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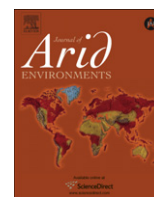
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Short Communication

Dieback affects forest structure in a dry Afromontane forest in northern Ethiopia

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ABSTRACT

Forests are highly susceptible to dieback under ongoing climate warming. In degraded forests, dead standing trees, or snags, have become such prominent features that they should be taken into account when setting management interventions. This study investigated (1) the extent and spatial pattern of standing dead stems of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* along an elevational gradient, and (2) the effect of dieback on forest stand structure. We quantified abundance, size, and spatial pattern of tree dieback in 57 plots (50 m × 50 m) established at 100 m intervals along five transects. The snag density and basal area (mean ± SE) of the two species combined were 147 ± 23 stems ha⁻¹ and 5.35 ± 0.81 m² ha⁻¹, respectively. The percentages of snags were extremely high for both *J. procera* (57 ± 7%) and *O. europaea* subsp. *cuspidata* (60 ± 5%), but showed a decreasing trend with increasing elevation suggesting that restoration is even more urgent at the lower elevations. Snags of the two species accounted for 31 and 45% of total stand density and basal area, respectively. Living stems exhibited truncated inverse-J-shaped diameter and height class distributions, indicating serious regeneration problems of these foundation species in the study area. In addition to direct interventions to assist recruitment of climax tree species, sites with high dieback would probably benefit from snag reduction to prevent fire incidents in the remaining dry Afromontane forests in northern Ethiopia.

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1. Introduction

Human disturbance (Darbyshire et al., 2003) and climate change (Dale et al., 2000; Garcia-Fayos and Gasque, 2002; Hemp, 2009) are major driving forces that shape forest ecosystems. Future warming is expected to exacerbate regional tree species dieback worldwide (Adams et al., 2009) thereby affecting regional carbon budgets. The suppression or loss of foundation tree species in tropical montane forests has acute and chronic impacts on fluxes of energy and nutrients, hydrology, food webs, and biodiversity (Ellison et al., 2005). So-called 'dieback', a special form of forest decline which affects only canopy trees, is known from several of the world's forest ecosystems (e.g. Mueller-Dombois, 1988). As far back as 1986, it was

shown that forests are highly susceptible to dieback under ongoing climate warming (Mueller-Dombois, 1988; Solomon, 1986). After a dwindling of interest in the late 1980s, forest dieback resulting from climate change has started to become a major focus of ecological research again (Allen, 2009; Boehmer, 2011).

The effects of forest disturbance on stand structure and diversity are more severe in dry than in mesic tropical forests (Nepstad et al., 2007). Similarly, lower elevations have warmer temperatures where a slight increase in temperature or a short drought can cause mass tree death (Adams et al., 2009; Gitlin et al., 2006; Segura et al., 2003). The occurrence of dead standing trees, or snags, in a forest is often considered as a notable sign of forest degradation. However, snags are also important ecological components of forest ecosystems (Franklin et al., 1987) as they serve as sources of nutrients (Kueppers et al., 2004), habitats for a wide range of plant and animal species (Harmon et al., 2000; Ohmann et al., 1994) and carbon stores (Kueppers et al., 2004). Because of these functions, understanding the extent of tree dieback and the spatial patterns of snags is useful in managing forest ecosystems (Craig and Friedland, 1991; Gitlin

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et al., 2006). However, in the tropics the status and roles of snags have been rarely studied (Grove, 2001).

Pollen studies in Kenya (Lamb et al., 2003) and northern Ethiopia (Darbyshire et al., 2003) indicate that the flora of East Africa has experienced several changes due to climate change and anthropogenic disturbances. The existing *Juniperus procera*-dominated dry Afromontane forests in northern Ethiopia, for instance, are secondary forest formations established during the fourteenth and eighteenth centuries (Darbyshire et al., 2003). *Juniperus*–*Olea*-dominated forests are of high ecological and economic importance in northern Ethiopia, but the few remaining forests are threatened by severe anthropogenic disturbance and drought (Aerts et al., 2006c; Tsegaye et al., 2010). Dieback during the past few decades has resulted in high densities of snags of *J. procera* and *O. europaea* subsp. *cuspidata* in the remaining forest fragments. Snags have become such prominent features of these forests that they should be taken into account when setting management interventions (Ganey, 1999; Marage and Lemperiere, 2005).

