DROUGHT EFFECTS ON REPRODUCTIVE AND GROWTH CHARACTERISTICS IN SEED ORCHARDS

TUĞRUL VAROL¹, HALİL BARIŞ ÖZEL^{1*} AND NEBİ BİLİR²

¹Forestry Faculty of Bartin University74100 Bartin, Turkey ²Forestry Faculty of Suleyman Demirel University, 32260 Isparta, Turkey *Corresponding author's email: halilbarisozel@gmail.com, Phone office +90378-2235153, Fax +90378-2235062

Abstract

Global climate change is one of the most important environmental problems, and it is also known that this change will lead to negative effects such as drought and increase in global temperature. This change is also estimated to increase its episodic effects negatively on growth and reproduction of the forest trees. In order to estimate the episodic or continuous effects of the drought, it is necessary to carry out studies based on long-term data. One of these studies are the investigation to be carried out on seed orchards that are one of the most important seed resources in forestry. Within this context, in this study, we determined to the reproductive and growth responses of the clones to the drought that continued in the most drought season (2012) for 2 subsequent years along with 65-year climate data for Red Pine (*Pinus brutia* Ten.) and Taurus Cedar (*Cedrus libani* Rich.). The relationships of SPEI values with seed characteristics and cone production were examined by using Spearman Correlation Analysis.

According to the results obtained from this study, it was found that the severe drought was effected the reproductive characteristics of both of red pine and cedar. The effect of drought on the number of cone (r=-0.810, P=0.022) in red pine and on the number of 1-year-old cones (r=-0.40, P=0.027) and on cone moisture (r=-0.715, P=0.022) in cedar was quite evident. These results indicate that approximately 65% of the change in number of cone in Red Pine and approximately 51% of the change in moisture content of the cones in cedar can be explained with the drought. From the data, it is clear that the drought is effective on the cone yield and seed characteristics in seed orchards of both of Red Pine and Taurus Cedar species.

Key words: SPEI, Drought, Seed orchard, Pinus brutia, Cedrus libani.

Introduction

Global climate change is affecting the life cycle of all living things.A considerable increase is observed in the number of studies (Mueller et al., 2005) examining the factors such as the increase in carbon dioxide and drought level related to the climate change that is effecting the ecosystem and its processes (Anon., 2006). The drought, which can lead to significant changes in vegetation especially in arid and semi-arid zones (Gibbens et al., 2005; Breshears et al., 2005), may also lead to changes in plant species diversity and compositions with the decrease in precipitations (Gitlin et al., 2006; Weltzin et al., 2003; Breshears et al., 2008). For instance; the pasture lands were dominant in Mexico in mid 1800s, it was observed in the vegetation maps prepared in 1998 that the potion of those lands decreased down to 1% in certain regions (Gibbens et al., 2005). The increase in drought does not only change the vegetation structure, but it also effects the land stability and land-plant (Farooq et al., 2009; Allen et al., 2010; Adams et al., 2009). Moreover, besides the direct effects of the drought such as limiting the photosynthesis (Felexas & Medrano, 2002; Medrano et al., 2002) and leading to changes in carbon retention in roots and shoots and in circulation of nutrients within the plant (Turtola et al., 2003), it has also indirect effects by affecting the secondary pests (Breshears et al., 2008). In many studies the relationship between vitality of the plant and the drought has been examined. The vitality has been linked to water stress and the change in reproductive activity of plant cover has not been examined (McDowell et al., 2008). The tolerance of tree species to drought is different.Considering the species, it has been determined

that the Juniperus species are more tolerant to drought than Pinus species (Breshears et al., 1997; Linton et al., 1998; Breshears et al., 2008). The effects of the drought on cedars have been determined and it has been specified that the drought tolerance of Cedrus libani is higher than that of Cedrus atlantica (Boydak, 2003). On the other hand, global warming and climate change that are the most important environmental problem of today also threatened the future of the forests. It is therefore required to take in-situ and ex-situ protective precautions in order to protect the genetic structures of all the tree species (Tunçtaner, 2007). In this parallel, the first precaution to be taken is to develop the seed orchards and seed plantations (Bilir et al., 2004; Koski & Antola, 2003). By significantly affecting the productivity of seed orchards, global warming and climate change also threatened the future of forest trees and productive forest lands (Zobel & Talbert, 1984; Carter, 1996; Wang et al., 2004). For this reason, the changes in forest gene sources caused from climate change and global warming should be examined periodically via actual techniques (Alfaro et al., 2014). The most important one among those gene sources is the seed orchards.

