Effects of stand age on litter quality, decomposition rate and nutrient release of Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani*)

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The influence of stand age on litter quality, decomposition rate and nutrient release was examined in pure stands of Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani* [Steven] Spach) differing in age (Fir_{38}, Fir_{60}, Fir_{90} and Fir_{100} years). The needle litters were collected and analysed for initial total carbon, cellulose, hemicellulose, lignin and nutrient concentrations (N, P, K, Ca, S, Mg, Mn and Fe). Initial litter quality parameters varied significantly among the four stand age classes. The Fir_{60} and Fir_{100} stands had higher total C than the Fir_{38} and Fir_{90} stands, while the Fir_{38} and Fir_{100} stands had higher N than the Fir_{60} and Fir_{90} stands. Mean cellulose and hemicellulose concentrations were highest in the Fir_{90} stand, while mean lignin concentration was highest in the Fir_{38} stand. Fir_{90} stand showed the highest ratios of C/N and Lignin/N. In general, the older fir stands showed higher Ca, Mg and K concentrations and lower P and S concentrations than the younger stands. The litter, however, showed higher a Mn concentration under the Fir_{60}. Mean Fe concentration was highest under the Fir_{38} stand and lowest under the Fir_{60} stand. Litter decomposition was studied in the field using the litterbag technique. The litterbags were placed on the soil under each stand age class and sampled every 6 months for 2 years. The interaction of stand age and time on the mass loss was significant (p<0.01). The repeated measures ANOVA showed that the main effect of time on the mass loss was also significant (p<0.001). Needle litters under Fir_{100} and Fir_{60} stands decomposed faster than the needle litters under Fir_{90} and Fir_{38} stands. The calculated times required for 50% mass loss were higher under Fir_{38} (1.35 y) and Fir_{90} (1.27 y) stands than under Fir_{100} (1.05 y) and Fir_{60} (1.06 y) stands. The litters in Fir_{38} and Fir_{90} stands need approximately 4 years for 95% mass loss compared to the litters in Fir_{60} and Fir_{100} stands, which need 3 years. In general, Ca, Mg and S concentrations increased over time, whereas K and Mn decreased. These results illustrate that stand age is a key factor to be considered when studying litter decomposition dynamics.

Keywords: Litter Quality, Stand Age, Litter Decomposition, Nutrient Release, Fir

Introduction

Plant litter decomposition has long been recognized as an essential process for nutrient cycling and organic matter turnover within ecosystems (Heal et al. 1997, Laskowski & Berg 2006). Decomposition rate is mainly affected by climate (temperature and precipitation) and by litter quality (carbon/nitrogen [C/N] ratio, lignin, N and lignin/N ratio – Heal et al. 1997, Sariyildiz 2000, Sariyildiz & Anderson 2003a). In general, climate factors govern decay rates at broad scales, whereas litter quality plays an important role in controlling decay rates at small scales (Couteaux et al. 1995, Sariyildiz & Anderson 2003b). Most of the studies on the topic investigated the influence on decay rates of either interspecific differences in litter quality within systems or differences among systems using the same litter (Fogel & Cromack 1977, Berg & Meentemeyer 2002, Inagaki et al. 2004, Joly et al. 2017). Moreover, considerable intraspecific variation in litter quality has been reported as related to factors such as tree canopy structure (Sariyildiz & Anderson 2003b), soil characteristics (Sanger et al. 1998, Hättenschwiler et al. 2003, Sariyildiz & Anderson 2005), topography (Sariyildiz et al. 2005) and hydrology (Carreiro et al. 1999). The differences in litter quality within tree species may also reflect both genotypic and phenotypic variations resulting from biotic and/or abiotic interactions. However, a considerable variation in litter traits under different tree genotypes has also been observed. For example, polyphenol concentrations in leaf and fine root litter vary inherently among four distinct populations of *Metrosideros polymorpha*, the dominant tree species in Hawaiian montane forests (Hättenschwiler et al. 2003).

While environmental heterogeneity and genetic variability have received some attention as sources of intraspecific litter quality and decay rate variability (Albert et

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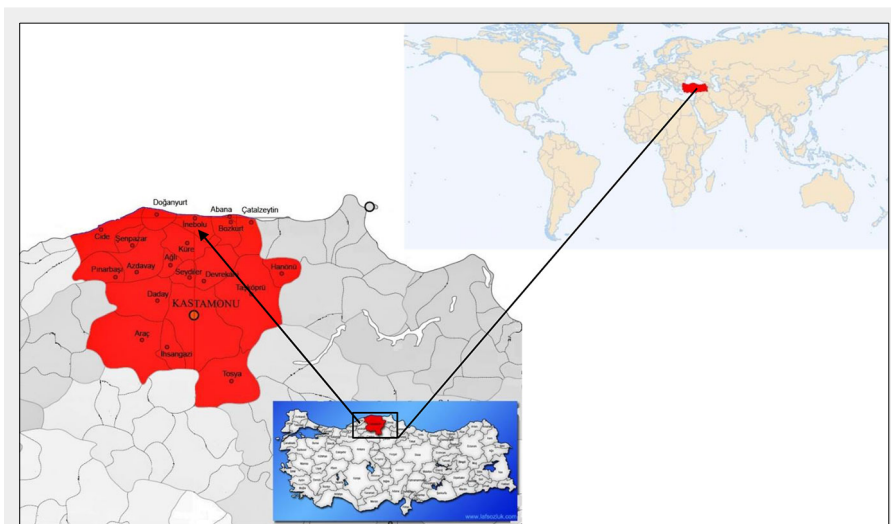@ Gamze Savaci (gsavaci@kastamonu.edu.tr)