Thus, the objectives of this study were (1) to quantify the extent and spatial patterns of snags of *J. procera* and *O. europaea* subsp. *cuspidata* along an elevational gradient, and (2) to examine the influence of dieback of these two species on the overall stand structure in a dry Afromontane forest in northern Ethiopia.

2. Methods

2.1. Study area

The study was conducted in the Desa'a forest (13°36'–13°56' N and 39°48'–39°51' E), which is located in a semi-arid environment in northern Ethiopia (Fig. 1). The study area lies between the mesic Tigrean plateau (2720 m a.s.l.) and the dry Afar lowlands (1400 m a.s.l. and below). The study site receives a mean annual rainfall of 532 mm (Abegaz, 2005). Climate here is influenced by elevation with a sharp decline in rainfall and an increase in temperature from the upland plateau to the eastern slopes. A large part of the study area is characterized by shallow soils and frequent rock outcrops of Enticho sandstone and Crystalline Basement (Asrat, 2002).

Desa'a forest is dry single-dominant Afromontane forest within the forest classification of northeast tropical Africa (Friis, 1992). The dominant species *J. procera* and *O. europaea* subsp. *cuspidata* are drought-tolerant species (Breshears et al., 2009; Cuneo and Leishman, 2006) widely occurring from Arabia to southern Africa. Local people noticed that dieback in the study area had occurred in the late 1980s due to extreme high temperature.

2.2. Data collection

Five transects were established perpendicular to the main slope (W–E) in 2008. Field data were collected in 57 plots (50 m × 50 m) established at 100 m intervals within the transects. In each plot, the height of stems >1.5 m tall and stem diameter at breast height (DBH) of stems >2 cm DBH of all individual woody plants were recorded. Stand density, height, DBH, and basal area for all trees, including snags, were calculated. We quantified the percentage of snags for each plot by counting the number of live stems and dead stems. Only *J. procera* and *O. europaea* subsp. *cuspidata* snags were considered because they are the dominant tree species that were heavily affected by dieback.

We analyzed the extent and spatial pattern of dieback along elevation in terms of the percentage of snags of the two species. Dieback index (DI) was defined as the proportion of snags per plot. The effect of dieback on the population structures of *J. procera* and *O. europaea* subsp. *cuspidata* was summarized using diameter and height class distributions. To quantify the changes in stand structure,

we compared stand density, diameter distribution, height distribution, and basal area with and without snags of the two species.

Since most of the data did not follow a normal distribution, we used non-parametric Kruskal–Wallis ANOVA to compare differences in stand structure (Siegel and Castellan, 1988). Linear regression was used to determine the relationship between elevation and percentages of snags. All tests of statistical significance were decided at $\alpha = 0.05$ level. Statistical analyses were performed in SPSS 13.0 for Windows (SPSS Inc., 2004).

3. Results

3.1. Extent and spatial patterns of snags

A total of 83 species belonging to 42 families was recorded in the 57 plots. Fabaceae, Lamiaceae, and Asteraceae were the dominant families. *J. procera* and *O. europaea* subsp. *cuspidata* were the two dominant tree species with relative abundance of 18 and 20%, respectively. The early-successional shrubs *Cadia purpurea*, *Tarchonanthus camphoratus*, and *Dodonaea viscosa* were the dominant woody species, occupying the most degraded parts of the forest. *J. procera* and *O. europaea* subsp. *cuspidata* snags were recorded in 31 (54%) and 49 (86%) of the plots, suggesting that tree dieback has occurred widely throughout the landscape. Mean (\pm SE) snag density (stems ha⁻¹) of *J. procera* and *O. europaea* subsp. *cuspidata* was 89 ± 16 and 91 ± 13 , respectively. Mean (\pm SE) snag basal area (m² ha⁻¹) of *J. procera* and *O. europaea* subsp. *cuspidata* was 3.12 ± 0.80 and 3.37 ± 0.46 , respectively. The dieback index was high for both *J. procera* ($57 \pm 7\%$) and *O. europaea* subsp. *cuspidata* ($60 \pm 5\%$).