In this study, it is aimed to determine the effects of climate change on the seed productivity of Red Pine and Taurus Cedar species that are widely used in forest studies carried out under various ecological conditions in Turkey.

Materials and Methods

In order to determine the effects of drought, SPEI (Standard Precipitation Evapotranspiration Index) values were correlated with the number of cones for *Pinus brutia*

and the number of male-female flowers at the ages of 1 and 2 years, the length, diameter and volume of the cone, the number of branches, moisture content of the cone, the number, length and width of the seeds in the cone, and the germination percentage values for Cedrus libani. These measurements were taken in Fethiye cedar and red pine seed orchards. The Red Pine seed orchard, first one of the seed orchards in Muğla-Fethiye where the study was carried out, was originated from Kaş-Karaçay, and it was constructed on 14.2 ha land in 1.3 Reclamation Zone by using 30 clones and 2263 saplings in year 1983. The Taurus Cedar seed orchard is the second seed orchards where the study was carried out, originated from Fethive-Esentepe, and was established on 5.4ha land in 1.2 Reclamation Zone by using 30 clones and 1503 saplings (Anon., 2014) (Fig. 1).

The statistical calculations for the calculation of SPEI values were made via the R 3.2.2 software. SPEI values were taken as the mean value of the 6-month vegetation period. Considering the SPEI values in vegetation periods between 1950 and 2014, the most drought year of last 64 years was found to be 2012 with the value of -1.30377. While year 2013 was the 4th most drought year with the value of -0.77142, year 2014 was 35th most drought year with the value of -0.04489. For this reason, even if the -1.30377 is in "moderately drought" class in SPEI classification, but it has been the most dry season of Fethiye region for last 65 years, it is accepted to be the severely dry,

while the year 2013 is accepted to be of moderate drought and the year 2014 is accepted to be of normal drought. The difference in cones and seeds due to the effects of drought was analyzed with bi-directional Variance analysis, where the Duncan test was performed after the multiple post hoc comparisons. 2 - variable linear correlation analysis was performed with Spearman correlation test.

Results and Discussions

The values obtained in red pine and cedar seed orchards under different drought levels were examined, it was observed that the drought led to different levels of influences in some components of those species (Tables 1 and 2). In cedar seed orchard; while the drought was not effective on the flowering percentage of female flowers and the number of male flowers, it was found to be effective on other variables (Table 2). Hence, in various studies that were carried out in seed orchards, it was reported that the female flowers are influenced from the changes in environmental factors than male flowers (Zobel &Talbert, 1984; Boydak 2003; Tunçtaner, 2007). It was determined that normal and severe drought types led to 54% decrease in the number of 1- and 2-year-old cones especially in cedar seed orchard, while the moderate drought led to 22% of decrease in the number of 1- and 2-year-old cones.

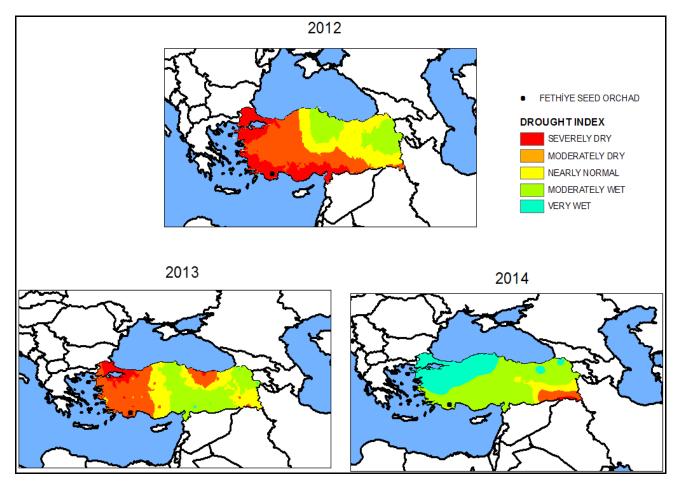


Fig. 1. The location of Fethiye seed orchard.