Fig. 1 - Location of the study area in northeast Turkey.

al. 2010), the role of stand age has been poorly addressed (Inagaki et al. 2004, Trap et al. 2013). Changes in photosynthesis, mineral nutrition, respiration, C allocation and hydrological function during stand development were reviewed in detail by Ryan et al. (1997). Some authors proposed that the quality and quantity of soil organic matter and nutrient turnover can be influenced by forest stand age and the related changes in community structure and composition (Inagaki et al. 2004). Moreover, litter decomposition can be affected by microclimatic changes due to variations in solar radiation, wind speed or rainfall interception related to the canopy structure (Chen et al. 1999, Welke & Hope 2005). Relative humidity, in particular, can increase in the course of secondary forest succession and promote decomposition (Lohbeck et al. 2014, Wang et al. 2014, Trogisch et al. 2016). However, there is evidence that plants can show considerable intraspecific variations in litter quality related to forest stand age (Sharma et al. 1985, Sharma & Ambasht 1987). For example, Trap et al. (2013) showed that for pure beech (*Fagus sylvatica*) stands with different ages (15, 65, 95 and 130 years), forest age is an important driver of litter quality variation. Notable results included decreasing Mg, N and K concentrations during stand development and varying hemicellulose, cellulose and lignin content.

In this study, we tested the hypothesis that litter quality of Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani* [Steven] Spach) changes during its 100-year life span while controlling for climate and soil conditions. Moreover, we hypothesised that variations in litter quality parameters affect litter decomposition and nutrient release.

Material and methods

Study site description and sampling

The study was conducted in pure fir-dominated stands around the town of Inebolu,

which is located in the north part of Kastamonu Province in northwest Turkey (41° 51′ 23″ N, 33° 45′ 36″ E – Fig. 1). Study site elevation is 1030 m a.s.l. The aspect is northeast (NE) with a mean slope of 25%. The study site has a characteristic Black Sea climate with warm and rainy winters and hot but rainy summers. According to weather data for 1960-2015 (Inebolu Meteorology Station, 64 m a.s.l.), mean annual precipitation is 1551 mm, ranging from 90.3 mm in July to 185.9 mm in December. The mean annual temperature is 9.3 °C, reaching highs in August (26.6 °C) and lows in February (2.7 °C). The parent rock of the study site is neritic limestone and schists covered with sandy loam and clay. According to the FAO forest soil classification system, the soil of the fir stand is brown forest soil, and the humus layers were mull.

The fir is an important tree species in Turkey. Here this genus is represented by five taxa: (i) *Abies nordmanniana* subsp. *nordmanniana* Spach; (ii) *Abies nordmanniana* subsp. *bornmuelleriana* Maltfelt; (iii) *Abies cilicica* subsp. *isaurica* Coode & Cullen; (iv) *Abies cilicica* subsp. *cilicica* Carr.; and (v) *Abies nordmanniana* subsp. *equi-trojani* Coode & Cullen. These taxa are distributed over 584,781 hectares, which accounts for 2.62% of the overall forest coverage. As an endemic taxon, Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani*) is distributed in the Central and Western Black Sea Region and South Marmara Region in Turkey (Mataraci 2012). Selective logging of the fir forests, which are natural forests in the region, is the main management type in the region.

Fir stands were classified into the following age classes according to average tree age: 38 (Fir$_{38}$), 60 (Fir$_{60}$), 90 (Fir$_{90}$) and 100 (Fir$_{100}$) years old. For each stand age class, three subplots (20 × 20 m = 400 m^2) were chosen. Freshly fallen fir-needle litters were collected from a total of twelve subplots (3 replicates × 4 age classes = 12 subplots). Litters showed no visible signs of

discolouration or fungal colonization. The needle litters were air-dried in the laboratory and then oven-dried at 40 °C for 48 h. The oven-dried samples were then stored in plastic bags at 6 °C until the analyses.

Stand characteristics (height, diameter and canopy closure) were measured in each subplot. Measurements of diameter at breast height (DBH) and tree height were conducted on three sample trees in each stand age class. DBH was measured using a diameter tape. Trees were cored at breast height to determine tree age using the dendrochronological approach. Tree heights were measured with a Blume-Leiss clinometer.

Soil samples were taken under the same trees from which the fir needle litter was collected. Soil samples were collected in an area of 0.5 × 0.5 m^2 at a distance of 2 m from the base of the trunk and at a depth of 0-20 cm. The moist field samples were sieved (< 2 mm) to remove stones, roots and macro-fauna and bulked to give a single representative soil sample for each age class. Stand and soil characteristics are shown in Tab. 1.

Needle litter and soil analysis

The stored needle litters were oven-dried at 85 °C, ground in a laboratory mill to a mesh fraction less than 1 mm and analysed for organic C, total N, P, K, Ca, Mg, S, Mn, Fe, ADF (acid detergent fibre), lignin and cellulose concentrations.

Organic C and N concentrations were measured using a CNH-S elementary analyser (EA 3000® v.3.0 single, Eurovector, Milan, Italy) according to the dry combustion method. Nutrient concentrations (P, K, Ca, Mg, S, Mn, Fe) in the needle litters were analysed using an energy dispersive X-ray Fluorescence Spectrometer (EDXRF Xepos II®, Spectro-Analytical Instruments GmbH, Kleve, Germany). Certified soil reference material (NIST SRM 2709) was used to assess the accuracy of the EDXRF analyses.