The DI of both species decreased with increasing elevation (Fig. 2) suggesting that tree dieback is more severe in the lower (drier) part of the landscape. The overall dieback index ranged from 0% at the higher elevations to 100% at the lower elevations.

3.2. Dieback and stand structure

The dieback of the two foundation species has significantly reduced stand stem density by 31% ($\chi^2 = 16.01$, $P < 0.001$) and stand basal area by 45% ($\chi^2 = 15.80$, $P < 0.001$) (Table 1).

High abundance of live *J. procera* and *O. europaea* subsp. *cuspidata* stems occurred above 2600 and 2400 m a.s.l., respectively (Fig. 3). The percentage of snags was higher for large diameter classes (>40 cm) for both species. The diameter and height class distributions of both species were truncated inverse-J-shaped indicating serious regeneration problems of these foundation species in the study area (Fig. 3).

4. Discussion

The extent of dieback was high for both species and had significantly affected the abundance and spatial distribution of *J. procera* and *O. europaea* subsp. *cuspidata*. The decreasing trend in the percentage of snags for both species along the elevational gradient suggests non-randomness of tree dieback in the study area. Trees at the lower and middle elevations, which are exposed to lower moisture and higher temperature conditions, were more affected. Studies have shown that the extent of drought-driven tree death increases along moisture stress gradients (Suarez et al., 2004). Lower elevations have warmer temperatures where a slight increase in temperature or a short drought can cause mass death of trees (Adams et al., 2009).

Dieback affects species composition and diversity by affecting certain species and size classes, and by changing the light environment of the understory (Engelbrecht et al., 2007; Slik, 2004).

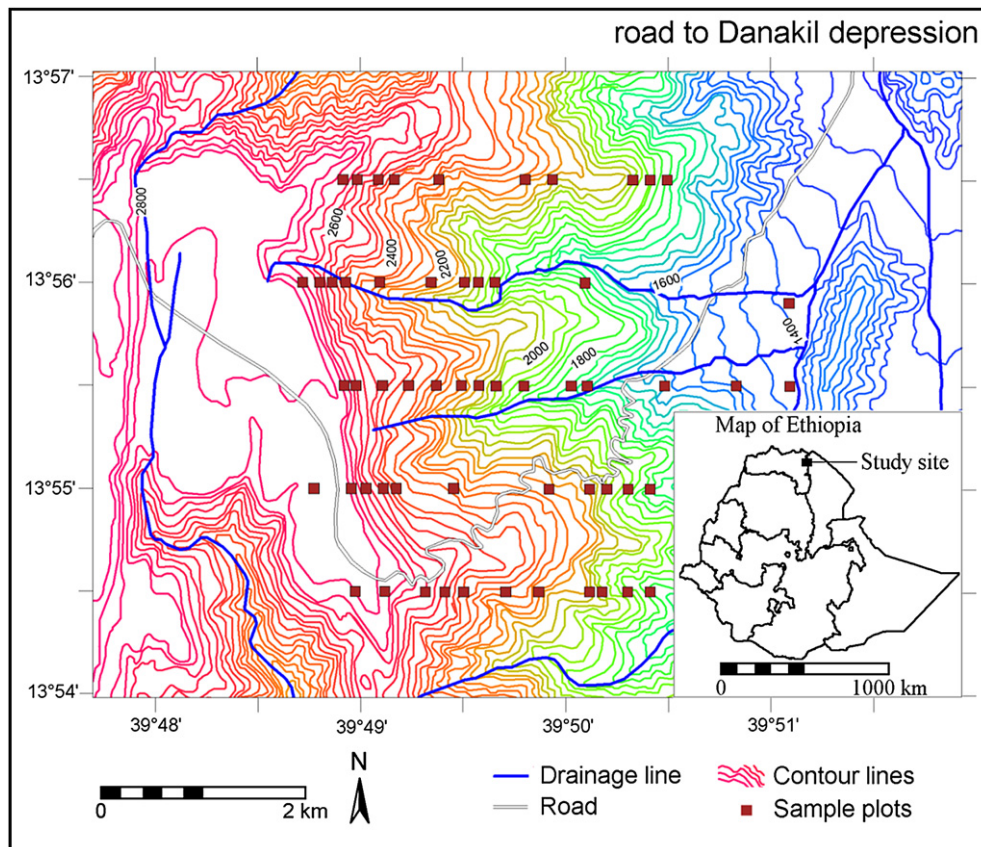


Fig. 1. Location of sample plots within the study area Desa'a Forest, northern Ethiopia.

