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Diffusion and seasonal dynamics of O_2 in woody debris from the Pacific Northwest, USA

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Abstract

O_2 is an important regulator of physiological processes involved in the decomposition of woody debris, yet O_2 levels and diffusion rates within decomposing logs are largely unknown. We examined how O_2 diffusion rates in decayed and sound wood varied with moisture and density, and we compared predicted with observed seasonal changes in oxygen concentration in logs in a Pacific Northwest old-growth *Pseudotsuga menziesii* forest. In the laboratory, the oxygen diffusion coefficient (D_{O2}) was determined in the longitudinal and radial (or tangential) directions on wood cores of varying moisture content and density. In the field, O_2 was measured in tubes inserted to three radial depths (2, 6 and 15 cm) within logs of two species (*Pseudotsuga menziesii* and *Tsuga heterophylla*) and five decay classes (where class 5 = most decayed). In both the radial and longitudinal directions, D_{O2} increased exponentially as the air filled pore space (AFPS) increased and as density decreased. In the field, mean O_2 concentrations in logs were not significantly different between species. Mean O_2 concentrations were significantly lower in the least decayed logs as compared to the most decayed logs. Mean O_2 concentrations decreased with radial depth only in decay class two logs. Seasonal O_2 levels did not consistently vary with log moisture, respiration, or air temperature. The comparison of the results from a model that assumes oxygen diffuses only in the radial direction to field data indicates that laboratory measurements of oxygen diffusion may underestimate field oxygen concentrations. Cracks, insect galleries and other passages in decayed logs, and longitudinal oxygen diffusion may account for this discrepancy. In the field, log oxygen concentrations were rarely as low as 2%, indicating anaerobic conditions may not be as common in logs as we previously thought. Oxygen limitations on decomposition may occur in relatively sound and/or water soaked wood, but probably not in decayed logs in a terrestrial setting.

Abbreviations: air filled pore space – (AFPS); TDR – time domain reflectometry

Introduction

The importance of woody debris in terrestrial carbon and nutrient cycles is well recognized (e.g. Harmon et al., 1986; Harmon and Sexton, 1996; Krankina et al., 1999). Woody debris contains a significant portion of the carbon stored in forest ecosystems. Changes in woody debris carbon stores are determined by the balance of inputs via tree mortality and outputs via respiration. Wood respiration is limited by available nitrogen and nitrogen fixation is thought to partially control respiration rates by providing a source of available nitrogen (Blanchette and Shaw, 1978; Cowling and Merrill, 1966). Thus, respiration and nitrogen fixation are key processes in the carbon and nitrogen cycles of dead wood. However, our understanding of the mechanisms that control these processes is still crude. For example, low levels of O_2 may explain low respiration rates in woody debris in cool, wet forests such as those in the Pacific Northwest of the United States (Harmon et al., 1986). However, O_2 levels in woody debris have rarely been monitored and O_2 diffusion processes in decayed wood have not been studied.

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Oxygen regulates many physiological processes in woody debris including respiration and nitrogen fixation (Scheffer, 1985; Silvester et al., 1982). Huang et al. (1977) measured the diffusion of dissolved O_2 in undecayed, chipped, liquid-saturated *Pseudotsuga menziesii* sapwood. Tarkow and Stamm (1960a,b) measured the diffusion of carbon dioxide and water vapor through undecayed veneers of *Picea sitchensis*. However, we do not know of any studies that have measured oxygen diffusion rates in decayed wood. Slightly more is known about oxygen levels in dead wood. Savely (1939) found O_2 concentrations as low as 9.4% in *Quercus* and *Pinus* logs from the deciduous forests of North Carolina. Paim and Beckel (1963) measured seasonal changes in O_2 partial pressure in decaying *Fagus grandifolia* logs from Ontario and found O_2 concentrations as low as 0.5% in partially submerged logs and as low as 3.4% in non-submerged logs.

In this study, we sought to answer the following questions: Can a simple model of radial oxygen diffusion in woody debris developed from laboratory measurements be used to predict oxygen concentrations of woody debris in the field? Do oxygen concentrations in woody debris inhibit respiration or nitrogen fixation? To answer these questions, we determined the effects of wood fiber orientation, density, and moisture on O_2 diffusion rates in wood in various stages of decay and measured seasonal changes in O_2 concentration within logs. We also used a model of O_2 diffusion in woody debris to compare predictions based on these diffusion data with the O_2 levels of logs in the field.