Acid detergent fibre (ADF), a-cellulose and lignin were determined using the ADF-sulphuric lignin method by Rowland & Roberts (1994). ADF was calculated as the mass loss after heating a 0.5 g tared sample for 1 h with acidified cetryltrimethyl ammonium bromide and filtering the suspension through a tared glass sinter, followed by drying and reweighing. Cellulose was calculated as the mass loss after acidification of the ADF with 72% H$_2$SO$_4$, and lignin was calculated from the residual mass of filtrate after ignition at 550 °C for 2 h.

Soil pH (H$_2$O) was measured in a 1:2.5 mixture of deionized water and soil using a glass calomel electrode (pH 5 Series meter, LaMotte, Chestertown, MSD, USA) after equilibration for 1 h in solution (Jackson 1962). Soil moisture content on fresh soil samples was calculated by weight loss after drying approximately 10 g of soil for 24 h at 105 °C (Allen 1989). Bulk density was determined by weight loss after drying the undisturbed soil cores. Soil texture (sand,

silt and clay) was determined using the hydrometer method of Bouyoucos (1962). All analyses were performed in triplicate.

Needle litter decomposition

The litterbag method (Bocock & Gilbert 1957) was used to measure the decomposition rates of the different needle litters in the field. Litterbags (20 × 20 cm) were made of 0.1-mm nylon with a mesh size of 1.5 mm to allow for inclusion of mesofauna but exclusion of macrofaunal detritivores.

Each bag was filled with 5 g of needle litter that was air-dried at room temperature until a constant weight was reached. Subsamples of the needle litter were taken to determine the moisture content by drying at 85 °C. For each age class, the litterbags were prepared and placed in the original site where the needle litter was collected.

The number of needle litterbags used in the field experiment was 80 (4 stand age classes × 4 removal dates × 5 replicates). The needle litterbags were numbered and fixed to the ground of the corresponding site with metal pegs. Five litterbags were harvested from each age class after 6, 12, 18 and 24 months to evaluate needle litter decay over time. Percentage loss of initial mass was calculated after drying samples at 85 °C.

The needle litter decomposition rate (k) was calculated from the percentage of dry mass remaining using an exponential decay model (Olson 1963 – eqn. 1)

$$W_t/W_o = e^{-kt} \qquad (1)$$

where W_t/W_o is the fraction of initial mass remaining at time t, t is the elapsed time (years) and k is the decomposition constant (y^{-1}). As suggested by Olson (1963), the times required for 50% and 95% mass loss were calculated as $T_{50} = 1/k$ and $T_{95} = 3/k$, respectively.

For each sampling, the remaining litter mass, C, N, P, K, Ca, Mg, S, Mn and Fe concentrations were expressed as percentages of the initial values (P_{ij}), according to the equation used by Baldantoni et al. (2013 – eqn. 2):

$$P_{ij} = \frac{C_{ij} \cdot W_i}{C_{0j} \cdot W_0} \cdot 100 \qquad (2)$$

where C_{oj} is the initial concentration of the j-th parameter analysed, W_o the initial litter weight, C_{ij} is the concentration of the j-th parameter at the i-th sampling and W_i is the litter weight at the i-th sampling.

Statistical analysis

Means and standard deviations of litter quality parameters and litter decomposition rates were calculated for each stand age class (4 age classes and 3 replicates per age class). A two-way ANOVA (analysis of variance) was applied to analyse the effects of the stand age classes and time on the initial litter quality parameters using the software SPSS® ver. 17.0 for Windows (IBM, Armonk, NY, USA). Following the re-

sults of the ANOVA, Tukey's HDS (Honestly Significant Difference) test (α = 0.05) was used to compare multiple litter quality parameters at each litter sampling time among age classes. Repeated measures ANOVA (RMANOVA) was adopted to test the effects of stand age class, time and their interactions on the differences in the litter decomposition rates.

Results

Fir stands, soil characteristics and litter chemistry

Stand characteristics and some mineral soil properties of the fir stand age classes are shown in Tab. 1. In general, the older stands (Fir₉₀ and Fir₁₀₀) had higher mean tree diameter, height, canopy closure and sand content and lower mean clay and silt contents than the younger stands (Fir₃₈ and Fir₆₀ – Tab. 1). The Fir₉₀ stand showed the highest soil pH (5.99 ± 0.37) compared

to the F₃₈, Fir₆₀ and Fir₁₀₀ stands, which had similar soil pH (5.00 ± 0.23, 5.15 ± 0.30 and 5.16 ± 0.14, respectively). Soil bulk density, however, was similar in all fir stand age classes.

Initial litter parameters and the ratios of C/N and lignin/N in the needle litters are given in Tab. 2. The results showed that there were significant intraspecific variations (*p*<0.001) in the chemical compositions of Kazdagi fir litters among the different stand age classes, which in turn affected their decomposition rates. Initial litter carbon concentrations in Fir₆₀ and Fir₁₀₀ stands were higher (53.5% ± 1.9% and 53.2% ± 1.0%, respectively) than in Fir₃₈ and Fir₉₀ stands (50.4% ± 1.7% and 49.7% ± 1.6%, respectively). However, initial litter N and lignin concentrations in Fir₆₀ and Fir₉₀ stands (the middle-aged fir stands) were lower (1.11% ± 0.11% and 1.00% ± 0.1% for N, 14% ± 1.0% and 18% ± 4.0% for lignin, respectively) than in Fir₃₈ and Fir₁₀₀ stands (1.49% ± 0.1%

Tab. 1 - Stand and soil characteristics for per stand age classes. Means with different alphabets in rows indicate significant (p<0.001) difference between the stand age classes.