		Treatments			ANOVA	
	Severely dry	Moderately dry	Near normal	F ^{1,2,3,4}	Р	
Count of cone (Pinus brutia)	12.39 ± 2.29^{b}	18.15 ± 3.26^{b}	$98.63 \pm 9.66^{\mathrm{a}}$	304.41	2.00 10-16	
Mean height (Cedrus libani)	$476.15 \pm 8.56^{\circ}$	530.99 ± 9.31^{b}	563.66 ± 10.22^{a}	24.94^{2}	7.27 10-11	
Block 1	$385.38 \pm 6.37^{\circ}$	432.65 ± 4.27^{b}	$461.33\pm7.07^{\mathrm{a}}$	40.55^{1}	4.19 10-14	
Block 2	$507.25\pm9.32^{\mathrm{b}}$	$567.78 \pm 12.85^{\rm a}$	$591.80 \pm 14.22^{\mathrm{a}}$	12.54^{1}	1.17 10-5	
Block 3	535.83 ± 11.96^{b}	$592.55 \pm 11.70^{\rm a}$	637.85 ± 13.15^{a}	17.31^{1}	2.60 10-7	
Mean diameter at breast height (Cedrus libani)	$123.28 \pm 2.85^{\circ}$	144.37 ± 2.59^{b}	162.93 ± 3.22^a	46.82^{2}	2.00 10-16	
Block 1	92.30 ± 3.18^{b}	126.43 ± 3.23^{a}	$135.83\pm2.76^{\mathrm{a}}$	55.96 ¹	2.00 10-16	
Block 2	137.25 ± 3.83^{b}	147.85 ± 5.27^{b}	173.30 ± 4.84^{a}	15.63 ¹	9.61 10-7	
Block 3	$140.28 \pm 3.53^{\circ}$	$158.83\pm3.06^{\text{b}}$	$179.65\pm5.94^{\mathrm{a}}$	20.38^{1}	2.56 10-8	
Mean volume (Cedrus libani)	$21.78\pm0.81^{\rm c}$	29.50 ± 1.24^{b}	35.79 ± 1.44^{a}	34.23 ⁴	2.42 10-14	
Block 1	17.22 ± 0.90^{b}	$20.73 \pm 1.28^{\text{b}}$	27.52 ± 1.90^{a}	13.31 ³	5.86 10-6	
Block 2	$20.68 \pm 1.21^{\text{b}}$	35.66 ± 2.32^{a}	33.44 ± 2.13^{a}	17.73 ³	1.72 10-7	
Block 3	27.85 ± 1.48^{b}	$32.11 \pm 1.93^{\text{b}}$	$46.40\pm2.46^{\rm a}$	22.83 ³	3.69 10-9	
Mean one year cones number (Cedrus libani)	52.57 ± 2.47	88.88 ± 5.41^{b}	$113.05\pm6.16^{\mathrm{a}}$	34.99^4	1.27 10-14	
Block 1	35.43 ± 2.69^{b}	$95.85 \pm 11.45^{\mathrm{a}}$	$89.28\pm9.35^{\mathrm{a}}$	14.52^{3}	2.17 10-6	
Block 2	$53.27 \pm 4.14^{\rm c}$	90.35 ± 7.67^{b}	$128.78\pm12.86^{\mathrm{a}}$	17.52^{3}	2.02 10-7	
Block 3	69.00 ± 4.04^{b}	80.45 ± 7.71^b	121.10 ± 10.22^{a}	12.30^{3}	1.35 10-5	
Mean two years cones number (Cedrus libani)	46.70 ± 1.20^{b}	82.05 ± 5.29^{a}	$79.65\pm5.03^{\mathrm{a}}$	20.11^4	5.20 10-9	
Block 1	$33.67 \pm 1.76^{\text{b}}$	63.82 ± 7.19^{a}	64.45 ± 7.14^{a}	8.90 ³	2.46 10-4	
Block 2	50.00 ± 4.22^{b}	$97.09 \pm 10.01^{\mathrm{a}}$	73.90 ± 7.15^{ab}	9.74 ³	1.19 10-4	
Block 3	56.44 ± 3.90^{b}	85.26 ± 8.68^{ab}	100.41 ± 9.99^{a}	7.83 ³	6.29 10 ⁻⁴	
Cone width (mm) (Cedrus libani)	32.13 ± 0.54^{b}	35.02 ± 0.53^a	34.74 ± 0.57^{a}	8.46 ¹	3.71 10-4	
Moisture of cones (%) (Cedrus libani)	36.13 ± 0.35^{b}	43.20 ± 0.42^{a}	44.05 ± 0.56^a	91.65 ¹	2.00 10-16	
Seed length in the one cone (mm) (Cedrus libani)	6.00 ± 0.10^{b}	6.80 ± 0.17^{a}	6.82 ± 0.16^{a}	10.22^{1}	8.08 10-5	