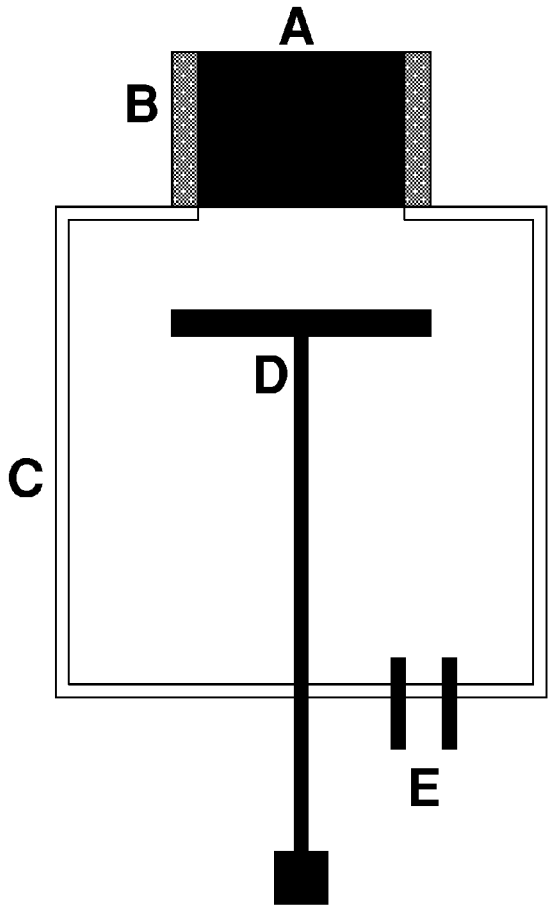

Figure 1. Diagram of a cross-section of the diffusion apparatus where A is the wood core, B is modeling clay, C is the diffusion chamber, D is the movable plate, and E designates ports used for obtaining gas samples and flushing the diffusion chamber with N_2.

Materials and methods

O_2 diffusion

O_2 diffusion coefficients (D_{O2}) in wood were determined using a core method developed for soils (Taylor, 1949). In this method an O_2 free diffusion chamber is separated from the atmosphere by a cylindrical sample of wood (Figure 1). O_2 accumulation in the diffusion chamber is then measured over time. A plate within the diffusion chamber can be moved to start or stop diffusion. Pure N_2 was used to thoroughly flush the diffusion chamber prior to measurement. Modeling clay was used to cover the sides of the wood cores and seal the space between the cores and the diffusion chamber. The change in O_2 concentration with time inside the diffusion chamber was measured by periodically withdrawing 0.5 mL gas samples. O_2 concentrations were measured with a Hewlett Packard model 5830 gas chromatograph fitted with a thermal conductivity detector and a Molecular Sieve 5A packed column. The effect of the diffusion apparatus and leakage were measured and corrected for (Taylor, 1949). D_{O2} was calculated by fitting the concentration data to a steady-state diffusion equation (i.e. Fick's first law; Taylor, 1949). To avoid violating the assumptions of a steady-state model of diffusion, we did not use data if O_2 concentrations within the diffusion apparatus were above 2%.

Samples of *Pseudotsuga menziesii* wood in various stages of decay taken from the H.J. Andrews Experimental Forest in the central Oregon Cascades were used to examine the influence of wood moisture

and density on O_2 diffusion. In addition, samples of nine species of sound wood of varying density (in order of increasing density: *Ochroma pyrimidale*, *Thuja plicata*, *Alnus rubra*, *Tilia americana*, *Picea sitchensis*, *Liriodendron tulipfera*, *Pseudotsuga menziesii, Acer macrophyllum*, and *Quercus garyana*) purchased from a local lumber supplier were used to examine the influence of density on O_2 diffusion. Wood samples were cut into cylindrical cores with a diameter of 5.2 cm and a height of 3.6 cm. For the decayed wood samples, 6 cores each were taken from low, moderate, and highly decayed *Pseudotsuga menziesii* samples. For the sound wood samples, 2 cores were cut from each of the nine species. Cores were cut to measure diffusion in the longitudinal (along the fiber) or radial (perpendicular to the fiber along an axis from the bark to the pith) direction. It was not always possible to cut sound wood cores for measuring diffusion in the radial direction, because it was often prevented by the fiber orientation in the lumber that the cores were cut from. Thus, sound cores were cut for measuring diffusion in the tangential (perpendicular to the fiber) instead of radial direction. Cores from decayed wood were sterilized in a cobalt 60 gamma irradiator with 2.5 Mrad prior to diffusion measurements to inhibit biological respiration. For the decayed wood cores, moisture was left at field conditions, decreased by drying, or increased by soaking in water. Sound wood cores were dried until the moisture content equilibrated with air humidity. The air filled pore space (AFPS) was calculated for each core using the following equation:

$$\text{AFPS} = 1 - (\text{Water Filled Pore Space}).$$

Water Filled Pore Space was determined by dividing the wood moisture content for a core by the maximum possible wood moisture content for that core (Wood $\text{Moisture}_{\text{max}}$). Wood moisture content was calculated as:

$$\text{Wood Moisture} = (\text{Wet Weight} - \text{Dry Weight}/\text{Dry Weight} * 100.$$

The maximum wood moisture (Wood $\text{Moisture}_{\text{max}}$) content of the wood cores was determined on cores submerged in water for at least one week with the moisture content calculated in the same fashion as unsubmerged cores. We did not observe any evidence of air spaces resulting from hydrophobic fungal hyphae. Density was determined for each core by dividing the dry weight by the wet volume.

O_2 concentrations within logs

To determine seasonal changes of O_2 in the field, we measured O_2 concentrations in logs in an old-growth stand in the Wind River Experimental Forest on the west slope of the southern Washington Cascades. Wet, cool winters and warm, dry summers characterize the climate of this site. Mean annual temperature and precipitation are 8.8 °C and 250 cm, respectively. Forests are dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* (Franklin and Dyrness, 1988).