Variable	Stand age classes (years)			
	Fir₃₈	Fir₆₀	Fir₉₀	Fir₁₀₀
Mean diameter (cm)	30.8 ± 1.4 [a]	41.5 ± 3.9 [b]	47.0 ± 3.0 [c]	48.0 ± 2.4 [c]
Mean height (m)	24 ± 2.0 [a]	35 ± 1.0 [b]	41 ± 2.0 [c]	42 ± 2.0 [c]
Canopy closure (%)	41-70	41-70	71-100	71-100
PH (H₂O)	5.16 ± 0.14 [a]	5.15 ± 0.30 [a]	5.99 ± 0.37 [b]	5.00 ± 0.23 [a]
Sand (%)	32 ± 3.0 [b]	8 ± 1.0 [a]	84 ± 3.0 [c]	76 ± 3.0 [c]
Clay (%)	42 ± 3.05 [b]	54 ± 2.0 [c]	8 ± 1.0 [a]	9 ± 1.0 [a]
Silt (%)	26 ± 0.58 [c]	38 ± 3.0 [d]	8 ± 4.0 [a]	15 ± 2.0 [b]
Soil bulk density (g cm⁻³)	1.12 ± 0.08 [a]	1.16 ± 0.28 [a]	1.04 ± 0.35 [a]	1.20 ± 0.35 [a]

Tab. 2 - Initial litter quality parameters from the 4 different fir stand age classes. Means with different alphabets in rows indicate significant (p < 0.001) difference between the stand age classes.

Parameters	Units	Stand age classes (years)			
		Fir₃₈	Fir₆₀	Fir₉₀	Fir₁₀₀
C	(%)	50.4 ± 1.7 [a]	53.5 ± 1.9 [b]	49.7 ± 1.6 [a]	53.2 ± 1.0 [b]
N	(%)	1.49 ± 0.1 [b]	1.11 ± 0.11 [a]	1.00 ± 0.1 [a]	1.39 ± 0.1 [b]
Hemicellulose	mg g⁻¹	497 ± 13.3 [a]	465 ± 12.0 [a]	619 ± 15.4 [b]	464 ± 6.0 [a]
Cellulose	mg g⁻¹	644 ± 6.0 [a]	729 ± 1.0 [b]	788 ± 7.0 [b]	670 ± 2.0 [a]
Lignin	(%)	24 ± 3.0 [b]	14 ± 1.0 [a]	18 ± 4.0 [b]	21 ± 2.0 [b]
C:N	ratio	34:01:00	48:01:00	50:01:00	38:01:00
L:N	ratio	16:01:00	13:01:00	18:01:00	15:01:00
Ca	mg kg⁻¹	23,630 ± 30 [a]	20,500 ± 20 [a]	33,080 ± 30 [b]	32,470 ± 30 [b]
Mg	mg kg⁻¹	2185 ± 21 [b]	1235 ± 15 [a]	3034 ± 25 [c]	2113 ± 21 [b]
K	mg kg⁻¹	6065 ± 15 [a]	6221 ± 15 [a]	7184 ± 16 [c]	7838 ± 17 [c]
P	mg kg⁻¹	1871 ± 3 [c]	1822 ± 3 [bc]	1780 ± 3 [b]	1570 ± 3 [a]
S	mg kg⁻¹	2073 ± 3 [b]	2023 ± 3 [b]	2120 ± 3 [b]	1998 ± 3 [b]
Mn	mg kg⁻¹	2339 ± 3 [c]	3044 ± 3 [d]	458 ± 1.3 [a]	2024 ± 3 [b]
Fe	mg kg⁻¹	1068 ± 3 [c]	421 ± 2.5 [a]	489 ± 2.1 [b]	494 ± 2.4 [b]

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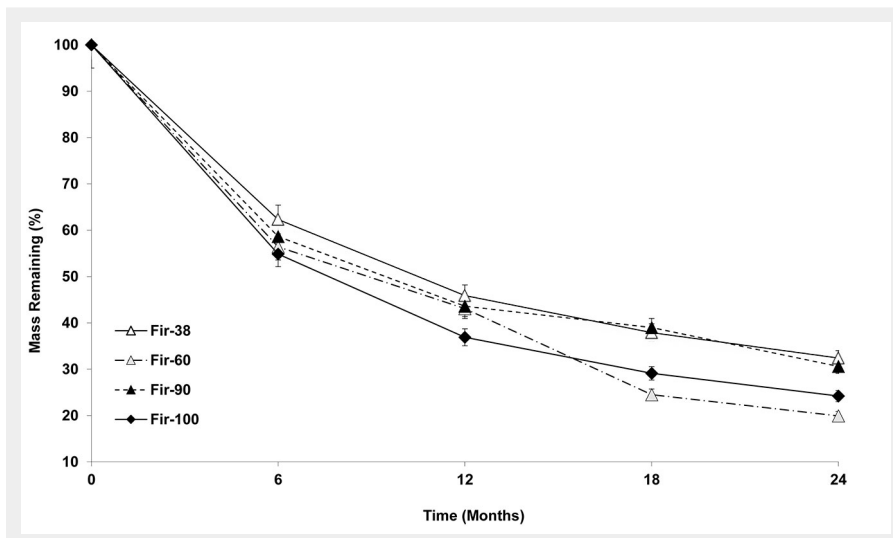
Fig. 2 - Mean mass loss of fir litters from the 4 different stand age classes.

and 1.39% ± 0.1% for N, 24% ± 3.0% and 21% ± 2.0% for lignin, respectively).