Table 1. Influence of dr	ought levels in cone (N	Mean ± SE) of <i>Pinus</i>	brutia and Cedrus libani.

¹: *F*(2,117), ²: *F*(2,357), ³: *F*(2,123), ⁴: *F*(2,363); ^{*a.b.c.*}: Duncan Multiple Range Test

Table 2. Influence of drought levels in seed (Mean±SE) of Cedrus libani.

	Treatments			ANOVA	
	Severely dry	Moderately dry	Near normal	F ^{1,2,3,4}	Р
Mean branch number	$22.37\pm0.39^{\rm c}$	26.48 ± 0.45^{b}	28.58 ± 0.56^{a}	45.03^{4}	2.00 10-16
Block 1	20.63 ± 0.71^{b}	26.28 ± 0.94^{a}	27.71 ± 0.90^a	18.29^{3}	1.12 10-7
Block 2	22.62 ± 0.71^{b}	26.96 ± 0.89^{a}	29.98 ± 1.20^{a}	14.51^{3}	2.21 10-6
Block 3	23.87 ± 0.70^{b}	26.21 ± 0.78^{ab}	28.04 ± 0.96^a	6.27^{3}	2.56 10-3
Mean male flower number	555.34 ± 30.64^{b}	751.89 ± 60.45^{a}	806.47 ± 54.49^{a}	6.79^{4}	1.27 10-2
Block 1	464.85 ± 47.78^{b}	887.38 ± 133.15^{a}	773.00 ± 78.17^{ab}	5.53 ³	5.00 10-2
Block 2	685.57 ± 47.74^{a}	679.81 ± 80.15^{a}	810.55 ± 106.02^{a}	0.86 ³	0.423
Block 3	523.63 ± 54.45^{b}	688.47 ± 80.95^{ab}	835.87 ± 90.07^{a}	4.10^{3}	1.88 10-2
Mean female flower numbers	63.99 ± 3.89^{b}	93.96 ± 5.36^{a}	84.97 ± 4.30^a	11.28^{4}	1.77 10-5
Block 1	47.08 ± 3.61^{b}	89.39 ± 6.45^{a}	71.19 ± 6.39^a	13.80^{3}	3.92 10-6
Block 2	74.40 ± 8.35^a	102.41 ± 10.04^a	108.51 ± 8.65^a	3.88 ³	2.32 10-2
Block 3	70.49 ± 6.16^{a}	90.08 ± 10.14^{a}	75.21 ± 5.07^a	1.94 ³	1.49 10-3
Conversion rate (%) of female flowers numbers to two years cones	55.64 ± 15.79^{ab}	50.66 ± 18.61^{b}	$59.97 \pm 14.54^{\mathrm{a}}$	9.68 ⁴	8.03 10-5
Block 1	56.80 ± 19.85^{ab}	51.81 ± 16.14^{b}	63.22 ± 16.86^a	3.82^{3}	0.0245
Block 2	$56.67 \pm 14.42^{\ a}$	$52.94\pm22.82^{\mathrm{a}}$	57.02 ± 13.37^a	0.55 ³	0.578
Block 3	$53.44 \pm 11.51 \ ^{ab}$	47.22 ± 15.19^{b}	59.66 ± 12.09^{a}	7.43 ³	8.98 10-4