The 18 logs that were used for oxygen measurement were selected randomly. Two *Pseudotsuga menziesii* and *Tsuga heterophylla* logs from each of five decay classes were selected except in decay class five where only one suitable log per species could be found. Decay class one logs are the least decayed and decay class five logs are the most (Harmon and Sexton, 1996). The logs were at least 30 cm in diameter and ranged up to 1 m in diameter.

Three PVC tubes with an inner diameter of 2.5 cm were tightly imbedded within each log to a depth of 2, 6, or 15 cm to monitor oxygen concentrations. Tubes were imbedded at least one meter from a log end to help reduce the influence of longitudinal oxygen diffusion. Tubes had unperforated sides and an open end that was in contact with the exposed wood surface (4.9 cm^2 exposed wood). Tube internal volume ranged from 60 ml in the 2 cm deep tubes to 125 ml in the 15 cm tubes. A bead of silicon caulk was applied along the edge of the tube in contact with the internal wood surface to help ensure a tight seal. Tubes were attached to the logs with screws to prevent movement and sealed to the log at the surface with caulk. In addition, silicon caulk was used to fill any spaces between the hole and tube. Each tube had a cap with a rubber septum to allow gas sample removal.

The tubes within each log were sampled monthly from April 1998 to April 2000. Four mL gas samples were withdrawn with a syringe and transferred to evacuated 3 mL gas sample containers. The septa of the gas sample containers were further sealed with wax to help prevent contamination. The O_2 concentration of the gas samples was determined within 24 h with a gas chromatograph (see O_2 diffusion section of the 'Materials and methods'). A gas mixing equation was used to correct for the average 0.02 mL of O_2 contamination that we found in the evacuated gas sample containers. In theory, the reduced pressure created by withdrawing 4 mL of gas from a 60 mL tube interior could increase O_2 concentration by up to 1.25% in the

syringe barrel from the inrush of atmospheric air into the syringe. This process could therefore elevate the O_2 concentrations of samples taken from tubes with low O_2 concentrations. We tested for this effect by additionally measuring O_2 in tubes with histories of low O_2 levels using gas sample containers left for a month on double-ended needles that also penetrated the log tube septum. The O_2 concentrations determined with both methods never differed by more than 0.5% even at O_2 concentrations as low as 3%. This indicates that airflow into the syringe barrel did not greatly influence measured O_2 concentrations.

Log moisture, respiration, and meteorological data

Log moisture was monitored in the logs using time domain reflectometry (TDR; Gray and Spies, 1995). The TDR method determines average wood volumetric water content in percent by measuring the elapsed time it takes an electromagnetic wave to travel the length of a pair of metal rods embedded in the wood. Two rods spaced 5 cm apart were inserted 30 cm into the logs resulting in a measured volume of approximately 47 cm^3(Gray and Spies, 1995). Readings from the rods were taken monthly or bimonthly from March 1998 to March 2000.

Log respiration in each of the eighteen study logs was monitored using soda-lime (Edwards, 1982). Jars with soda lime were left for 24 h roughly once per month (23 times from March 1998 to March 2000) in lidded buckets sealed to the logs with silicone caulk and attached with long screws. One bucket was attached to each log and the exposed wood surface area was 706 cm^2 for each bucket. Control buckets with jars of soda-lime were used to correct for leakage of CO_2 into the buckets from the atmosphere.

Monthly temperature and precipitation data were from the National Oceanic and Atmospheric Administration's data archives for the Carson Fish Hatchery weather station in Washington. The weather station is approximately 7 km from the study site and is at a similar elevation.

Statistical and modeling analysis

Statistical analysis including linear regression, analysis of covariance (ANCOVA), and calculation of means and 95% confidence limits were performed with SAS (1985). Linear regression was used to develop relationships between wood moisture, density and the log of the O_2 diffusion coefficients. ANCOVA was used to test for significant differences among the means of the O_2 levels from all sampling dates for the two species, five decay classes, and three tube depths with the distance of the tubes from the nearest broken end of the log included as a covariate. This part of the study used a split-plot experimental design and the analyses were performed using the appropriate procedures and random effects for this design. Means and confidence intervals of the O_2 concentrations at each sampling date were used to examine seasonal changes in O_2 concentrations.

For this study, we consider relationships to be statistically significant when the p-value was less than 0.05. The 95% confidence limits on figures provide a simple visual method to compare means. Using the terminology of Ramsey and Schafer (1995), we use the phrase 'conclusive evidence' of a difference between two means to describe situations where confidence limits do not overlap at all and 'strong evidence' to describe situations where confidence limits may overlap but not enough to include the mean being compared.