The Fir$_{90}$ stand had the highest litter cellulose and hemicellulose concentrations (788 ± 7.0 and 619 ± 15.4 mg g^{-1}, respectively) compared to the other 3 age classes, which showed relatively similar hemicellulose concentrations (~465 mg g^{-1}); however, for cellulose concentration, age class order

was Fir$_{60}$ (729 ± 1.0 mg g^{-1}), Fir$_{100}$ (670 ± 2.0 mg g^{-1}) and Fir$_{38}$ (644 ± 6.0 mg g^{-1} – Tab. 2). Initial litter C/N ratios were higher in Fir$_{60}$ and Fir$_{90}$ (48:1 and 50:1, respectively) than in Fir$_{38}$ and Fir$_{100}$ (34:1 and 38:1, respectively). The Fir$_{90}$ stands also had a higher initial litter lignin/N ratio (18:1) than the Fir$_{60}$ and Fir$_{100}$ stands (16:1 and 15:1, respectively). However, the Fir$_{60}$ stands showed

the lowest initial lignin/N ratio (13:1). In general, the middle-age fir stands (Fir$_{60}$ and Fir$_{90}$) had lower N and lignin concentrations but higher cellulose concentrations and C/N ratios compared to the younger (Fir$_{38}$) and older (Fir$_{100}$) fir stands (Tab. 2).

Overall, initial litter Ca, Mg and K concentrations were higher in the older fir stands (Fir$_{90}$ and Fir$_{100}$) than in the younger fir stands (Fir$_{38}$ and Fir$_{60}$ – Tab. 2). Initial litter, P and Mn concentrations, however, were lower in the older fir stands than in the younger fir stands. Initial Fe concentration was highest in the youngest fir stand (F$_{38}$) as compared to the other fir stands, which had similar Fe concentrations (Tab. 2). Initial litter S concentration did not vary among the fir stand age classes.

Needle litter mass losses

Fig. 2 shows the remaining mass of the fir needle litter in the four different stand age classes over 24 months. According to the ANOVA results, the main effects of time and the interaction of time and stand age on mass loss were all significant (p<0.001). These results demonstrate that litter mass losses of fir varied significantly between the sampling times and between the fir stand age classes.

After 6 months, the needle litters in Fir$_{100}$ and Fir$_{60}$ stands showed higher mean mass losses (45% and 44%, respectively) than in Fir$_{90}$ and Fir$_{38}$ (41% and 38%, respectively). There was a 7% difference in needle-mass losses between the oldest and youngest stands. At 12 months, the needle litter under Fir$_{100}$ still had the highest mass losses (63%), while Fir$_{38}$ had the lowest (54%). The needle litters had similar mass loss under Fir$_{60}$ (57%) and Fir$_{90}$ (57%). The differences in needle mass losses between the oldest and the youngest stands were higher at 12 months (by 9%) than at 6 months. At 18 months, the needle litters under Fir$_{60}$ de-

Tab. 3 - Annual decomposition constant (*k*) and the time (year) required for 50% [T$_{50}$ (y)] and 95% mass loss [T$_{95}$ (y)] under 4 different fir stand age classes.

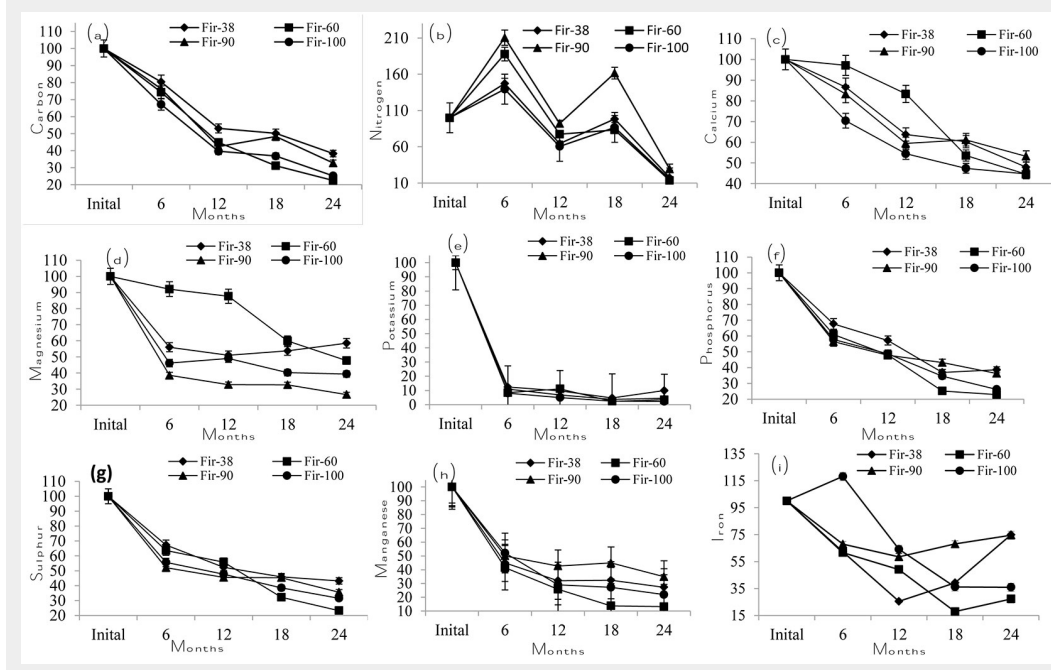| Parameters	Stand age classes (years)			
	Fir$_{38}$	Fir$_{60}$	Fir$_{90}$	Fir$_{100}$
k (yr^{-1})	-0.743	-0.948	-0.788	-0.944
r^2	0.975	0.519	0.946	0.979
F	p<0.001	p<0.001	p<0.001	p<0.001
T$_{50}$ (y)	1.35	1.05	1.27	1.06
T$_{95}$ (y)	4.04	3.16	3.81	3.18

