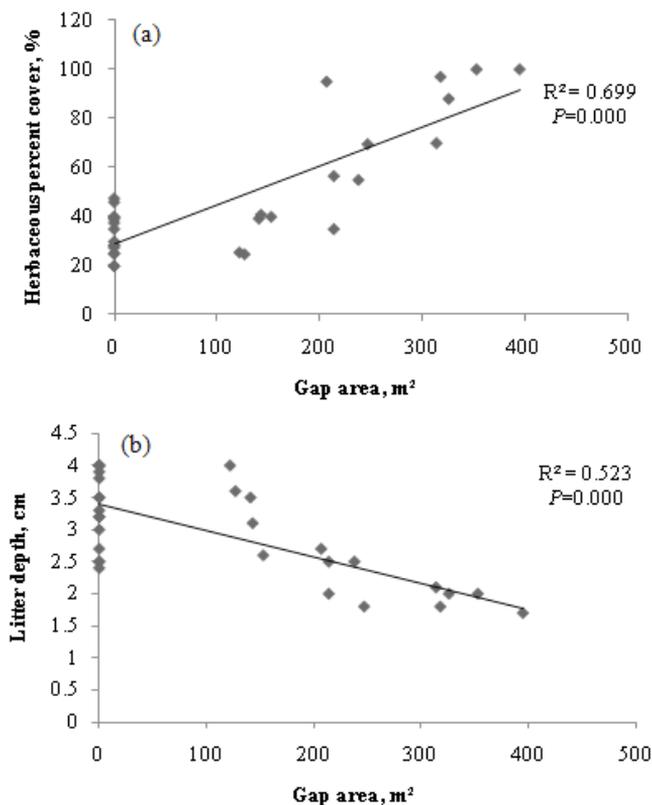


Fig. 1. Relationship between gap area and herbaceous percent cover (a), and litter depth (b) in different canopy gap sizes. Gap size under closed canopy was considered as 0.

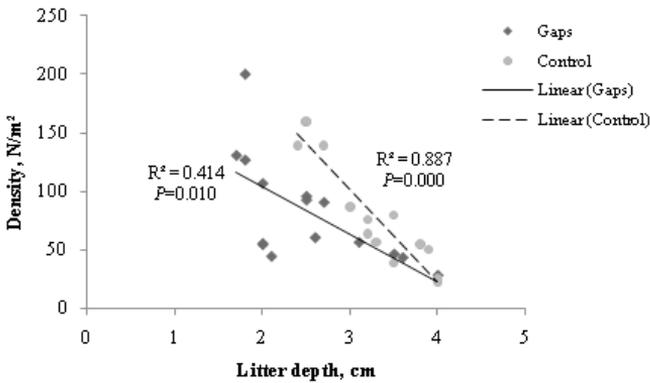


Fig. 2. Relationship between litter depth and seedling density in gaps (solid line), and under closed canopy (dotted line).

with the results of Naaf and Wulf (2007) and Wang and Liu (2011). Forest gaps created by partial harvesting generate ecological niches for various species regeneration as a result of micro-environmental heterogeneity (Li et al. 2005). Moreover, gaps generally increase available resources, particularly light (Denslow 1987, Romell et al. 2008) and soil moisture (Griffiths et al. 2010). Therefore, competition for obtaining these resources is lower in canopy gaps (Cahill and Casper 2002) within which seedling growth and diversity are higher than in control areas.

Species diversity and richness in medium size gaps were significantly greater than in control areas because gaps promote the establishment of shade intolerant species before crown closure (Wang and Liu 2011). Results from Albanesi et al. (2005) obtained in fir forests and those of Pourbabaei et al. (2013) in beech forests also showed that a gap range of 200–300 m² was the most suitable size for establishing and diversifying tree regeneration.

In small canopy gaps, species diversity and richness were only slightly higher than in closed canopy likely because of very small differences in environmental

conditions such as light and nutrient availability (Fahey and Puettmann 2007). Small differences in percent herbaceous cover were also observed between small gaps and control areas (Fig. 1a). These small differences were likely related to the effect of surrounding trees which substantially shade the gap perimeter and even the gap center (Gagnon et al. 2004). Therefore, small canopy gaps were not associated with changes in forest

floor plant communities which can thus be considered as relatively stable (Promis et al. 2012). The small differences between small canopy gaps and control areas can even disappear over a short period of time because of canopy closure which would likely prevent the development of many species, especially the shade intolerant ones (Franklin et al. 2002). Hence, these gaps will be mostly filled by shade-tolerant tree species, which can lead to a decline in regeneration diversity and richness (Anderson and Leopold 2002).