To examine the implications of our laboratory O_2 diffusion results, we used a model of nitrogen fixation in dead wood that generates log O_2 concentrations from diffusion and respiration rates (Hicks, 2000). These predictions were compared to the seasonal O_2 levels obtained from the field. This model uses a modified form of Fick's First Law to estimate oxygen diffusion rates in the radial direction. The oxygen diffusion rate (DIFF, mol d^{-1}) is controlled by log moisture, density and oxygen content:

$$\mathrm{DIFF} = \mathrm{DIFMAX} * \mathrm{SA/THIK} * \mathrm{MSTIDD} * \mathrm{DENIDD} * \mathrm{O2IDD},$$

where DIFMAX (mol O_2 m^{-1} d^{-1}) is a reference diffusion rate of O_2 through wood calculated from D_{O2}, SA (m^2) is the surface area available for diffusion, and THIK (m) is the distance that O_2 must diffuse through. Three indices describe the effect of log moisture (MSTIDD), density (DENIDD) and oxygen content (O2IDD) on the oxygen diffusion rate. Indices range from zero to one and are used to reduce DIFMAX when any conditions controlling diffusion are limiting. Respiration rates used in the model are modified by log temperature, moisture, oxygen concentration, and substrate quality. Log temperature and moisture were estimated using meteorological data from the Carson Fish Hatchery NOAA weather station in Washington. All logs used in model runs were 50 cm in diameter. For model predictions and field data, we compared the average of the O_2 concentra-

Table 1. Coefficients for slopes and y-intercepts for equations fit to O_2 diffusion data relating the diffusion coefficient (D_{O2}) to AFPS and wood density. Equations were of the form: $\log(D_{O2}) = m*x + b$

Decay	Wood Variable (x)	Fiber Orientation	m	b	R^2	*p*-value	*N*
Present	AFPS	Radial	2.01	−5.72	0.66	<0.01[a]	9
Present	AFPS	Longitudinal	3.40	−5.58	0.95	<0.01[a]	9
Present	Density	Radial	−4.58	−2.46	0.99	0.03[a]	3
Present	Density	Longitudinal	−4.06	−1.18	0.86	0.25	3
Absent	Density	Tangential	−1.84	−4.07	0.36	0.09	9
Absent	Density	Longitudinal	−1.51	−2.64	0.37	0.08	9

[a]Indicates significance at p-values < 0.05.

tions at three radial depths (2, 6 and 15 cm) from *Pseudotsuga menziesii* and *Tsuga heterophylla* logs for each decay class examined.

Results

O_2 diffusion

In the radial and longitudinal directions, D_{O2} increased exponentially with AFPS (Figure 2). The lines fitted to the log-transformed radial and longitudinal data explain much of the variation in the data as indicated by R^2 values of 0.66 and 0.95, respectively (Table 1). The regression results indicate that D_{O2}increased from 1.88×10^{-6} cm^2 s^{-1} at zero AFPS to 1.94×10^{-4} cm^2 s^{-1} at an AFPS of 1.0 in the radial direction, and increased from 2.64×10^{-6} cm^2 s^{-1} at zero AFPS to 6.62×10^{-3} cm^2 s^{-1} at a AFPS of 1.0 in the longitudinal direction. D_{O2} was higher in the longitudinal direction when compared to the radial direction and this difference increased as AFPS increased. Thus, D_{O2} in the longitudinal direction was 1.4 and 34 times greater than D_{O2} in the radial direction at zero and 1.0 AFPS, respectively.

As wood density increased, D_{O2} decreased exponentially (Figures 3 and 4). The rate of D_{O2} decrease was lower in the longitudinal direction than in the radial or tangential directions (Table 1). In addition, the rate of D_{O2} decrease was lower for sound as compared to decayed wood. For decayed wood with a theoretical density of zero, D_{O2} in the longitudinal direction was 19 times greater than D_{O2} in the radial direction (6.63×10^{-2} and 3.46×10^{-3} cm^2 s^{-1}, respectively). At a decayed wood density of 0.5, D_{O2} in the longitudinal direction was 35 times greater than D_{O2} in the radial direction (6.15×10^{-4} and 1.78×10^{-5} cm^2 s^{-1}, respectively). For sound wood with a theoretical density of zero, D_{O2} in the longitudinal direction was 27 times greater than D_{O2} in the tangential direction (2.28×10^{-3} and 8.56×10^{-5} cm^2 s^{-2}, respectively). At a sound wood density of 0.5, D_{O2} in the longitudinal direction was 39 times greater than D_{O2} in the tangential direction (4.02×10^{-4} and 1.03×10^{-5} cm^2 s^{-1}, respectively).

O_2 levels within logs

In the field, mean O_2 concentrations for the two log species and for the three radial depths within the logs were not significantly different, whereas the means for the decay classes and combinations of decay class and depth were significantly different (Table 2; Figures 5 and 6). The covariate (distance of the tubes from the end of the logs) bordered on meeting the criteria for significance with a p-value of 0.0656 (Table 2). Average O_2 concentration rose from 15.1% in decay class one logs to approximately 20.5% in decay classes three through five (Figure 5c). Mean O_2 concentrations decreased significantly with radial depth in decay class two logs from 18.6% at a depth of 2 cm to 11.4% at a depth of 15 cm, but O_2 concentrations did not consistently vary with depth in the other decay classes (Figure 6).