Because of *J. procera* and *O. europaea* subsp. *cuspidata* are dominant climax species, total stand density and basal area were significantly affected by dieback. The wider gap created in the diameter distribution (Fig. 3) due to tree dieback suggests that the stand structure did not recover after the dieback period. The return to the pre-disturbance status is hampered by slow growth and poor regeneration of the species (Aerts et al., 2006b; Aynekulu et al., 2009). The increase in canopy gaps caused by dieback leads to higher soil temperature and reduces soil moisture availability, the major limiting factors for regeneration of many dry Afromontane tree species (Teketay, 1997). Moreover, dieback also reduced the availability of nurse trees for a successful establishment of seedlings

(Aerts et al., 2007; Mueller et al., 2005). Dieback strongly affected the reproductive range (10–40 cm) of *J. procera* (Couralet et al., 2005), which may influence the maintenance of a viable plant population.

Dieback was more pronounced in large trees, particularly in the case of *J. procera*. Since large trees use more water per unit time than smaller trees (Meizner, 2003). The higher dieback rate of larger trees following elevated temperatures may be related to the higher vulnerability of larger trees to xylem cavitations especially during extreme drought conditions (Brodrribb and Cochard, 2009).

Higher tree dieback at the lower elevation has pushed the distribution of *J. procera* and *O. europaea* subsp. *cuspidata* to the higher

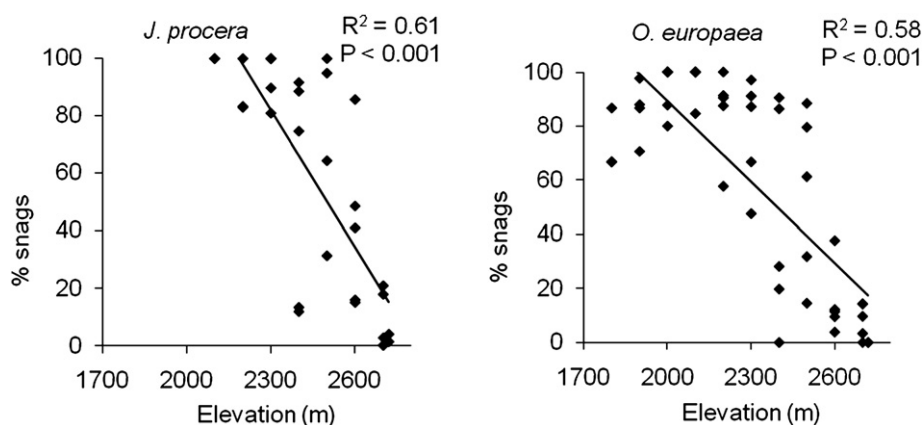


Fig. 2. Changes in percentage of snags of *J. procera* and *O. europaea* subsp. *cuspidata* along an elevational gradient in a dry Afromontane forest, northern Ethiopia.

Table 1
Stand structure of live stems and snags of *J. procera* and *O. europaea* subsp. *cuspidata* in northern Ethiopia.

Attribute	Live	Dead (Snag)	% Dead
Stem density (stems ha ⁻¹)			
<i>J. procera</i>	133	89	40.9
<i>O. europaea</i> subsp. <i>cuspidata</i>	63	91	59.1
All others	226	8	3.4
Basal area (m ² ha ⁻¹)			
<i>J. procera</i>	2.91	2.78	48.9
<i>O. europaea</i> subsp. <i>cuspidata</i>	2.55	3.08	54.7
All others	1.85	0.03	1.6