Species diversity and richness were not significantly different between large canopy gaps and control areas. This result is likely related to the larger exposition to full sunlight and high temperatures in large canopy gaps, conditions that promotes the growth of herbaceous species which, in turn, limit the establishment and development of tree seedlings. This is supported by significant positive relationship between the percent cover of herbaceous species and gap size (Fig. 1a). Therefore, the germination, establishment and spatial arrangement of regeneration in large gaps may be influenced by the presence of abundant herbaceous spe-

cies, which compete for light, water and nutrients (George and Bazzaz 2003, Page and Cameron 2006, Hagemann et al. 2012). The presence of herbaceous species can negatively affect seed germination conditions and thus reduce the abundance of seedlings (Frochot et al. 1996, Grant et al. 2003, Godefroid et al. 2005). Our results also indicated that species richness in small, medium, and large gaps were greater than that of control areas in accordance with the results of other studies (Runkle 1982, Denslow 1995, Busing and White 1997, Li et al. 2005, Sapkota et al. 2009).

Overall, regeneration density between gaps and control areas were similar in agreement with results of Nagel et al. (2010) observed in forests of Bosnia and Herzegovina. Accordingly, in Amazonian forests, no significant differences were observed in seedling densities between artificial gaps and closed canopy, 12 years after gap formation (d'Oliveira and Ribas 2011).

The establishment, growth, survival and density of tree seedlings can also be affected by litter cover (Molofsky and Augspurger 1992). Indeed, litter cover can directly or indirectly influence plant establishment by modifying soil temperature and moisture, water and nutrient availability, herbivory, and plant competition (Ganade and Brown 2002, Dupuy and Chazdon 2008). In addition, litter can act as a mechanical barrier against seed germination and seedling establishment (Hutchinson et al. 2005). Accordingly, we found significant negative relationship between litter depth and tree seedling density both in canopy gaps and under closed canopy (Fig. 2). However, litter in large gaps was significantly shallower than in small gaps as already observed by Mountford et al. (2006) and Griffiths et al. (2010). Al-

though the shallower litter and the canopy openness associated with large gaps can positively affect seed germination and regeneration establishment (Dupuy and Chazdon 2008), too large gaps can have the opposite effect by reducing seedling density through increasing competition by herbaceous, shade-intolerant species (Albanesi et al. 2005, Mihok et al. 2005). Our results clearly show that litter depth affected tree seedling density, and that these effects depended on gap size such that increasing litter depth reduced seedling density in both gaps and control areas.

Conclusion

The application of selection cutting resulted in the formation of canopy gaps of different sizes. These gaps, together with small-scale natural disturbances, create a mosaic of habitat conditions that diversify the forest (Mallik et al. 2014). Canopy gaps provide suitable conditions for the establishment of seedlings and are a major driver of beech-dominated forest dynamics of Northern Iran.

Canopy gap creation through selection cuttings must be prioritized to maintain the ecological stability of these beech-dominated forests while allowing sustainable production. This silvicultural treatment should help preserve the natural uneven-aged structure of these forests, which promotes environmental heterogeneity and tree species diversity. According to our results, medium-sized gaps were associated with maximum regeneration density while maintaining suitable herbaceous cover, litter depth and seedling diversity. For future application of the selection cutting system in these forests, it is thus recommended to create canopy gaps ranging from 200 to 300 m². If possible, this

silvicultural system should be accompanied by the timely removal of herbaceous species to reduce competition with newly established seedlings.

