

Carbon dynamics and nutrients in different decay stages of coarse woody debris in natural Hyrcanian forests, Northern Iran

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ABSTRACT

The relationship between the degree of decay, carbon dynamics, and nutrients of coarse woody debris (CWD) were examined in the experimental forest of Kheirudkenar – Nowshahr as a part of Hyrcanian forests in Northern Iran. CWD (snag and log) with an average middle diameter more than 7.5 cm was recorded in 50 ha. For snag CWD, species type, diameter at the breast height and height, while for log CWD, species type, the average diameter and their length were determined and recorded. In the case of non-circular CWD cross-sections especially in the higher decay stages, diameter was determined by tape. All CWD were categorized in three diameter classes and the degree of their decay (snag and log) was determined. The CWD nutrients examined throughout taking a piece from each CWD and analysing them in the laboratory (60 specimens). The C/N ratio of CWD was obtained separately for diameter classes and degrees of decay. All data were tested for probability of fit to normal distribution. To identify the most influential gradients, principal component analysis (PCA) was applied. The nutrients in the trunk CWD in different diameter classes and degrees of decay showed that in most cases, there is a significant difference between them. The results of the C/N ratio of the total trunk of CWD showed that this ratio decreases by elevating the degree of decay and by upraising the diameter classes of CWD. The degrees of decay of CWD were majority related to N, C/N ratio, C and K respectively. This research demonstrated that the nitrogen and carbon concentrations among the decay classes and species type of CWD should be considered.

Keywords: Beech, CWD, C/N ratio, Hornbeam, PCA.

Article type: Research Article.

INTRODUCTION

Coarse woody debris (CWD) has a high ecological relevance and contributes significantly to crucial ecological processes in forest ecosystem, playing an essential role in forest productivity, nutrition cycles, carbon pools, community regeneration, biodiversity (Martin *et al.* 2021). The amount of CWD is strongly dependent on management regime, stand age, disturbance (Bantle *et al.* 2014), and stand succession stage. CWD is an important and necessary factor and a huge source of organic matter in forest ecosystems. CWD stabilizes the soil (Vrška *et al.* 2015) and plays an important role in the nutrient cycle (Cosmo *et al.* 2013; Yuan *et al.* 2014), especially the carbon cycle (Yuan *et al.* 2014). In addition, by long-term storage, dead woods help reduce global warming by storing carbon in habitats (Dudley *et al.* 2004). Carbon storage is a key process for managing the concentration of atmospheric carbon dioxide in natural forests (Heidari Safari Kouch *et al.* 2015), which is determined by the

degree of degradation and decay of the wood. Various factors affect decay and decomposition rate, including wood type, temperature, wood moisture content, annual rainfall, physical and chemical nature of the wood, as well as the population of fungal and the other decomposers (Garrett *et al.* 2007 & 2008). The stability and maximum storage of carbon in CWD is determined based on the stability and resistance of wood against decomposition (Mason *et al.* 2013; Moghimian *et al.* 2020). The decomposition of these dead woods plays a key role in the carbon cycle (Koster *et al.* 2015). In addition, during the decomposition period, the ratio of carbon to nitrogen rises (Yang *et al.* 2010; Bantle *et al.* 2014) and the amount of nitrogen declines after decomposition (Bantle *et al.* 2014). Also, elevating the carbon storage content in CWD, leads to reduction in the greenhouse gases (Mason *et al.* 2013) and elevating the nutrients in it during the degradation process (Yang *et al.* 2010). On the other hand, the process of decomposition of CWD is due to change in physical and chemical structure (Vanderwel *et al.* 2006), so that during the decomposition of wood, carbon is slowly released. In this way, if the rate of decomposition of wood is high, the amount of carbon storage will also decrease, depending on the type of species and the rate of decomposition of different species. The more the rate of gradual decomposition of wood and the resistance of the wood to decay is high, the amount of carbon storage increases and it stays in the ecosystem longer (Mason *et al.* 2013). Decomposition of various stages of dead tree plays an important role in global greenhouse gases related to climate changes (Koster *et al.* 2015). Therefore, climate changes increase the diversity and severity of pest and insect attacks, thus lead to elevation in the mortality and drought rate of trees. Tree mortality reduces carbon in natural forests, which is a major factor in changing carbon storage among forest stands (Mason *et al.* 2013). So, a huge amount of carbon is produced by CWD that plays a role in biomass, and accumulates for centuries. On the other hand, all the carbon in the forest is made from biomass, which improves the physical and chemical properties of snag dead woods (Mason *et al.* 2013). These dead woods play an important role in ecology and forest management (Yuan *et al.* 2014; Cousins *et al.* 2015). Numerous studies have been conducted on carbon storage, the food element cycle, and the decomposition of coarse woody debris (CWD). Wu *et al.* (2019) found that three factors, including increasing ultraviolet radiation, nitrogen decomposition and global warming accelerate the decomposition of CWD in forest ecosystems. Nitrogen level in CWD drops at each stage of decomposition (Bantle *et al.* 2014) and CWD is a source of nitrogen (Bantle *et al.* 2014). In addition, in semi-deciduous forests, nitrogen concentration in dead woods increased by elevating in degradation classes (Koster *et al.* 2015). The dynamics of CWD is based on carbon storage and decomposition rate (Russell *et al.* 2015). All the carbon in the forest was biomass and the tree destruction classes exhibited a gradual and slow elevation in carbon concentration (Cousins *et al.* 2015). In managed forests, CWD plays a very important role in carbon storage and for a long time, contributes to the stability of carbon storage in natural ecosystems (Olajuyigbe *et al.* 2011). CWD also affects the sustainability of carbon storage, which can accumulate over several centuries and plays as a main component and key role in biomass (Schmid *et al.* 2016; Mason *et al.* 2013). The amount of carbon storage in CWD of different species and decay stages has affected the biomass (Cosmo *et al.* 2013) and also, in different tree species, high levels of carbon enter the soil from CWD (Bantle *et al.* 2014). Accordingly, the main objectives of the present study were to (i) disclose the amount of CWD, (ii) quantity the types, tree species, decay stages and diameter classes of CWD, carbon dynamics and nutrients in different decay stages of CWD in study area where is remnant of virgin forests in Hyrcanian region.