¹: *F*(2,117), ²: *F*(2,357), ³: *F*(2,123), ⁴: *F*(2,363); ^{*a,b,c*}: Duncan Multiple Range Test

In red pine plantation, the severe drought and moderate drought led to 87% and 81% decreases, respectively in the number of cones. Thus, considering the Duncan test results in red pine plantation, it was observed that the severe drought and moderate drought did not lead to significant change, while all three drought types led to statistically significant differences in first year. Thus, as a result of drought it has been reported that significant damages occurred in gene sources of coniferous species except the pines, while the pines were damaged less because they have more tolerant growth course and genetic base (Aber et al., 2001; Alfaro et al., 2014). At the end of second year, statistically significant differences $(p \ge 0.01)$ were observed in red pine seed orchard in terms of the number of cone and the seed productivity (Table 1). Accordingly, it was observed that only the severe drought type has led difference in the number of cone and the seed productivity. On the other hand, it was found in Taurus Cedar seed orchard that the drought was effective on all of the determined quantitative parameters (p > 0.001) (Table 2). Accordingly, it was determined that all the drought types decreased the number and development of mean height, diameter at breast height, and length and width and moisture of cone by 5-50%. In various studies on the protection of different gene species, it has been reported that especially the drought negatively affected the height development and width development and formation of male and female flowers and pollen production by 28.6-65.4% (Gitlin et al., 2006; Gienapp et al., 2008). On the other hand, selection of venues for seed orchards has been more important than other climatic regions for sustainability of cone production (Schmidtling, 1987).

On the cone productivity and seed characteristics in seed orchards, besides the number of clones and the genetic structure, the environmental factors have also significant effect. Within this context, the effect of gene changes in environmental factors on the gene sources should be periodically examined, and the relationship of environmental factors with those parameters should be investigated (Bilir et al., 2002; Bilir et al., 2003). Within the scope of this study the relationships of SPEI values with cone production and seed characteristics were examined by using Spearman Correlation Analysis. According to the results obtained, p > 0.005 is for the length and number of seed in cedar seed orchard, while p < 0.005 for other variables. The most statistically significant values were obtained in the number of cone (r=-0.810, P=0.022) in red pine and the number of 1-yearold cones (r=-0.40, P=0.027) and cone moisture (r=-0.715, P=0.022) in Taurus Cedar. These results indicate that approximately 65% of the change in the number of cones in red pine species and approximately 51% of the change in moisture content of cedar cones can be explained with the drought. The studies investigating the relationships of environmental factors (temperature, precipitation, moisture etc.) with development in seed sources, cone production, and seed characteristics are seen scarce especially in Turkey, the number of original studies on this topic are really insufficient. It was determined in studies on relationships of environmental factors and biological diversity that there were strong relationships between cone and seed production and seed characteristics. However, it has been determined by Eprom (1997) that there is an important relation between drought period and photosynthesis level in Taurus Cedar. In a study on Abies alba about this topic, it was demonstrated that there was a relationship at 73.2% level at p > 0.01 confidence level between drought/water stress and growth/seed productivity (Macias et al., 2006; Skrøppa et al., 2007). Similarly in another study carried out in North America, a positive and significant relationship at 82.4% level was found between annual ring development of trees and drought (Stahle et al., 2007). Yurkonis & Meiners (2006) investigated the effects of drought on photosynthesis and biodiversity and found 73.5% and negative relationship between drought stress and photosynthesis and 79.7% and negative relationship between drought stress and herbal biodiversity.