References

- ABRARI VAJARI K., JALILVAND H., POURMAJIDIAN M.R., ESPAHBODI K., MOSHKI A. 2011. Effects of canopy gap size and ecological factors on species diversity and beech seedling in managed beech stands in Hyrcanian forest. *Journal of Forestry Research* 23(2): 217–222.
- ALBANESI E., GUGLITTA O., MERCURIO I., MERCURIO R. 2005. Effects of gap size and within gap position on seedlings establishment in silver fir stands. *Forest Journal* 2(4): 358–366.
- ANDERSON K.L., LEOPOLD D.J. 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. *Torrey Botanical Society* 129: 238–250.
- ANONYMOUS 2003. Forestry plan series No. 7 Lumiere. Department of natural resources, Guilan province. 379 p.
- BERG E.C., VAN LEAR D.H. 2004. Yellow-poplar and oak seedling density responses to wind-generated gaps. In: Connor, KF (Eds.). Proceedings of the 12th biennial southern silvicultural research conference. Department of Agriculture, Forest Service, Southern Research Station. Asheville, NC. February 24–28, 2003: 254–259.
- BROCKWAY D.G., OUTCALT K.W. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. *Forest Ecology and Management* 106: 125–139.
- BUSING R.T., WHITE P.S. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* 78: 562–568.
- CAHILL J.F., CASPER J.R. 2002. Canopy gaps are sites of reduced belowground plant competition in a productive old field. *Plant Ecology* 165: 207–215.
- CLINTON B.D., BORING L.R., SWANK W.T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influence of topographic position and evergreen understory. *American Midland Naturalist* 132: 308–319.
- DENSLOW J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology* 18: 431–451.
- DENSLOW J.S. 1995. Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications* 5: 962–968.
- DIACI J., ADAMIC T., ROZMAN A. 2012. Gap recruitment and partitioning in an old-growth beech forest of the Dinamic Mountains: Influences of light regime, herb competition and browsing. *Forest Ecology and Management* 285: 20–28.
- D'OLIVEIRA M.V.N. 2009. Forest regeneration in artificial gaps after two years of canopy cover in the state of Acre: Western Amazon. In: Goncalvez R.C., L. C. de Oliveira (Eds.). Embrapa Acre: science and technology for sustainable development of the southwestern Amazon. Embrapa Acre. cap. 3, Rio Branco, AC: 68–96.
- D'OLIVEIRA M.V.N., RIBAS L.A. 2011. Forest regeneration in artificial gaps twelve years after canopy opening in Acre state Western Amazon. *Forest Ecology and Management* 261: 1722–1731.
- DUGUID M.C., FREY B.R., ELLUM D.S., KELTY M., ASHTON M.S. 2013. The influence of ground disturbance and gap position on understory plant diversity in upland forests of southern New England. *Forest Ecology and Management* 303: 148–159.
- DUPUY J., CHAZDON R.L. 2008. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *Forest Ecology and Management* 255: 3716–3725.
- FAHEY R.T., PUETTSMANN K.J. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *Journal of Ecology* 95: 1098–1109.
- FRANKLIN J.F., SPIES T.A., VAN PELT R., CAREY A.B., THORNBURGH D.A., BERG D.R., LINDENMAYER D.B., HARMON M.E., KEETON W.S., SHAW D.C., BIBLE K., CHEN J. 2002.

Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155: 399–423.

FROCHOT H., WEHRLÉN L., COLLET C. 1996. Effect of grasses and shrubs on the growth of young Oak stand. Reims, France. Tome 1: 191–197.

GAGNON J.L., JOKELE E.J., MOSER W.K., HUBER D.A. 2004. Dynamics of artificial regeneration gaps within a longleaf pine flatwoods ecosystem. *Forest Ecology and Management* 172: 133–144.

GANADE G., BROWN V.K. 2002. Succession in old pastures of central Amazonia: role of soil fertility and plant litter. *Ecology* 83: 743–754.

GEORGE L.O., BAZZAZ F.A. 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gilliam, F.S., Roberts, M.R. (Eds.). *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford: 265–282.

GODEFROID S., PHARTYAL S., WEYEMBERGH G., KOEDAM N. 2005. Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. *Forest Ecology and Management* 210: 91–105.

GRANT D.W., PETERS D.P.C., BECK GK., FRALEIGH H.D. 2003. Influence of an exotic species, *Acroptilon repens* (L.) DC on seedling emergence and growth of native grasses. *Plant Ecology* 166: 157–166.

GRIFFITHS R.P., GRAY A.N., SPIES T.A. 2010. Soil properties in old-growth Douglas-fir forest gaps in the western Cascade Mountains of Oregon. *Northwest Science* 84(1): 33–45.

HAGEMANN U., KELEN G.V.D., WAGNER S. 2012. Comparative assessment of natural regeneration quality in two northern hardwood stands. *Northern Journal of Applied Forestry* 30(1): 5–15.

HUTCHINSON T.F., BOEMER R.E.J., SUTHERLAND S., SUTHERLAND E.K., ORTT M., IVERSON L.R. 2005. Prescribed fire effects on the herbaceous layer on mixed-oak forests. *Canadian Journal of Forest Research* 35: 877–890.

KREBS C.J. 1999. *Ecological methodology*: AddisonWesley Longman Menlo Park. California. 620 p.

LEGOUT A., NYS C., PICARD J.F., TURPAULT M.P., DAMBRINE E. 2009. Effects of storm Lothar (1999) on the chemical composition of soil solution and on herbaceous cover, humus and soils (Fougeres, France). *Forest Ecology and Management* 257: 800–810.

LI Q.Z., BOGAERT J., NIJS I. 2005. Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation. *Ecography* 28: 777–790.

MALLIK A.U., KREUTZWEISER D.P., SPALVIERI C.M. 2014. Forest regeneration in gaps seven years after partial harvesting in riparian buffers of boreal mixedwood streams. *Forest Ecology and Management* 312: 117–128.

MARVI-MOHADJER M.R. 2011. *Silvicultural*. Tehran: Tehran University Press. 386 p.

MIHOK B., GALHIDY L., KELEMEN K., STANDOVAR T. 2005. Study of gap – phase regeneration in managed beech forest: relations between tree regeneration and light, substrate features and cover of ground vegetation. *Acta Silvatica and Lingaria Hungarica* 1: 25–38.