MATERIALS AND METHODS

Study area

The research area, covering 950 ha, was located in the experimental forest of Kheirudkenar-Nowshahr as a part of Hyrcanian forests in north of Iran (Fig. 1). The altitude range is 1150-1350 m and the mean slope is 30% on the southwest-facing. The average annual temperature and annual rainfall are 15.9°C and 1300 mm, respectively, and the climate belongs to the temperate zone. The study area is an uneven-aged high forest that is mostly dominated by Beech (*Fagus orientalis* Lipsky) and Hornbeam (*Carpinus betulus* L.) followed by other species (*Ulmus glabra* Huds., *Quercus castaneifolia* C.A.Mey., *Alnus subcordata* C.A.Mey., *Acer velutinum* Boiss. and *Tilia begonifolia* Steven). The average canopy is more than 80% with relatively moderate regeneration. (Anonymous 2010).

Research Method

According to previous studies and documents, some of areas including 4 unmanaged stands (compartment) with approximately 50 ha (after decreasing side effects of neighbour area) represent the least human influenced of

forest and have been concluded as virgin forest. These areas were considered as study area. In addition, all CWD (snag and log) with an average middle diameter more than 7.5 cm was recorded (Amiri *et al.* 2015). The distance-azimuth method (Meour 1993) was used to determine the position of the all CWDs in the study area. For snag, the type of species, diameter at breast height and height, while for log, species type, the average diameter and their length were determined and recorded. For non-circular cross-sections of CWD, especially in the higher decay stages, diameter was determined by tape. The degree of CWD decay (snag and log) was determined using the modified proposed method of Christensen & Vesterdal (2003; Table 1).

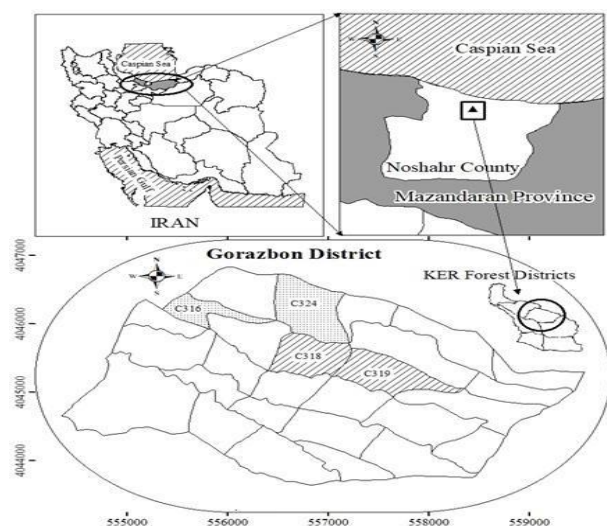


Fig. 1. Geographic location of the study area in Kheyroud Educational-Research Forest.

Table 1. Decay classification for CWD; Modified from Christensen & Vesterdal (2003).

Decay phases	Bark	Twigs branches	Softness	Surface	Shape
D1	intact or missing only in small patches, more than 50%	present	hard or knife penetrate 1-2 mm	covered by bark, outline intact	Circle
D2	missing or less than 50%	only branches (>3 cm) present	hard or knife penetrate less than 1 c	smooth, outline intact	Circle
D3	missing	missing	begin to be soft, knife penetrate 1-5 cm	smooth or crevices present, outline intact	Circle
D4	missing	missing	soft, knife penetrate more than 5 cm	large crevices, small pieces missing, outline intact	circle or elliptic
D5	missing	missing	soft, knife penetrate more than 5 cm	large pieces missing, outline partly deformed	flat elliptic, covered by soil

All deadwoods were categorized in three diameter classes including small-diameter (7.5-32.5 cm), medium-diameter (32.5-57.5 cm, and large-diameter (>57.5 cm; Sagheb-Talebi & Schutz 2002), and also five degrees of decay (Table 1 and Fig. 2). In the study area predominant frequency of deadwood mainly belonged to beech and hornbeam. Other species exhibited very low frequency and even some decay classes were not observed. Accordingly, once studying other species, CWD nutrients was not abandoned due to the lack of sufficient samples. To measure the nutritional elements of CWD, from the stump or the end part of the trunk of the CWD (beech and hornbeam) in each parcel, 3 samples in each diameter class and each degree of decay were taken randomly and mixed together, considering as a combined sample (3 diameter classes \times 5 decomposition classes \times 4 parcels as replications). In total, 60 specimens were taken with the difference that the hornbeam CWD was not present in

the region with the degree of decay one. It was placed in special bags and transferred to the laboratory. Then, carbon, phosphorus, potassium and nitrogen of the CWD samples were measured using standard methods (Gubena & Soromessa 2017; Álvarez-DaÁvila *et al.* 2017).