elevations (Fig. 3) by about 500 m, and this can lead to a shift in the forest–shrubland ecotone. The problem is more severe for *O. europaea* subsp. *cuspidata* than for *J. procera*, because *O. europaea* subsp. *cuspidata* largely occurs in the lower elevations (Fig. 3). Such a shift in

structural composition and the openness of the canopies due to tree dieback also changes the understory light conditions and encourages the establishment of pioneer species (Slik, 2004). Similarly, dry Afromontane forests in northern Ethiopia, which were dominated by *J. procera* and *O. europaea* subsp. *cuspidata* prior to anthropogenic and natural disturbance, have been gradually replaced by encroaching light-demanding shrubs and herbs such as *Cordia purpurea* and *Tarchonanthus camphoratus*. An expansion of the shrubland vegetation from lower elevation drier sites to forests was also observed in central Ethiopia (Woldu and Ingvar, 1991). Thus, dieback in the study area's dry Afromontane forests may further lead to a gradual replacement of high canopy trees by pioneer shrub and herb species.

The dieback of the two dominant tree species has significantly reduced the living stand density and basal area. Both species have smaller seedling and sapling populations. However, many questions regarding the potential effects of climate change on forest dynamics

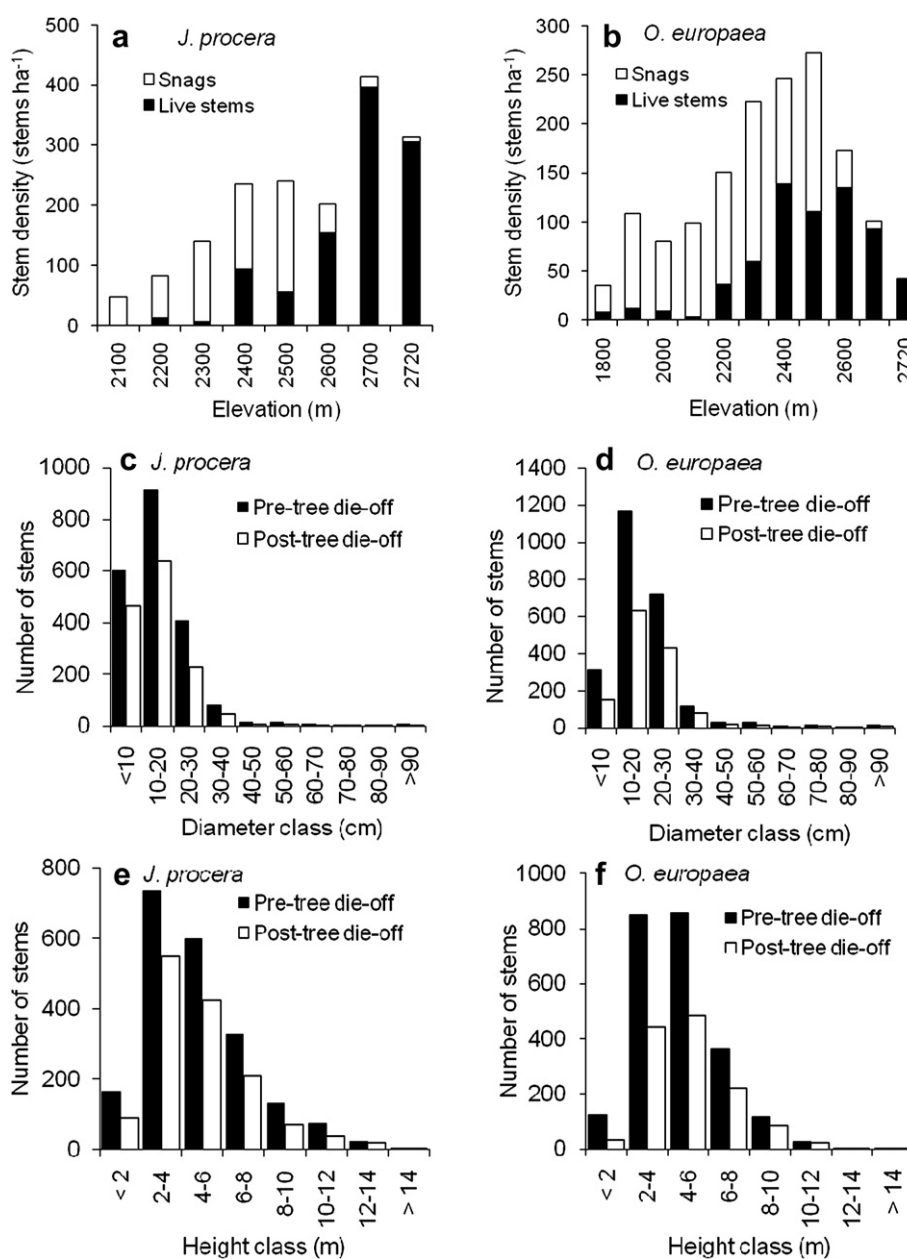


Fig. 3. Changes in live stem and snag densities along an elevational gradient (a, b). Changes in diameter class distribution (c, d) and height class distribution (e, f) before (live stems + snags) and after (live stems) dieback in a dry Afromontane forest, northern Ethiopia.

and species ranges remain unanswered and require further research. Besides continued pressure on the *J. procera* and *O. europaea* subsp. *cuspidata* trees for their economic value, dieback of these species is a major concern in the tree-scarce landscapes in northern Ethiopia. Thus, it is important to reduce further anthropogenic pressure on the forest to restore the population of the two species. It is also important to increase their seedling population through assisted restoration interventions (see e.g. Aerts et al., 2006a). Sites with high snag density should also be carefully managed to reduce potential fire incidents.