Log O_2 concentrations, moisture, and respiration varied seasonally (Figure 7). There was convincing evidence that O_2 levels were significantly lower and varied more in decay class one and two logs in comparison to logs in decay classes three through five (Figure 7a). In addition, O_2 concentrations dropped dramatically and significantly in November 1998 coinciding with an increase in precipitation and moderate temperatures in this month (Figure 7a,b). There was

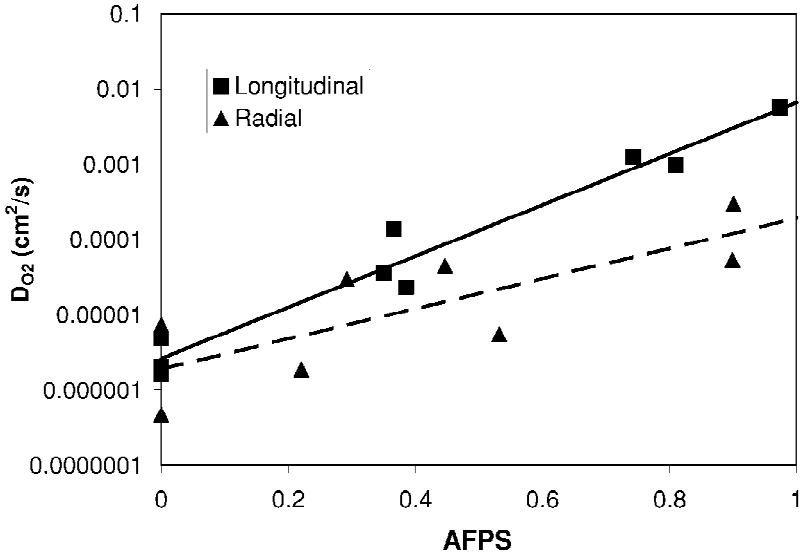

Figure 2. The relationship of the O_2 diffusion coefficient (D_{O2}) with the air filled pore space (AFPS) in decayed *Pseudotsuga menziesii* wood cores of various densities.

Table 2. *p*-values from ANCOVA results for testing if wood species, tube depth within the log, decay class or their interactions affect mean O_2 concentrations

Effect	*p*-value
Species	0.9188
Tube Depth	0.1225
Decay Class	0.0046[a]
Species × Depth	0.5715
Species × Decay Class	0.5618
Depth × Decay Class	0.0032[a]
Species × Depth × Decay Class	0.9651
Distance of tube from the log end	0.0656

[a]Indicates significance at *p*-values < 0.05.

no indication of a consistent seasonal pattern in log O_2 concentrations associated with the patterns of log moisture, respiration, and air temperature. Log moisture levels were generally higher as decay class increased (Figure 7b). In decay class five logs, moisture levels peaked around 300% from November through May then declined to nearly 150% in August through October. Moisture levels varied much less in decay classes one through three. The respiration rates of the logs generally tracked average monthly temperatures; although, there was more variation in the respiration data in comparison to the monthly temperatures (Figure 7b).

Model predictions

In general, modeled log O_2 concentrations either underestimated or overestimated field O_2 concentrations when the model used parameters calculated from laboratory diffusion data from the radial or longitudinal directions, respectively (Table 3). Differences between model and field estimates were much greater for decay class one logs than for decay class five logs. Model predictions closely tracked seasonal changes in field data in decay class five logs when model parameters were estimated from diffusion data from the longitudinal direction, but not when parameters for the radial direction were used (seasonal changes in O_2 are not shown because predicted and observed data consistently disagreed). Model predictions did not closely track seasonal changes in field O_2 concentrations in decay class one logs.

Discussion

O_2 Diffusion

Our results for the relationships of D_{O2} with AFPS in decayed wood agree with other studies of O_2 diffusion. Taylor (1949) measured O_2 diffusion in soil and found a similar exponential decrease of D_{O2} with increasing moisture. In addition, Huang et al. (1977) measured diffusion of dissolved oxygen in liquid-saturated *Pseudotsuga menziesii* sapwood and found

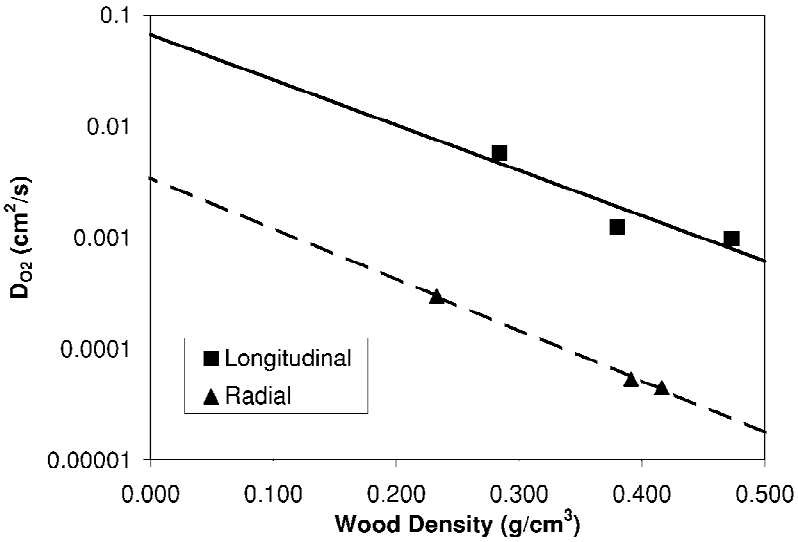

Figure 3. The relationship of the oxygen diffusion coefficient (D_{O2}) with the density of decayed *Pseudotsuga menziesii* wood. The regression lines are extended beyond the range of the data to allow comparison of our results to theory and other studies. Statistical inference only applies within the range of the data.