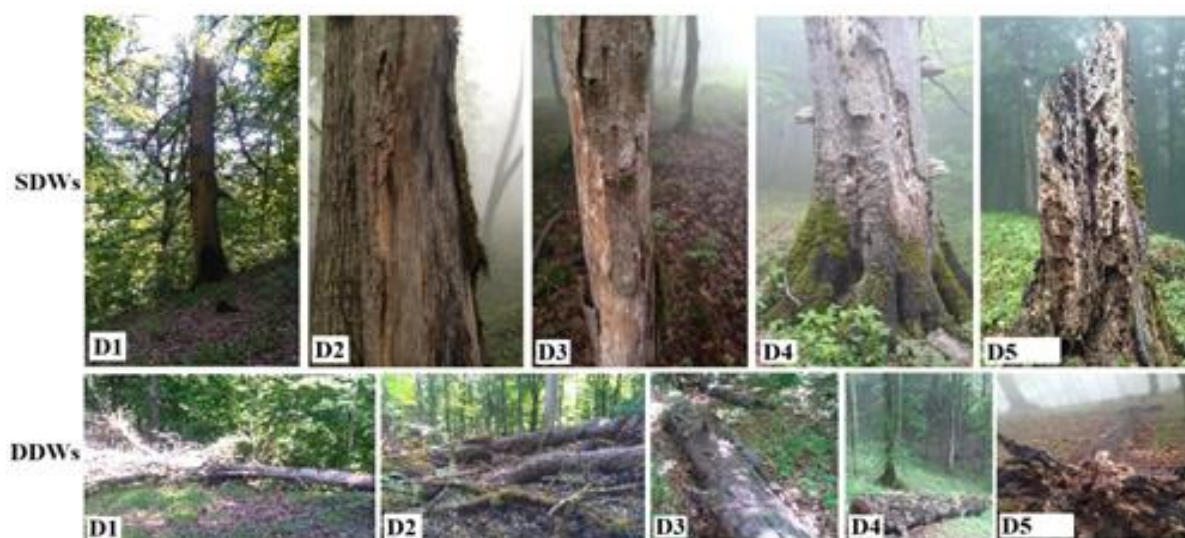


Fig. 2. Different decay stages of CWD.

Statistical data analysis

All data were tested for probability of fit to normal distribution by a Kolmogorov-Smirnov test. Then, One-Way ANOVA was used to compare nutrients and C/N trunk Beech and Hornbeam CWD. To identify the most influential gradients, principal component analysis (PCA) was applied to the factors that were found to be related to decay classes, but were mostly independent from each other. PCA is the ordination technique that constructs the theoretical variable that minimizes the total residual sum of squares after fitting straight lines to the data (Jongman *et al.* 1995). In the case of PCA, all the data were standardized to zero mean and unit variance, and the analysis was done on the correlation matrix. All statistical analysis was done using SPSS version 16 and Pc-Ord version 5.

RESULTS

Descriptive analysis

The results of the descriptive statistics of beech and hornbeam CWD in the studied forest are presented in Table 2. The density per hectare of beech snag CWD (3.35) was higher than that of log CWD (2.85), but the volume per hectare was the opposite. In the case of the hornbeam, the volume per hectare of log CWDs (0.50) was higher despite the higher density of snag CWD (1.15) compared to log CWD (0.60), while in the case of the other species, the density per hectare (0.6) was higher despite the volume per hectare (0.4). In total the density per hectare and the volume per hectare of beech CWD is higher than hornbeam CWD.

Table 2. Descriptive statistics of Beech and Hornbeam CWD.

	Beech		Hornbeam	Other species	
	Snag	Log	Snag	Log	Snag and Log
Density (n.ha ⁻¹)	3.35	2.85	1.15	0.60	0.6
Volume (m ³ .ha ⁻¹)	2.25	8.60	0.20	0.50	0.4

Other species (*Ulmus*, *Quercus*, *Alnus*, *Acer* and *Tilia*).

The nutrients of the CWD

The results of the average amount of nutrients in the trunk of CWD (snag and log) of beech and hornbeam are presented according to the diameter classes and degrees of decay. The nutrients in the trunk CWD in the diameter classes and the degrees of decay showed that there was no significant difference (Table 3).

Table 3. Results of comparing nutrients of trunk CWD based on diameter classes and decay stages.

	CWD (Beech and Hornbeam)			
	C (%)	P (%)	K (%)	N (%)
	CWD	CWD	CWD	CWD
Diameter class (cm)				
Small	57.5 ^a	0.4 ^a	0.1 ^a	0.5 ^a
Medium	57.4 ^a	0.4 ^a	0.09 ^a	0.6 ^a
Large	57.3 ^a	0.3 ^a	0.07 ^a	0.7 ^a
Decay stage				
D1	58 ^a	0.4 ^a	0.1 ^a	0.4 ^a
D2	57.5 ^a	0.5 ^a	0.1 ^a	0.6 ^a
D3	57.4 ^a	0.6 ^a	0.1 ^a	0.7 ^a
D4	57.3 ^a	0.4 ^a	0.1 ^a	1 ^a
D5	57.2 ^a	0.2 ^a	0.1 ^a	0.8 ^a

Note. a: there is no significant difference at 95% confidence level.