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References

- Abegez, A., 2005. Farm Management in Mixed Crop-Livestock Systems in the Northern Highlands of Ethiopia, PhD dissertation. Wageningen University and Research Center, Wageningen.
- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional dieback under global-change-type drought. *Proceedings of the National Academy of Sciences of the USA* 106, 7063–7066.
- Aerts, R., Maes, W., November, E., Negussie, A., Hermy, M., Muys, B., 2006a. Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management* 230, 23–31.
- Aerts, R., November, E., Van der Borgh, I., Behailu, M., Hermy, M., Muys, B., 2006b. Effects of pioneer shrubs on the recruitment of the fleshy-fruited tree *Olea europaea* ssp. *cuspidata* in Afromontane savanna. *Applied Vegetation Science* 9, 117–126.
- Aerts, R., Van Overtveld, K., Haile, M., Hermy, M., Deckers, J., Muys, B., 2006c. Species composition and diversity of small Afromontane forest fragments in northern Ethiopia. *Plant Ecology* 187, 127–142.
- Aerts, R., Negussie, A., Maes, W., November, E., Hermy, M., Muys, B., 2007. Restoration of dry Afromontane forest using pioneer shrubs as nurse plants for *Olea europaea* ssp. *cuspidata*. *Restoration Ecology* 15, 12–138.
- Allen, C.D., 2009. Climate-induced forest dieback: an escalating global phenomenon? *Unasylva* 231/232 (60), 43–49.
- Asrat, A., 2002. The Rock-Hewn churches of Tigray, northern Ethiopia: a geological perspective. *Geoarchaeology* 17, 649–663.
- Aynekulu, E., Denich, M., Tsegaye, D., 2009. Regeneration response of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* to enclosure in a dry Afromontane forest in northern Ethiopia. *Mountain Research and Development* 29, 143–152.
- Boehmer, H.J., 2011. Vulnerability of tropical montane rain forest ecosystems due to climate change. In: Hans Günter Brauch, H.G., Spring, U.O., Mesjasz, C., Grin, J., Kameri-Mbote, P., Chourou, B., Dunay, P., Birkmann, J. (Eds.), *Coping with Global Environmental Change, Disasters and Security – Threats, Challenges, Vulnerabilities and Risks. Hexagon Series on Human and Environmental Security and Peace*, vol. 5. Springer-Verlag, Berlin – Heidelberg – New York, pp. 789–802.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree dieback in response to global change-type drought: mortality insights from decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7, 185–189.
- Brodribb, T.J., Cochard, H., 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* 149, 575–584.
- Coureaud, C., Sass-Klaassen, U., Sterck, F., Bekele, T., Zuidema, P.A., 2005. Combining dendrochronology and matrix modelling in demographic studies: an evaluation for *Juniperus procera* in Ethiopia. *Forest Ecology and Management* 216, 317–330.
- Craig, B.W., Friedland, A.J., 1991. Spatial patterns in forest composition and standing dead red spruce in montane forests of the Adirondacks and northern Appalachians. *Environmental Monitoring and Assessment* 18, 129–143.
- Cuneo, P., Leishman, M.R., 2006. African Olive (*Olea europaea* subsp. *cuspidata*) as an environmental weed in eastern Australia: a review. *Cunninghamia* 9, 545–577.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., 2000. The interplay between climate change, forests, and disturbances. *Science of the Total Environment* 262, 201–204.