Table 3. Average O_2 concentration in decay class one and five logs from 1999 from a model and field data. Modeled results used diffusion parameters calculated from data for the radial or longitudinal directions

Data source	Parameter source	Average O_2 (%)	
		Decay Class 1	Decay Class 5
Model	Radial	8.6	18.1
Model	Longitudinal	18.9	20.9
Field		15.2	20.7

D_{O2} in the longitudinal and radial directions to be 1.4 $\times 10^{-6}$ and 7.6 $\times 10^{-6}$ cm^2 s^{-1}, which is 6 to 40% of the D_{O2} for water (approximately 2.0 $\times 10^{-5}$ cm^2 s^{-1} at 20 °C; Lide, 1998). At an AFPS of zero, we found D_{O2} was 9–13% of the D_{O2} in water for diffusion in the radial and longitudinal directions, respectively. Huang et al. (1977) used sound sapwood and selected for wide annual rings, which may explain the higher D_{O2} they found for the longitudinal direction.

Our results for the relationships of D_{O2} with wood density generally agree with other studies of O_2 diffusion. Studies of O_2 diffusion in soil and sound wood found similar exponential decreases of D_{O2} with increasing bulk density (Huang et al., 1977; Taylor, 1949). In addition, if density alone is controlling diffusion rates, the D_{O2} in wood should equal the D_{O2} in air (approximately 2.1 $\times 10^{-1}$ cm^2 s^{-1} at 20 °C; Lide, 1998) when wood density equals air density (approximately 0.001 g cm^3 at standard temperature and pressure). As expected, our predicted D_{O2} values for wood approach the D_{O2} for air as wood density theoretically approaches zero (Figures 3 and 4).

Higher rates of O_2 diffusion in the longitudinal direction when compared to the radial or tangential direction can be explained by wood structure (Figures 3–5). Longitudinal diffusion is faster than radial diffusion, because wood tracheids and vessels form passages in the longitudinal direction that facilitate diffusion. These passages reduce the cell wall thickness per unit distance that a gas must diffuse through when the gas is traveling along the longitudinal direction as compared to the radial direction (Tarkow and Stamm, 1960a).

The convergence of radial and longitudinal D_{O2} values as AFPS approaches zero agrees with theory and previous results (Figure 2; Huang et al., 1977; Tarkow and Stamm, 1960a). As water fills wood pore spaces, radial and longitudinal O_2 diffusion rates should converge, because O_2 diffuses much more slowly in water than through air (Lide, 1998). This should reduce the relative differences between the longitudinal and radial directions. In dry, undecayed wood veneers, Tarkow and Stamm (1960a) found D_{CO2} to be approximately 650 times greater in

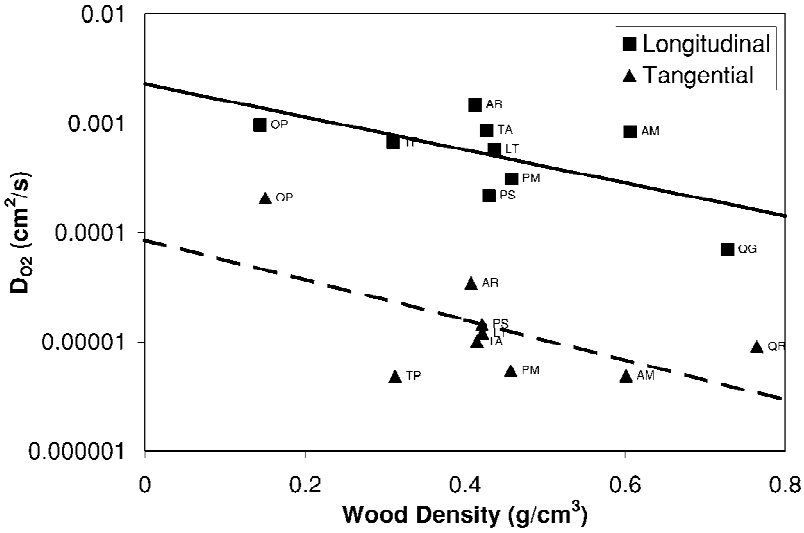

Figure 4. The relationship of the oxygen diffusion coefficient (D_{O2}) with the density of sound wood from nine species (in order of increasing density: *Ochroma pyrimidale*, *Thuja plicata*, *Alnus rubra*, *Tilia americana*, *Picea sitchensis*, *Liriodendron tulipfera*, *Psedotsuga menziesii, Acer macrophyllum*, and *Quercus garyana*; initials of each species appear to the right of the data point).

the longitudinal as compared to the radial direction, while Huang et al. (1977) found longitudinal D_{O2} to be 5.5 times greater than radial D_{O2} in undecayed wood chips that were water saturated. The smaller relative differences between D_{O2} for radial and longitudinal directions found in our study likely result from comparing different wood species and decay amounts. In addition, comparing O_2 and CO_2 diffusion rates further complicates matters.