The amounts of nutrients in the trunk beech CWD (Table 4) depicts that the percentage of carbon in the trunk CWD is significantly different in the three diameter classes. There was no significant difference in the nutrients of the trunk Beech CWD between the diameter classes and the degrees of decay (Table 4).

Table 4. Results of comparing nutrients of trunk Beech CWD based on diameter classes and decay stages

	Beech CWD			
	C (%)	P (%)	K (%)	N (%)
	CWD	CWD	CWD	CWD
Diameter class (cm)				
Small	57.5 ^a	0.4 ^a	0.1 ^a	0.5 ^a
Medium	57.4 ^a	0.5 ^a	0.1 ^a	0.5 ^a
Large	57.2 ^a	0.3 ^a	0.07 ^a	0.5 ^a
Decay stage				
D1	58 ^a	0.4 ^a	0.1 ^a	0.4 ^a
D2	57.7 ^a	0.5 ^a	0.1 ^a	0.6 ^a
D3	57.6 ^a	0.4 ^a	0.1 ^a	0.7 ^a
D4	57.2 ^a	0.4 ^a	0.1 ^a	0.7 ^a
D5	57.4 ^a	0.2 ^a	0.1 ^a	0.8 ^a

Note. a: there is no significant difference at 95% confidence level.

Table 5 depicts that in the three diameter classes of hornbeam CWD, the percentage of trunk phosphorus CWD in the small and medium-diameter classes were significantly different. The nutrients in the trunk Hornbeam CWD in the diameter classes and the degrees of decay exhibited no significant difference (Table 5). The C/N ratio was also obtained for beech and hornbeam CWD and whole species (Table 6). In terms of diameter classes and degrees of decay, for beech and hornbeam CWD and whole species, the rate of decay between the trunk CWD was significantly different. Noteworthy, the ratio of C/N in all CWD and in their trunks decreased by the elevated degree of decay, likewise, by upraising in the diameter of the CWD, this rate was elevated.

PCA of different decay classes in relation to the characteristics of CWD trunk

Principle component (PCA) was used to determine the relationship between the physical and chemical characteristics of the trunk CWD and the degrees of decay. First, the data was standardized. The results of the eigenvalues, the percentage of variance and the percentage of cumulative variance of components (Table 7) showed that the first and second components have the highest value of eigenvalues. This means that these two

axes explain the highest variance (more than 62%) of the trunk CWD characteristics in relation to the degrees of decay. In other words, the results of these two components are close to reality and can be interpreted.

Table 5. Results of comparing nutrients of trunk Hornbeam CWD based on diameter classes and decay stages.

	Hornbeam CWD			
	C (%)	P (%)	K (%)	N (%)
	CWD	CWD	CWD	CWD
Diameter class (cm)				
Small	57.4 ^a	0.3 ^a	0.1 ^a	0.6 ^a
Medium	57.4 ^a	0.3 ^a	0.08 ^a	0.7 ^a
Large	57.4 ^a	0.3 ^a	0.07 ^a	0.8 ^a
Decay stage				
D1	-	-	-	-
D2	57.4 ^a	0.5 ^a	0.1 ^a	0.6 ^a
D3	57.3 ^a	0.7 ^a	0.1 ^a	0.7 ^a
D4	57.1 ^a	0.3 ^a	0.1 ^a	1.3 ^a
D5	57 ^a	0.3 ^a	0.1 ^a	0.7 ^a

a: there is no significant difference at 95% confidence level.

Table 6. Results of C/N values comparison of trunk beech, hornbeam and total CWD.

	Hornbeam	Beech	Total
	C/N	C/N	C/N
Diameter class (cm)			
Small	52.2	82.1	63.9
Medium	82	81.7	81.9
Large	82	95.7	95.7
Decay stage			
D1	-	82.9	82.9
D2	38.3	115.4	81.7
D3	95.5	115.2	75.7
D4	81.6	63.6	68.2
D5	81.4	57.7	52.3

Note. a: there is no significant difference at 95% confidence level.

Table 7. Eigenvalues and individual and accumulative variances of first 3 PCs.

Components	eigenvalue	Variance (%)	Cumulative variance (%)
1	2.043	40.865	40.865
2	1.061	21.218	62.083
3	0.940	18.791	80.874

Table 8. depicts the eigenvectors of characteristics of the trunk CWD with the first and second axes of PCA. The degrees of decay of CWD (beech and hornbeam) exhibited the most positive relationship with potassium (0.3175) and nitrogen (0.6442; Table 8). Based on the second PCA axis, carbon (-0.8162) and potassium (0.4959) of trunk displayed the highest relationship with the degrees of decay of beech and hornbeam CWD. Fig. 5 illustrates a diagram of the conformity of the first and second axes.

Table 8. Eigenvectors of PCA axes and relation between decay stages via the trunk CWD.