MILLINGTON J.D.A., MICHAEL B.W., MEGAN S.M., JIANGUO L. 2012. A compositional gap regeneration model for managed northern hardwood forests. *Forest Ecology and Management* 253: 17–27.

MOLOFSKY J., AUGSPURGER C.K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68–77.

MOUNTFORD E.P., SAVILL P.S., BEBBER D.P. 2006. Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry* 79: 389–408.

MUELLER D.D., ELLENBERG H. 1989. *Aims and methods of vegetation ecology*. John Wiley and Sons. 547 p.

MUSCOLO A., SIDARI M., BAGNATO S., MALLAMACI C., MERCURIO R. 2010. Gap size effects on above- and below- ground processes in a silver fir stand. *European Journal of Forest Research* 129: 355–365.

- NAAF T., WULF M. 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. *Forest Ecology and Management* 244: 141–149.
- NAGEL T.A., SVOBODA M., RUGANI T., DIACI J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. *Plant Ecology* 208: 307–318.
- NASCIMENTO A.R.T., ARAÚJO G.M., GIROLDO A.B., SILVA P.P.F. 2012. Gap area and tree community regeneration in a tropical semi deciduous forest. *Tropical Forests* 388: 140–154.
- PAGE L.M., CAMERON A.D. 2006. Regeneration dynamics of Sitka spruce in artificially created forest gaps. *Forest Ecology and Management* 221: 260–266.
- POURBABAEI H., HADADI-MOGHADAM H., BEYGOM-FAGHIR M., ABEDI T. 2013. The influence of gap size on plant species diversity and composition in beech forests, Ramsar, Mazandaran Province, North of Iran. *Biodiversitas* 14(2): 89–94.
- PROMIS A., GÄRTNER S., REIF A., CRUZ G. 2012. Effects of canopy gaps on forest floor vascular and non-vascular plant species composition and diversity in an uneven-aged *Nothofagusbetuloides* forest in Tierra del Fuego, Chile. *Community Ecology* 13(2): 145–154.
- ROMELL E., HALLSBY G., KARLSSON A., GARCIA C. 2008. Artificial canopy gaps in a *Macaranga* spp. dominated secondary tropical rain forest-effects on survival and above ground increment of four under-planted dipterocarp species. *Forest Ecology and Management* 255: 1452–1460.
- RUNKLE J.R. 1982. Patterns of disturbance in some old-growth Mesic forests of eastern North America. *Ecology* 63: 1533–1546.
- RUNKLE J.R. 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (Eds). *The ecology of natural disturbance and patch dynamics*. Academic Press: New York: 17–34.
- SAGHEB-TALEBI K., ABAZARI B., NAMIRANIAN M. 2005. Regeneration process in natural uneven-aged Caspian beech forests of Iran. *Schweizerische Zeitschrift fuer Forstwesen* 156: 477–480.
- SAPKOTA I.P., TIGABU M., ODEN P.C.H. 2009. Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. *Journal of Forestry Research* 20(1): 7–14.
- SEFIDI K., MARVI MOHADJER M.R., MOSANDI R., COPENHEAVER C.A. 2011. Canopy gaps and regeneration in old-growth Oriental beech (*Fagus orientalis* Lipsky) stands, northern Iran. *Forest Ecology and Management* 262: 1094–1099.
- SCHLIEMANN S.A., BOCKHEIM J.G. 2011. Methods for studying treefall gaps: a review. *Forest Ecology and Management* 261: 1143–1151.
- SCHWARTZ G., LOPES J.C.A., MOHREN G.M.J., PEÑA-CLAROS M. 2013. Post-harvesting silvicultural treatments in logging gaps: A comparison between enrichment planting and tending of natural regeneration. *Forest Ecology and Management* 293: 57–64.
- STANCIU P.T., O'HARA K.L. 2005. Regeneration growth in different light environments of mixed species, multiaged, mountainous forest of Romani. *European Journal of Forest Research* 125: 151–162.
- VAN DAM O. 2001. *Forest filled with gaps: Effects of gap size on water and nutrient cycling in tropical rain forest: A study in Guyana*. Publisher Tropenbos-Guyana programme. Georgetown, Guyana. 208 p.
- WANG G., LIU F. 2011. The influence of gap creation on the regeneration of *Pinus tabuliformis* planted forest and its role in the near-natural cultivation strategy for planted forest management. *Forest Ecology and Management* 262: 413–423.
- YAMAMOTO S.I., NISHIMURA N., TORIMARU T., MANABE T., ITAYA A., BECEK K. 2011. A comparison of different survey methods for assessing gap parameters in old-growth. *Forest Ecology and Management* 262: 886–893.