Possible explanations for the lower rate of D_{O2} decrease with increasing wood density in the longitudinal as compared to the radial and tangential directions depend on whether the wood was sound or decayed (Table 1). In sound wood, structural changes in wood anatomy that are related to density increase (i.e. more cell wall per unit volume) possibly decrease tangential diffusion to a greater degree than longitudinal diffusion. In decayed wood, cracks and passages that form as decay progresses and density decreases should reduce the importance of fiber orientation.

Similarly, the cracks and passages that form as decay progresses may also explain the lower rate of D_{O2} decrease with increasing wood density for sound wood as compared to decayed wood (Table 1). The breakdown of cell walls creates additional air paths that facilitate gas movement through wood to a greater degree than do the structural changes that accompany density decrease in sound wood.

O_2 levels within logs

The patterns of O_2 concentration among the different decay classes and between the two species can be explained by patterns of wood density and respiration. Wood density decreases with decay (Harmon et al., 1986; Harmon and Sexton, 1996). Respiration and decomposition rates also tend to decrease with the degree of decay (Harmon et al., 1986; Hicks et al., 2002a). Lower O_2 levels in decay class one and two logs relative to decay classes three through five result from relatively high respiratory consumption of O_2 and relatively low O_2 diffusion rates in the denser wood of decay classes one and two. *Pseudotsuga menziesii* and *Tsuga heterophylla* have similar wood densities and respiration rates during decomposition, thus they should have similar average O_2 levels (Harmon and Sexton, 1996; Hicks et al., 2002a; Sollins et al., 1987).

The interaction of decay class and depth was unexpected. We expected O_2 levels to decrease with radial depth in each decay class because the distance for O_2 to diffuse increases. In addition, we assumed that respiration rates would be relatively constant along the length of the log, and that spacing the tubes at least one meter from the ends of the logs would avoid the influence of longitudinal oxygen diffusion (Paim and Beckel, 1963). However, the decrease of O_2 with radial depth only occurred in decay class two logs (Figure 6). The nearly constant, near atmospheric ($\sim$21%), values in decay classes three through five are

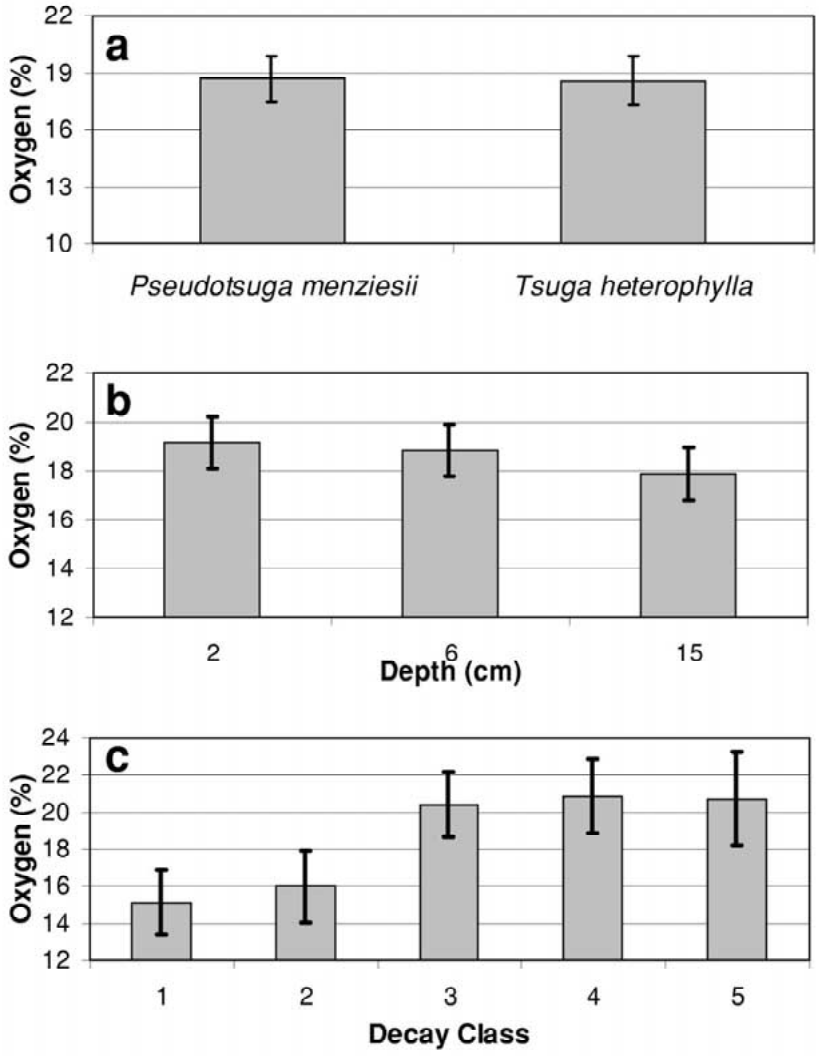

Figure 5. Mean oxygen concentrations and 95% confidence intervals in logs for different (a) species, (b) radial depths within the logs, and (c) decay classes. Means are calculated by pooling data for all species, depths, and decay classes.