Trunk properties	PC1	PC2
Carbon	-0.1209	-0.8162
Potassium	0.3175	0.4959
Phosphorus	-0.2409	-0.0433
Nitrogen	0.6442	-0.2150
C/N	-0.6416	0.1995

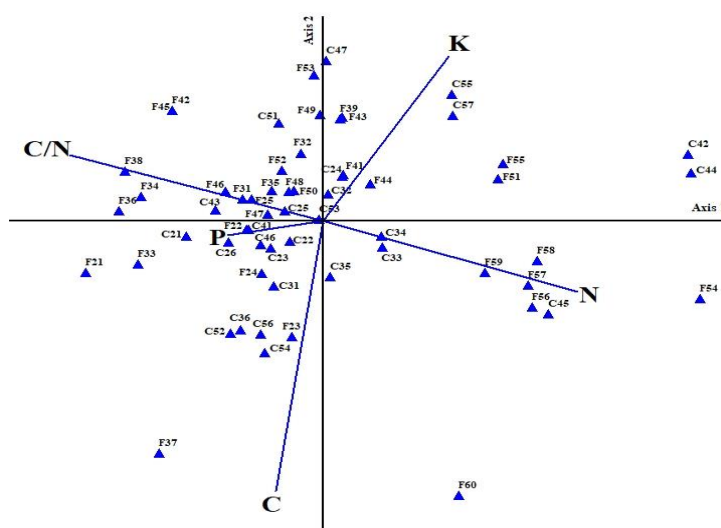


Fig. 5. A 2-dimensional principal components analysis of trunk properties and decay stages (C: Carbon; K: Potassium; P: Phosphorus; N: Nitrogen; F21: *Fagus*, C21: *Carpinus* and numbers show decay stages and frequency respectively).

DISCUSSION

In the present study, the nutrient elements of the CWD trunk were evaluated according to the degree of decay and diameter classes and also identified the most influential gradient. Although dead woods have low commercial and economic value, they have fundamental ecological values. In the forest, organic matter is added to the forest soil from high disturbances or underground sources (Emtiyazi 2002). In general, plant organic matter contains about 15-60% cellulose, 10-30% hemicellulose, 30-50% lignin and 2-5% protein (Kogel-Knabner 2002). Dead woods are a huge source of cellulose and a large amount of organic matter that, over time, enter into the biological cycle of forest soil by decomposing (Lutz *et al.* 1966; Spears & Lajtha 2004; Cousins *et al.* 2015). Cellulose is one of the most abundant components of plant residues and is often associated with hemicellulose and lignin. In the life cycle and death of the forest ecosystem, the material taken from the soil enters the forest again after the death of the organism. Notably, cellulose is the main source of carbon storage in the forest (Cousins *et al.* 2015), which is slowly released in the forest during the decomposition processes. Dead wood is a combination of internal and external skin materials, inside and outside the wood. The share of each of these parts varies depending on the species, size and age of the tree. The inner skin, which is a combination of cambium and phloem, is rich in sugar and generally decomposes much faster than other wood compounds (Harmon *et al.* 1986). Inside wood, in many species, has a large portion of the CWD. It decomposes relatively later, since it contains the antifungal and anti-

insect extracts and may have more density. The results of the density of beech and hornbeam CWD showed that its value in CWD of beech is higher than that of hornbeam CWD. Such a result was to be expected, since the structure of the forest under study is seed borne inconsistent with the dominant beech-hornbeam type. The density of CWD (log and snag) of the two species with volume per hectare showed that despite the small number per hectare, they have allocated a larger volume. The latest data show that the volume of CWD in the untouched Hyrcanian beech forests is between 7 and 196 m³/ha per hectare and an average of 56 m³/ha (Sagheb-Talebi *et al.* 2020). According to another study, the volume of CWD in the forests of Northern Iran is 5-54 m³/ha (Mataji *et al.* 2014). Other results also show that the volumetric inventory of CWD in the forests of Northern Iran is lower than in European forests, which may be due to some reasons such as species type, temperature fluctuations and decomposition rate (Amanzadeh *et al.* 2013). According to studies, the density of CWD is directly related to the mortality rate of trees (Yan *et al.* 2007). On the other hand, the elevated temperature due to climate change has led to the increased tree mortality, which in turn tends to an upraised density of CWD (Pennisi 2009). Examining the nutrients in the trunk CWD showed that in different diameter classes, the percentage of carbon, potassium and nitrogen in the trunk of CWD is higher, and also the highest percentage of nutrients is related to carbon. This element makes up the largest percentage of dead wood tissue (Kooch 2012) and is known as an energy supplier for metabolism in plant tissues (Zibilske 1994). On the other hand, CWD are one of the main factors in carbon balance in ecosystems (Harmon *et al.* 2011). In the present study, the percentage of nitrogen exhibited an increasing trend by elevating diameter of CWD and degree of decay class, consistent with results obtained by Noh *et al.* (2017), Holub *et al.* (2001) and Ganjegunte *et al.* (2004). The upraised nitrogen content in the trunk of CWD may also be affected by the stabilization of nitrogen and its entry occurs through precipitation into the trunk of CWD (Klockow *et al.* 2014). CWD releases nutrients through the decomposition process (Palviainen *et al.* 2010), depending on climatic conditions and species. Factors such as wood moisture, average annual temperature, and decomposers also affect the rate of decomposition of CWD (Beets *et al.* 2008). The released nutrients can be absorbed through the soil and to be available to soil microorganisms (Zhou *et al.* 2007). Effect of dead wood decomposition on soil varies depending on soil characteristics and nutrient conditions (Thiffault *et al.* 2006). The nutrients in CWD function as factors in improving the biodiversity and abundance of ectomycorrhizal fungi (Graham *et al.* 1994). Due to the release, nutrients by CWD play an important role in storage of nutrients in ecosystems (Augusto *et al.* 2008). The results obtained from the decay rate values (C/N) showed that for hornbeam, beech and whole species, this amount for the trunk of CWD is higher. In general, the rate of decay in the trunk of CWD in different diameter classes revealed an increasing trend. Furthermore, different degrees of decay showed a decreasing trend in the trunk of the CWD. Also, by the elevated degree of decay in all CWD, the C/N ratio declines, which is consistent with the results of Creed *et al.* (2004). In addition, Yang *et al.* (2010) and Mogimian *et al.* (2020) reported that as the decay upraises, the amount of carbon in the CWD declines, however, the amount of nitrogen increases. The C/N ratio also drops by the elevated decay. The increased nitrogen level may be due to the activity of fungi and bacteria (Brunner & Kimmis 2003) that stabilize nitrogen and precipitation (Garrett *et al.* 2008). Dissolution of carbon of CWD also results in nitrogen inactivity (Fierer *et al.* 2001). As mentioned earlier, the increase in nitrogen and, in contrast, the reduction of carbon in the trunk of CWD upon an elevated degree of decay may be the cause of this trend. The results of PCA showed that the most important factors in relation to the degree of decay included nitrogen, carbon and potassium. Other variables such as phosphorus are placed in the next order. So that, Eshaqi Rad *et al.* (2009) have considered the phosphorus, organic matter and exchanged cations to be important in the distribution of species in beech forest communities. Noh *et al.* (2017) and Yang *et al.* (2010) also reported that by the increased decay, the nitrogen trunk CWD also rises.