Fig. 3 - Variation in total C (a), N (b), Ca (c), Mg (d), K (e), P (f), S (g), Mn (h) and Fe (i) concentrations in fir litters during decomposition period (24 months) from the 4 different stand age classes.

composed much faster and had the highest values (76%), followed by Fir_{100} (71%), Fir_{90} and Fir_{38}, which had the same mass losses (62%). The differences in the needle mass losses between the oldest and the youngest stands at 18 months were much higher (14%). At 24 months, the needle litters under Fir_{60} had the highest mass loss (80%), followed by Fir_{100} (76%), Fir_{90} (69%) and Fir_{38} (68%). The differences in the needle mass losses between the oldest and the youngest stands at 24 months were still higher (12%).

Decay rates (k) and the time required for 50% [T_{50} (y)] and 95% mass loss [T_{95} (y)] for the needle litters from the different stand age classes are given in Tab. 3. The decay rates of the needle litters were higher in Fir_{60} and Fir_{100} stands (-0.948 and -0.944, respectively) than in Fir_{38} and Fir_{90} stands (-0.743 and -0.788, respectively). The calculated times required for 50% mass loss were higher in Fir_{38} (1.35 y) and Fir_{90} (1.27 y) than in Fir_{100} (1.06 y) and Fir_{60} (1.05 y). A similar order was seen for the time required for 95% mass loss, indicating that the needle litters under Fir_{38} and Fir_{90} need approximately 4 years to lose 95% of mass compared to the needle litters under Fir_{60} and Fir_{100}, which need less time (~3 y).

Initial litter C, P, K, Mg, Ca, S, Mn and Fe concentrations all decreased over time (Fig. 3). Initial N concentration also decreased over time but had two peaks at the 6-month and 18-month intervals (Fig. 3b). The needle litters in the middle age stands (Fir_{60} and Fir_{90}) had higher peaks than Fir_{38} and Fir_{100}. At the 12-month and 24-month intervals, N concentration in the needle litters decreased. Initial C, P and S concentrations decreased linearly and did not show any significant differences among the fir stand age classes (Fig. 3a, Fig. 3f and Fig. 3g, respectively). Initial K concentration showed a sharp decrease at the 6-month interval but remained relatively stable after that (Fig. 3e). Initial Ca, Mn and Fe concentrations also decreased over time but varied among the fir stand age classes (Fig. 3c, Fig. 3h and Fig. 3i, respectively).

Discussion

Variation in fir litter quality with stand age classes

In temperate ecosystems, initial litter quality parameters (mainly lignin and nitrogen concentration) largely influence litter decomposition rates, which in turn influences the turnover of associated carbon and nutrients as a dominant source of organic matter input to the soil (Melillo et al. 1982, Aerts 1997). Initial litter quality also affects nitrogen availability for plants and soil N dynamics (Hobbie 2000). Many studies have shown that higher litter C/N and lignin/N ratios are associated with slow rates of net soil N mineralization (Scott & Binkley 1997, Satti et al. 2003). The specific quality of the litter that plants produce is,

therefore, a key trait for the functioning of ecosystems (Trap et al. 2013).

To our knowledge, no study has directly investigated the forest stand age-related variability in litter quality of Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani* [Steven] Spach) and its consequences for litter decomposition processes. Our results indicated that initial N and lignin concentration in fir needle litter was lower in the middle-age fir stands compared to the younger- and older-age fir stands. Similar findings were also reported by Inagaki et al. (2004) who found that N and lignin concentrations in leaf litter were lower in middle-aged forests than in young forests. The authors state that in the middle-aged forests, tree density decreases due to thinning practices or competition among individuals; and the N capital in the biomass increases, especially for evergreen species, indicating that N becomes a less limiting resource. They concluded that changes in N demand for plants are likely a major factor affecting lignin production in leaf litter. In contrast to those findings, Trap et al. (2013) who studied pure beech (*Fagus sylvatica*) forest stands differing in age (15, 65, 95 and 130 years) found that lignin and lignin/ N ratios were highest in stands of intermediate age.

In the present study, significant differences were evident in nutrient concentrations among the age classes of the fir stands; however, the differences did not clearly show a linear increase or decrease pattern with the stand age classes. Other researchers have also stated that the effect of the nutrient concentrations on litter due to stand age was not continuous (Welke & Hope 2005). Trap et al. (2013) found significantly high Mg, N and K litter concentrations in 15-year-old stands of pure beech that subsequently decreased with increasing stand age; Mn, on the other hand, was the only nutrient analysed that was highest in the oldest stands. They attributed the observed differences among stands of different ages to (i) the relative abundance of sun and shade leaves and (ii) increasing intraspecific competition for soil nutrients with increasing tree age (Ryan et al. 1997).