- Darbyshire, I., Lamb, H., Umer, M., 2003. Forest clearance and regrowth in northern Ethiopia during the last 3000 years. *The Holocene* 13, 537–546.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3, 479–486.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, 80–83.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *BioScience* 37, 550–556.
- Friis, I., 1992. Forests and Forest Trees of Northeast Tropical Africa: Their Natural Habitats and Distribution Patterns in Ethiopia, Djibouti and Somalia. Her Majesty's Stationery Office, London.
- Ganey, J.L., 1999. Snag density and composition of snag populations on two National Forest in northern Arizona. *Forest Ecology and Management* 117, 169–178.
- García-Fayos, P., Gasque, M., 2002. Consequences of a severe drought on spatial patterns of woody plants in a two-phase mosaic steppe of *Stipa tenacissima* L. *Journal of Arid Environments* 52, 199–208.
- Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.I., Kennedy, K., Munoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* 20, 1477–1486.
- Grove, S.J., 2001. Extent and composition of dead wood in Australian lowland tropical rainforest with different management history. *Forest Ecology and Management* 154, 35–53.
- Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research* 30, 76–84.
- Hemp, A., 2009. Climate change and its impact on the forests of Kilimanjaro. *African Journal of Ecology* 47, 3–10.
- Kueppers, K.J., Southon, J., Baer, P., Harte, J., 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. *Oecologia* 141, 641–651.
- Lamb, H., Darbyshire, I., Verschuren, D., 2003. Vegetation response to rainfall variation and human impact in central Kenya during the past 1100 years. *The Holocene* 13, 285–292.
- Marage, D., Lemperiere, G., 2005. The management of snags: a comparison in managed and unmanaged ancient forests of the southern French Alps. *Annals of Forest Science* 62, 135–142.
- Meizner, F.C., 2003. Functional convergence of plant responses to the environment. *Oecologia* 134, 1–11.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology* 93, 1085–1093.
- Mueller-Dombois, D., 1988. Towards a unifying theory for stand-level dieback. *Geojournal* 17 (2), 249–251.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P., Cardinot, G., 2007. Mortality of large trees and lianas following experimental drought in an Amazon rain forest. *Ecology* 88, 2259–2269.
- Ohmann, J.L., McComb, W.C., Zumravi, A.Z., 1994. Snag abundance for primary cavity-nesting birds on nonfederal forest lands in Oregon and Washington. *Wildlife Society Bulletin* 22, 607–620.
- Segura, G., Balvanera, P., Durán, E., Pérez, A., 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology* 169, 259–271.
- Siegel, S., Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York, NY.
- Slik, J.W., 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* 141, 114–120.
- Solomon, A.M., 1986. Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* 68, 567–579.
- SPSS 13.0 for Windows, 2004. SPSS Inc., Chicago, IL, USA.
- Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in Northfagus-site, climatic sensitivity and growth trends. *Journal of Ecology* 92, 954–966.
- Teketay, D., 1997. Seedling populations and regeneration of woody species in dry Afromontane forests of Ethiopia. *Forest Ecology and Management* 98, 149–165.
- Tsegaye, D., Moe, S.R., Vedeld, P., Aynekulu, E., 2010. Land-use/cover dynamics in Northern Afar rangelands, Ethiopia. *Agriculture, Ecosystems and Environment* 139, 174–180.
- Woldu, Z., Ingyar, B., 1991. The shrubland vegetation in western Shewa, Ethiopia and its possible recovery. *Journal of Vegetation Science* 2, 173–180.