CONCLUSION

The present study demonstrated that the nitrogen and carbon concentrations among the decay classes and species type of CWD should be considered. Decay rates were related to C/N ratio, which drops by the elevated degrees of decay or CWD diameter. Whether CWD is a pure source of nutrients such as carbon, which are added to the soil by the rotting of these elements and form a cycle of transferring nutrients from the CWD to the soil, depends on the type of species and the length of decay of the CWD. However, clearly it is only in the long run that CWD can play such a role in the nutrient cycle. In short, CWD are a constant source of nutrients. In other words, the

transfer of nutrients such as carbon to the soil is not significant. On the other hand, examining the amount of CWD can show the outcomes of climate change and land use change.

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REFERENCES

- Álvarez-DaÁvila, E, Cayuela, L, GonzaÁlez-Caro, S *et al.* 2017, Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS ONE*, 12: 0171072. <https://doi.org/10.1371/journal.pone.0171072>.
- Amanzadeh, B, Sagheb-Talebi, Kh, Foumani, BS, Fadaie, F, Camarero, JJ & Linares, JC 2013, Spatial distribution and volume of dead wood in unmanaged Caspian Beech (*Fagus orientalis*) forests from Northern Iran. *Forests*, 4: 751-765.
- Amiri, M, Rahmani, R & Sagheb-Talebi, KH 2015, Canopy gaps characteristics and structural dynamics in a natural unmanaged oriental beech (*Fagus orientalis* Lipsky) stand in the north of Iran. *Caspian Journal of Environmental Sciences*, 13: 259-274.
- Anonymous 2010, Forest Management Plan Gorazbon District of Khyrud Forest. Department of Forestry and Forest Economics, Faculty of Natural Resources, University of Tehran, Karaj, pp. 191-273.
- Augusto, L, Meredieu, C, Bert, D, Trichet, P, Porte, A, Bosc, A, Lagane, F, Loustau, D, Pellerin, S, Danjon, F, Ranger, J & Gelpe, J 2008, Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. *Annals of Forest Science*, 65: 808–822.
- Bantle, A, Borken, W & Matzner, E 2014, Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition. *Forest Ecology and Management*, 334: 277-283. <http://dx.doi.org/10.1016/j.foreco.2014.09.015>.
- Beets, PN, Hood, IA, Kimberley, MO, Oliver, GR, Pearce, SH & Gardner, JF 2008, Coarse woody debris decay rates for seven indigenous tree species in the central North Island of New Zealand. *Forest Ecology and Management*, 256, 548-557.
- Brunner, A & Kimmnis, JP 2003, Nitrogen fixation in coarse woody debris of Thuja plicata and Tsuga heterophylla forests on northern Vancouver Island. *Canadian Journal of Forest Research*, 33: 1670-1682.
- Christensen, M & Vesterdal, L 2003, Nat-Man WP7 report: prepared by members of Work-package7 in the Nat-Man project (Nature-based Management of beech in Europe) funded by the European Community 5th framework programme. Nat-Man Working Report, No. Vol. 25.
- Cosmo, DL, Gasparini, P, Paletto, A & Nocetti, M 2013, Deadwood basic density values for national-level carbon stock estimates in Italy. *Forest Ecology and Management*, 295: 51-58, <http://dx.doi.org/10.1016/j.foreco.2013.01.010>.
- Cousins, SJM, Battles, JJ, Sanders, JE & York, RA 2015, Decay patterns and carbon density of standing dead trees in California mixed conifer forests. *Forest Ecology and Management*, 353: 136–147. <https://doi.org/10.1016/j.foreco.2015.05.030>.
- Creed, IF, Webster, KL & Morrison, DL 2004, A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. *Canadian Journal of Forest Research*, 34: 744–753. <https://doi.org/10.1139/x03-212>.
- Dudley, N & Equilibrium Vallauri, D 2004, Deadwood living forests. *WWF Report*, pp. 1-19. DOI: assets.panda.org/downloads/deadwoodwithnotes.
- Emtiyazi, G 2002, Microbiology, University of Isfahan Press, 185 p.
- Fierer, N, Schimel, JP, Cates, RG & Zou, J 2001, Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. *Soil Biology and Biochemistry*, 33: 1827–1839