Conclusions

In order to ensure the continuity of seed sources in Red Pine and Taurus Cedar seed orchards in Muğla-Fethiye region and to realize the forestation with mentioned tree species, it is required to periodically follow the effect of environmental factors on seed orchards and to establish new in-situ and ex-situ gene sources for these species in case of risky situations.

Acknowledgement

We would like to thank the Directorate of Forest Trees and Seeds Reclamation Research Institute supporting this study carried out in seed orchard.

References

- Aber, J., R.P. Neilson, S., Mcnulty, J.M. Lenihan, D. Bachelet and R.J. Drapek. 2001. Forest processes and global environmental change: predicting the effects of individual and multiple stressors. *Bio. Sci.*, 51: 735-751.
- Adams, H.D., M. Guardiola-Claramonte, G.A. Barron-Gafford, J.C. Villegas, D.D. Breshears, C.B. Zou, P.A. Troch and T.E. Huxman. 2009. Temperature sensitivity of droughtinduced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*, 106(17): 7063-7066.
- Alfaro, R.I., B. Fady, G.G. Vendramin, I.K. Dawson, R.A. Fleming, C. Sáenz-Romero, R.A. Lindig-Cisneros, T. Murdock, B. Vinceti, C.M. Navarro, T. Skrøppa, G. Baldinelli, Y.A. El-Kassaby and J. Loo. 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *Forest Ecol. & Manag.*, 333: 76-87.
- Allen, C.D., A.K. Macalady, H. Chenchouni, D. Bachelet, N. Mcdowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E.H. (Ted) Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J.H. Lim, G. Allard, S. W. Running, A. Semerci and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol. & Manag.*, 259(4): 660-684.
- Anonymous. 2006. Change 2006. IPCC guidelines for national greenhouse gas inventories.[2013-04-28]. http://www. ipccnggip. iges. or. jp./public/2006gl/index. html.

1229

- Anonymous. 2014. *Turkey Seed Orchard Situation Report*. Seed Breeding Research Institute, Ankara, 35p.
- Bilir, N., K.S. Kang and D. Lindgren. 2003. Fertility variation and effective number in the seed production areas of *Pinus radiata* and *Pinus pinaster*. Silvae Genetica, 52(2): 45-88.
- Bilir, N., K.S. Kang and H. Ozturk. 2002. Fertility variation and gene diversity in clonal seed orchards of *Pinus brutia*, *Pinus nigra* and *Pinus sylvestris* in Turkey. *Silvae Genetica*, 51(2-3): 112-116.
- Bilir, N., K.S. Kang, D. Zang and D. Lindgren. 2004. Fertility variation and status number between a base population and a seed orchard of *Pinus brutia*. *Silvae Genetica*, 53(4-5): 161-163.
- Boydak, M. 2003. Regeneration of Lebanon cedar (*Cedrus libani* A. Rich.) on karstic lands in Turkey. *Forest Ecol. & Manag.*, 178(3): 231-243.
- Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Flouyd, J. Belnap, J.J. Anderson, O.B. Myers and C.W. Meyer. 2005. Regional vegetation die-off in response to globalchange-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, 102(42): 15144-15148.
- Breshears, D.D., O.B. Myers, C.W. Meyer, F.J. Barnes, C.B. Zou, C.D. Allen, G. Nathan and W.T. Pockman. 2008. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, 7(4): 185-189.
- Breshears, D.D., O.B. Myers, S.R. Johnson, C.W. Meyer and S.N. Martens. 1997. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. J. Ecol., 85: 289-299.
- Carter, K.K. 1996. Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Can. J. For. Res.*, 26: 1089-1095.
- Eprom, D. 1997. Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*). *J. Exp. Bot.*, 48(10): 1835-1841.
- Farooq, M., A. Wahid, N. Kobayashi, D. Fujita and S.M.A. Basra. 2009. Plant drought stress: effects, mechanisms and management. *In Sustainable Agriculture*. Springer Netherlands. pp. 153-188.
- Flexas, J. and H. Medrano. 2002. Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. *Ann. Bot.*,89(2): 183-189.
- Gibbens, R.P., R.P. Mcneely, K.M. Havstad, R.F. Beck and B. Nolen. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. *J. Arid Environ.*, 61(4): 651-668.
- Gienapp, P., C. Teplitsky, J.S. Alho, J.A. Mills and J. Merila. 2008. Climate change and evolution disentangling environmental and genetic responses. *Mol. Ecol.*, 18: 167-178.
- Gitlin, A.R., C.M. Sthultz, M.S. Bowker, S. Stumpf, K.L. Paxton, K. Kennedy, A. Munoz, J.K. Bailey and T.G. Whitham. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Cons. Biol.*,20(5): 1477-1486.