Variation in initial litter quality parameters among fir subspecies

The initial litter C and N concentrations of *Abies nordmanniana* subsp. *equi-trojani* were partly comparable with the findings of other studies and occasionally lower or higher than their results depending on the fir subspecies used in their studies. Wei et al. (2020) found that initial C concentration for *Abies fabri* was 51.3%, which was similar to the initial litter C concentration (51.7%) for *Abies nordmanniana* subsp. *equi-trojani*. Jagodzinski et al. (2019) studied *Abies alba* stands ranging from 8-115 years old (12 different aged tree stands) in southern Poland and found that C concentration ranged from 50.4% (8 years old) to 52.7% (93 years old). A study by Wu et al. (2014)

showed that initial carbon and N concentrations of *Abies faxoniana* were 52% and 1.12%, respectively. Similarly, in a study of *Abies faxoniana* tree stands in western Sichuan, China, Wu et al. (2010) found that initial C and N values were 51.6% and 0.92%, respectively. Sariyildiz et al. (2005) reported that for *Abies nordmanniana* subsp. *bornmuelleriana* Maltfelt, initial litter was 47% C and 1.10% N. Accordingly, *Abies nordmanniana* subsp. *equi-trojani* had lower initial litter lignin concentrations (from 14% to 24%) than the litters of *Abies alba* (mean 30.5%) and *Abies nordmanniana* subsp. *bornmuelleriana* (mean 36%) but similar values with the litter of *Abies faxoniana* (mean 25%).

Initial litter hemicellulose and cellulose concentrations of *Abies nordmanniana* subsp. *equi-trojani* were much higher than the values reported for *Abies alba* (Hobbie et al. 2006), which were 199.9 mg g^{-1} for cellulose and 123.4 mg g^{-1} for hemicellulose. The same was true for *Abies nordmanniana* subsp. *bornmuelleriana* Maltfelt, which had initial litter cellulose concentrations between 260 mg g^{-1} and 290 mg g^{-1} (Sariyildiz et al. 2005). Palosuo et al. (2005) found 416 mg g^{-1} for initial cellulose and 303 mg g^{-1} for initial lignin in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands. Wu et al. (2010) noted that initial lignin and cellulose concentrations for *Abies faxoniana* trees were 418.3 mg g^{-1} and 294.5 mg g^{-1}, respectively. Mean C/N ratios in the litters of *Abies nordmanniana* subsp. *equi-trojani* (from 34:1 to 50:1) were similar to the litter of *Abies nordmanniana* subsp. *bornmuelleriana* Maltfelt, ranging from 38:1 to 51:1. However, mean lignin/N ratios were lower in the litters of *Abies nordmanniana* subsp. *equi-trojani* (from 13:1 to 18:1) than in the litter of *Abies nordmanniana* subsp. *bornmuelleriana* Maltfelt, ranging from 25:1 to 45:1. Palosuo et al. (2005) found that C/N ratios and lignin/N for Douglas-fir were 56:1 and 45:1, respectively.

When comparing the findings of other studies with the initial litter P and K concentrations found in the present study, our values are higher than the values found for *Abies alba* (Hobbie et al. 2006), which were 1180 mg g^{-1} for P and 2200 mg g^{-1} for K. Our initial Ca and Mg concentrations were also much higher than the values found for *Abies alba* (Hobbie et al. 2006), which were 12,400 mg g^{-1} for Ca and 800 mg g^{-1} for Mg.

Variation in mass losses with stand age classes

Our results indicate that decomposition rate did not vary monotonically with the increase in stand age of fir. Needle litters under Fir_{100} and Fir_{60} stands decomposed faster than the needle litters under Fir_{90} and Fir_{38} stands. The faster rate of litter decomposition in Fir_{60} and Fir_{100} stands noted in the present study was associated with a lower value of lignin/N ratio (13:1 and 15:1, respectively) in the litter samples compared to Fir_{38} and Fir_{90} (16:1 and 18:1, re-

spectively). It is generally argued that decomposition is relatively faster with litter of lower lignin content and in sites with a warm and humid climate; dry, wet and cold climates and poor litter quality would inhibit litter decomposition processes (Laskowski & Berg 2006, Berg et al. 2010, Currie et al. 2010). Several studies have also reported significant correlations between lignin content or the lignin/N ratio and decay rates for a variety of litter types (Fogel & Cromack 1977, Berendse et al. 1987, Sariyildiz 2015). For example, Melillo et al. (1982) found strong, negative, linear relationships between initial lignin/N ratios and mass-loss rates of leaf litter from northern hardwoods and other areas. The conditions for microorganisms were possibly more favourable in Fir_{100} and Fir_{60} stands than Fir_{90} and Fir_{38} stands, resulting in the higher litter decomposition rates. Because lignin is a resistant substrate, more time is required for microbial decomposition; therefore, organic substances with large amounts of lignin decompose over longer periods (Sariyildiz 2000). The lignin content was highest in Fir_{38} and lowest in Fir_{60}, which may have affected litter decomposition. Long-term climate changes have the greatest effect on litter decomposition and carbon sinks. Such changes are not only related to temperature changes, but to seasonal precipitation changes as well, which can be more influential (Klopatek 2008). Similarly, Fogel & Cromack (1977) stated that the rapid decomposition of litter was due to excessive temperature differences (especially since it affects the water-soil regime), and that the mass-loss rate of coniferous species significantly affected the mass.

On the other hand, age-related forest stand changes in forest structure influence the quality and quantity of organic matter input and thus nutrient turnover (Inagaki et al. 2004, Trap et al. 2009). Additionally, structural changes of the canopy layer during succession can also affect the microclimate on the forest floor due to alterations in solar radiation, wind speed or rainfall interception (Chen et al. 1999, Shen et al. 2012). As shown by other studies, forest development over time can result in substantial changes in fir stand conditions, especially microclimate factors (Aerts 1997), soil fauna (Chauvat et al. 2009), soil microbial community composition (Smithwick et al. 2005) and nutrient cycling efficiency (Trap et al. 2009), which are seen as the most influential factors on litter mass loss.