- Ganjugunte, GK, Condrón, LM, Clinton, PW, Davis, MR & Mahieu, N 2004, Decomposition and nutrient release from radiate pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management*, 187: 197-211. DOI: 10.1016/S0378-1127(03)00332-3.
- Garrett, LG, Davis, MR & Oliver, GR 2007, Decomposition of coarse woody debris, and methods for determining decay rates. *New Zealand Journal of Forestry Science*, 37: 227-240.
- Garrett, LG, Oliver, GR, Pearce, SH & Davis, MR 2008, Decomposition of *Pinus radiata* coarse woody debris in New Zealand. *Forest Ecology and Management*, 255: 3839-3845.
- Graham, RT, Harvey, AE, Jurgensen, MF, Jain, TB, Tonn, JR & Pagedumroese, DS 1994, Managing coarse woody debris in forests of the rocky-mountains. *USDA Forest Service Intermountain Research Station Research Paper*, 477: 1-13.
- Gubena, AF & Soromessa, T 2017, Variations in forest carbon stocks along environmental gradients in Egdu Forest of Oromia Region, Ethiopia: Implications for sustainable forest management. *American Journal of Environmental Protection*, 6: 1-8.
- Heidari Safari Kouchi, A, Rostami Shahraji, T & Iranmanesh, Y 2015, Comparison of allometric equations to estimate the above-ground biomass of *Populus alba* species (Case study; poplar plantations in Chaharmahal and Bakhtiari Province, Iran). *Caspian Journal of Environmental Sciences* 13: 237-246.
- Harmon, ME, Franklin, JF, Swanson, FJ, Sollins, P, Gregory, SV, Lattin, JD, Anderson, NH, Cline, SP, Aumen, NG, Sedell, JR, Lienkaemper, GW, Cromack, K & Cummins, KW 1986, Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15: 133-302, [https://doi.org/10.1016/S0065-2504\(08\)60121-X](https://doi.org/10.1016/S0065-2504(08)60121-X).
- Harmon, ME, Bond-Lamberty, B, Tang, J & Vargas, R 2011, Heterotrophic respiration in disturbed forests: a review with examples from North America. *Journal of Geophysical Research*, 116: 117.
- Holub, SM, Spears, DH & Lajtha, KA 2001, Reanalysis of nutrient dynamics in coniferous coarse woody debris. *Canadian Journal of Forest Research*, 31: 1894-1902. DOI: 10.1139/cjfr.
- Jongman, RHG, Ter Braak, CJF & Van Tongeren, OFR 1995, Data analysis in community and landscape ecology. *Cambridge University Press*, 127 p.
- Klockow, PA, D'Amato, AW, Bradford, JB & Fraver, S 2014, Nutrient concentrations in coarse and fine woody debris of *Populus tremuloides* Michx.-dominated forest, northern Minnesota, USA. *Silva Fennica*, 48: 962. <http://dx.doi.org/10.14214/sf>.
- Kogel-Knabner, I 2002, The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol Biochem*, 34: 139-162, DOI: 10.1016/S0038-0717(01)00158-4.
- Kooch, Y 2012, Response of earthworms' ecological groups to decay degree of dead trees (Case study: sardabrood forest of chalous, Iran). *European Journal of Experimental Biology*, 3: 532-538.
- Koster, K, Metslaid, M, Engelhart, J & Koster, E 2015, Deadwood basic density, and the concentration of carbon and nitrogen for main tree species in managed hemiboreal forests. *Forest Ecology and Management*, pp: 35-42, <https://doi.org/10.1016/j.foreco.2015.06.039>.
- Lutz, J, Harold, R, Chandler, F & Morris, KG 1966, *Forest soils*, New York. 514 p.
- Martin, M, Tremblay, JA, Ibarzabal, J & Morin, H 2021, An indicator species highlights continuous deadwood supply is a key ecological attribute of boreal old-growth forests. *Ecosphere*, 12: 1-19.
- Mason, NWH, Bellingham, PJ, Carswell, FE, Peltzer, DA, Holdaway, RJ & Allen, RB 2013, Wood decay resistance moderates the effects of tree mortality on carbon storage in the indigenous forests of New Zealand. *Forest Ecology and Management*, 305: 177-188, <http://dx.doi.org/10.1016/j.foreco.2013.05.028>.
- Mataji, a, Sagheb-Talebi, Kh & Eshaghi-Rad, j 2014, Deadwood assessment in different developmental stages of beech (*Fagus orientalis* Lipsky) stands in Caspian forest ecosystems. *International Journal of Environmental Science and Technology*, 11: 1215-1222, <https://link.springer.com/article/10.1007/s13762-014-0532-0>
- Meour, M 1993, Characterizing spatial patterns of trees using stem-mapped data. *Forest Science*, pp: 756-775. <https://doi.org/10.1093/forestscience/39.4>.
- Moghimian, M, Jalali, SGh, Kooch, Y & Rey, A 2020, Downed logs improve soil properties in old-growth temperate forests of northern Iran. *Elsevier*, 30: 378-389, [https://doi.org/10.1016/S1002-0160\(17\)60424-7](https://doi.org/10.1016/S1002-0160(17)60424-7).
- Noh, NJ, Yoon, TK, Kim, RH, Bolton, NW, Kim, CH & Son, Y 2017, Carbon and Nitrogen Accumulation and Decomposition from Coarse Woody Debris in a Naturally Regenerated Korean Red Pine (*Pinus densiflora* S. et Z.) Forest. *Forests*, 8: 4-13, DOI: 10.3390/f8060214.