- Koski, V. and J. Antola. 2003. National tree breeding and seed production programme for Turkey 1994-2003, The Research Directorate of Forest Tree Seeds and Tree Breeding, Ankara, Turkey, 52p.
- Linton, M.J., J.S. Sperry and D.G. Williams. 1998. Limits to water transport in Juniperus osteosperma and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Funct. Ecol.*, 12(6): 906-911.
- Macias, M., L. Andreu, O. Bosch, J.J. Camarero and E. Gutierrez. 2006. Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its South-western distribution limit. *Climate Change*, 79: 289-313.
- McDowell, N., W.T. Pockman, C.D. Allen, D.D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D.G. Williams and E.A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178(4): 719-739.
- Medrano, H., J.M. Escalona, J. Bota, J. Gulias and J. Flexas. 2002. Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. *Ann. Bot.*, 89(7): 895-905.
- Mueller, R.C., C.M. Scudder, R. Porter, C.A. Talbot Trotter and T.G. Gehring. 2005. Whitham. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol., 93(6): 1085-1093.
- Schmidtling, R.C. 1987. Locating pine seed orchards in warmer climates: benefits and risks. *Forest Ecol. & Manag.*, 19(1-4): 273-283.
- Skrøppa, T., K. Kohmann, Ø. Johnsen, A. Steffenrem and Ø.M. Edvardsen. 2007. Field performance and early test results of offspring from two Norway spruce seed orchards containing clones transferred to warmer climates. *Can. J. Forest Res.*, 37(3): 515-522.
- Stahle, D.W., F.K. Fye, E.R. Cook and R.D. Griffin. 2007. Treering reconstructed megadroughts over North America since A.D. 1300. *Climate Change*, 83: 133-149.
- Tunçtaner, K. 2007. Forest Genetics and Tree Breeding. Turkey Foresters Association. Education Series 2, Ankara, 470 p.
- Turtola, S., A.M. Manninen, R. Rikala and P. Kainulainen. 2003. Drought stress alters the concentration of wood terpenoids in Scots pine and Norway spruce seedlings. J. Chem. Ecol., 29(9): 1981-1995.
- Wang, W., B.T. Anderson, R.K. Kaufmann and R.B. Myneni. 2004. The relation between the North Atlantic Oscillation and SSTs in the North Atlantic basin. J. Climate., 17: 4752-4759.
- Weltzin, J.F., M.E. Loik, S. Schwinning, D.G. Williams, P.A. Fay, B.M. Haddad, J. Harte, T.E. Huxman, A.K. Knapp, G. Lin, W.T. Pockman, M.R. Shaw, E.E. Small, M.D. Smith, S.D. Smith, D.T. Tissue and J.C. Zak. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, 53(10): 941-952.
- Yurkonis, K.A. and J.J. Meiners. 2006. Drought impacts and recovery are driven by local variation in species turnover. *Plant Ecol.* 184: 325-336.
- Zobel, B. and J. Talbert. 1984. *Applied Forest Tree Improvement*. John Wiley & Sons Inc. New York, 505 pp.

(Received for publication 29 April 2016)