Other studies using fir or different tree species have also found contrasting results with litter mass losses related to stand age. Klaus (2018) noted that the litter decomposition rates for balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) needles increased slightly with increasing stand age. Welke & Hope (2005) studied Douglas-fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*) aged 10-25, 50-65 and >85 years old and found that Douglas fir lit-

ter decayed more in old stands than in younger stands, while the opposite trend was seen for birch litter. Yu et al. (2014) assessed four Chinese fir plantations (7, 16, 23 and 29 years old) and found that litter decomposition rates decreased between the 7- and 16-year-old plantations, then significantly increased from the 16- to 23-year-old plantations and reached a peak in the 29-year-old plantations. Trogisch et al. (2016) found that litter decomposition declined with forest stand age. Their results clearly showed that microclimatic site conditions were more favourable for litter decomposition in young forest stands. A study by Brun et al. (2008) also showed that Scots pine needles in the 118-year-old stands decayed less than in the 70- and 53-year-old stands. Sharma & Ambasht (1987) found that $T_{1/2}$ value for *Alnus nepalensis* mass was lowest in the 30-year stand and highest in the 56-year stand, indicating that mass loss was much faster in the 30-year stand.

Variation in mass losses and nutrients during litter decomposition

As demonstrated by several authors (Sariyildiz & Anderson 2003a, Pérez-Suárez et al. 2012), the general trend in litter decomposition processes is initially rapid and then slows down. A similar trend was also seen in our study for fir litter decomposition (Fig. 2). The litters of Fir_{38}, Fir_{60}, Fir_{90} and Fir_{100} respectively lost 54%, 57%, 57% and 63% of their initial weight in the first year (0-12 months) compared with 14%, 23%, 12% and 13% losses in the second year (12-24 months). Initially, accelerated litter decomposition rates are mainly attributed to easier degradation of water-soluble organic compounds, while the later, slower litter decomposition rates are mostly due to difficulties in microbial degradation and mineralization of chemically recalcitrant complex compounds, such as polyphenols and lignin. Researchers have shown that litter N concentration has a strong, positive influence on initial litter decay (<3 months), as higher concentration of this element is associated with faster decomposition rates, while lignin and C/N ratios determine later rates of decomposition (Aber et al. 1990).

Mean mass loss in the fir stands was 58% after 12 months and 74% after 24 months. These values were much higher than the values shown by Sariyildiz & Küçük (2008) for fir (31% and 52%, respectively). Wei et al. (2020) noted that throughout the experiment, the dry weight loss rate of fir litter was 32%. The decay-rate coefficients (k) for fir litters (ranging from -0.743 to -0.948 in this study) were comparatively higher than the -0.370 k value reported by Sariyildiz & Küçük (2008). Klaus (2018) noted that the decay-rate coefficients (k) for balsam fir aged 1, 13, 16, 28 and 29 years were -0.26, -0.34, -0.31, -0.35 and -0.36, respectively, after 12 months.

Research suggests that nutrient concentrations vary to some extent during the de-

composition period. An increase in litter N concentration (Fig. 3b) followed by a decline over time, as observed in this study, is similar to the patterns found in other studies (Bubb et al. 1998, Singh et al. 1999). Increases in N concentration could be attributed to the addition of N from exogenous sources to microbial biomass (Melillo et al. 1982, Sinsabaugh et al. 1993). Among the nutrients, initial litter K and Mn (Fig. 3e and Fig. 3h, respectively) were lost from the decomposing litter mostly during the first 6 months. This indicates an initial leaching loss of K because of its solubility. The relative elemental transfer from the decomposing litter generally demonstrates that potassium is highly mobile and nitrogen is the least mobile (K > Ca > P > N). The results of Laskowski et al. (1995a, 1995b) revealed an initial rapid decrease in K concentration followed by stabilisation or a slow increase. Similarly, Brais et al. (1995) demonstrated for *Abies balsamea* that K, Ca and Mg concentrations decreased with time. Gosz et al. (1973) reported an increase in absolute phosphorus content in deciduous litter during the first year of decomposition. However, Edmonds (1980) found that phosphorus was rapidly lost in the first three months, and absolute weights never exceeded initial weights in *A. rubra* and *A. nepalensis* litter. Sharma & Ambasht (1987) demonstrated that the 30-year stand had a higher rate of phosphorus loss than the other stands, while the 56-year stand had the lowest rate. We did not study the differences in soil nutrient status and microclimate conditions of the different stand age classes of the fir species; however, the results indicate that those factors should be taken into account to fully understand the differences in the decomposition process among the different stand age classes.

Conclusion

Our results indicate that forest stand age is an important driver of intraspecific variability in fir litter quality parameters and decomposition rates with associated consequences for ecosystem functioning. The decomposition rate did not vary monotonically with increases in fir stand age. However, the results have clearly shown that the faster decomposition rates in Fir_{60} and Fir_{100} stands are associated with a lower value of lignin/N ratio in the litter samples compared to Fir_{38} and Fir_{90} stands. Unfortunately, these forest age-related intraspecific variations in litter quality and mass losses are unprecedented and largely unexplained. There is clearly a need for further studies focusing on those topics, their variation and their potential driving forces on soil processes.

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