- Olajuyigbe, SO, Tobin, B, Gardiner, P & Nieuwenhuis, M 2011, Stocks and decay dynamics of above- and belowground coarse woody debris in managed Sitka spruce forests in Ireland. *Forest Ecology and Management*, 262: 1109–1118. DOI: 10.1016/j.foreco.2011.06.010.
- Palviainen, M, Finer, L, Laiho, R, Shorohova, E, Kapitsa, E & Vanha-Majamaa, I 2010, Phosphorus and base cation accumulation and release patterns in decomposing Scots pine, Norway spruce and silver birch stumps. *Forest Ecology and Management*, 260: 1478-1489.
- Pennisi, E 2009, Western U.S. forests suffer death by degrees. *Science*, 323, 447.
- Russell, M, Fraver, SH, Aakala, T, Gove, JH, Woodall, CHW, D'Amato, AW & Ducey, MJ 2015, Quantifying carbon stores and decomposition in dead wood: A review. *Forest Ecology and Management*, 350: 107-128, <https://doi.org/10.1016/j.foreco.2015.04.033>.
- Sagheb-Talebi, Kh, Parhizkar, P, Hassani, M, Amanzadeh, B, Hemmati, A, Khanjani-Shiraz, B, Amini, M, Mohammadnejad Kiasari, Sh, Mirkazemi, SZ, Karimidoost, A, Maghsoudlou, MK, Mortazavi, M, Karandeh, M, Delfan Abazari, B, Moghadasi, D, Dastangoo, D, Mashayekh, V & Sayadi Marzdashti, A 2020, Preliminary results of survey on stand structure in permanent research plots of Hyrcanian intact beech forests. *Iranian Journal of Forest and Poplar*, 17 p. [In press, In Persian].
- Sagheb-Talebi, Kh & Schütz, J-Ph 2002, The structure of natural oriental beech (*Fagus orientalis*) in the Caspian region of Iran and potential for the application of the group selection system. *Forestry*, pp. 465-472. <https://doi.org/10.1093/forestry/75.4>.
- Schmid, AV, Vogel, CHS, Liebman, E, Curtis, PS & Gough, CHM 2016, Coarse woody debris and the carbon balance of a moderately disturbed forest. *Forest Ecology and Management*, 361: 38-45, DOI: 10.1016/j.foreco.2015.11.001.
- Thiffault, E, Pare, D, Belanger, N, Munson, A & Marquis, F 2006, Harvesting intensity at clear-felling in the boreal forest: impact on soil and foliar nutrient status. *Soil Science Society of America Journal*, 70: 691–701.
- Vanderwel, MC, Malcolm, JR & Smith, SM 2006, An integrated model for snag and downed woody debris decay class transitions. *Forest Ecology and Management*, 234: 48-59, <https://doi.org/10.1016/j.foreco.2006.06.020>
- Vrška, T, Práveřtivy, T, Janík, D, Unar, P, Šamonil, P & Král, K (2015) Deadwood residence time in alluvial hardwood temperate forests—A key aspect of biodiversity conservation. *Forest Ecology and Management*, 357: 33-41, <http://dx.doi.org/10.1016/j.foreco.2015.08.006>.
- Wu, CH, Wang, H, Mo, Q, Zhang, ZH, Huang, G, Kong, F, Liu, Y & Wang, GG 2019, Effects of elevated UV-B radiation and N deposition on the decomposition of coarse woody debris. *Science of the Total Environment*, 663: 170-176, <https://doi.org/10.1016/j.scitotenv.2019.01.271>
- Yuan, J, Cheng, F, Zhao, P, Qiu, R, Wang, L & Zhang, SH 2014, Characteristics in coarse woody debris mediated by forest developmental stage and latest disturbances in a natural secondary forest of *Pinus tabulaeformis*. *Acta Ecologica Sinica*, 34: 232-238, <https://doi.org/10.1016/j.chnaes.2014.05.001>.
- Yan, ER, Wang, XH, Huang, JJ, Zeng, FR & Gong, L 2007, Long-lasting legacy of forest succession and forest management: characteristics of coarse woody debris in an evergreen broad-leaved forest of Eastern China. *Forest Ecology and Management*, 252: 98-107.
- Yang, FF, Li, YL, Zhou, Gi, Wenigmann, KO, Zhang, DQ, Wenigmann, M, Liu, SZ & Zhang, QM 2010, Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. *Forest Ecology and Management*, 259: 1666-1672.
- Zibilske, LM 1994, Carbon mineralization. In: Weaver RW, Angle J S, Bott omley PS, Eds. Methods of soil analysis. Part 2. Microbiological and biochemical properties. Madison, WI, USA. *Soil Science Society of America*, pp. 64 -835.
- Zhou, L, Dai, L, Gu, H & Zhong, L 2007, Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. *Journal of Forest Research*, 18: 48-54.

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