likely a result of the relatively high O_2 diffusion rates in these lower density logs when compared to decay class one and two logs. The pattern in decay class one cannot be explained unless longitudinal O_2 diffusion and/or patchily distributed respiration activity is influencing O_2 levels. We measured the distance of the tubes from the nearest broken end of the log and included it as a covariate to test if longitudinal diffusion might be influencing O_2 levels in the tubes. The borderline significance of the covariate is suggestive that the distance of the tubes from the end of the logs was influencing O_2 levels in some of the logs. However, there is no way to tell if the mechanism producing this effect is longitudinal diffusion or something else such as patterns of respiration or moisture. The relatively dry and constant moisture content of heartwood early in the decay process of logs (Harmon and Sexton, 1995) suggests that longitudinal diffusion rates might be higher in decay class one than in later decay classes. A patchy distribution of respiration may also explain the results for decay class one logs. It was not uncommon in decay class one logs for tubes at depths of 2 or 6 cm to have much lower O_2 levels (3–6%) when compared to levels at the 15 cm depth (10–20%). Logs are colonized in a patchy manner with many microbial decomposers introduced by channelising insects (Carpenter, 1988). This should lead to a patchy distribution of respiration activity in the early decay stages of the

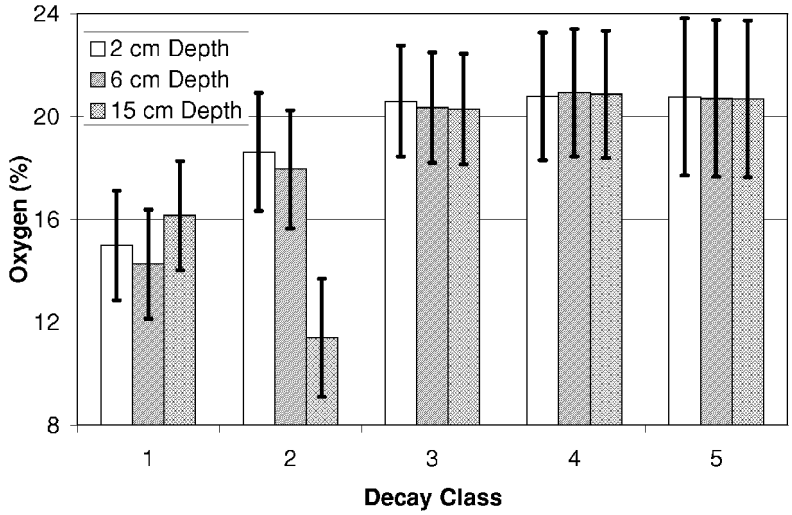

Figure 6. Mean oxygen concentrations and 95% confidence intervals for different combinations of radial depths within the logs and decay classes. Means are calculated by pooling data for all species.

log. This patchy distribution probably changes to a relatively uniform distribution in decay class two logs and this may account for the decrease of O_2 with depth in that class.

In an apparent contrast to our results, Paim and Beckel (1963) found O_2 levels to generally decrease with the radial depth within logs in a forest in Ontario, Canada. However, they sampled only *Fagus grandifolia* logs inhabited by *Orthosoma brunneum* beetles. These beetles do not inhabit logs until they have been on the ground several years, making them most similar to decay class two logs in our study.

The seasonal pattern of moisture with decay class agrees with previous studies of wood moisture. Harmon and Sexton (1995) measured changes in seasonal fluctuations in the moisture content of decay class one *Pseudotsuga menziesii* and *Tsuga heterophylla* logs in the Pacific Northwest and found little seasonal variation in the average moisture content of logs. They also found the maximum moisture content of logs to increase with decreasing density. In addition, Harmon and Sexton (1995) noted that runoff of throughfall decreases and drying rates increase as density decreases. Thus, the low-density logs of decay classes four and five are more likely to wet up and dry out to a greater degree than higher density logs.

The dramatic decrease in O_2 concentrations in November 1998 coincided with increased precipitation (Figure 7a,b). Log moisture as measured by TDR also increased in decay classes four and five at these times, but not in decay classes one through three. However, TDR measures the average moisture concentration along a pair of metal rods that passed through the bark, sapwood, and heartwood of the logs. It is likely that the moisture content of the outer portions of logs (primarily bark and sapwood) in all decay classes also increased in November. This is supported by Harmon and Sexton (1995), who found that heartwood moisture content was relatively constant, while bark and sapwood moisture contents decreased in the summer and were maximum in the fall and winter. It is likely that the outer portions of logs in all decay classes had greater seasonal moisture fluctuations than the inner portions. We hypothesize that a wetting event in November 1998 triggered reduced O_2 diffusion rates, and possibly high respiration rates. Although temperatures were cool, high respiration rates could result from scavenging by the decomposer community of the remains of microorganisms that died from previous low moisture availability in the outer portions of the logs.

In November 1999, O_2 levels also dropped in all decay classes; however, the decrease is neither as large nor as significant as in November 1998 (Figure 7a). We may have missed this second rewetting event or a more gradual log rewetting may have spread the decrease out over time. We would have expected respiration rates to also increase in November 1998; however, in this month respiration rates were measured 2 weeks after O_2 levels were measured possibly missing the ef-

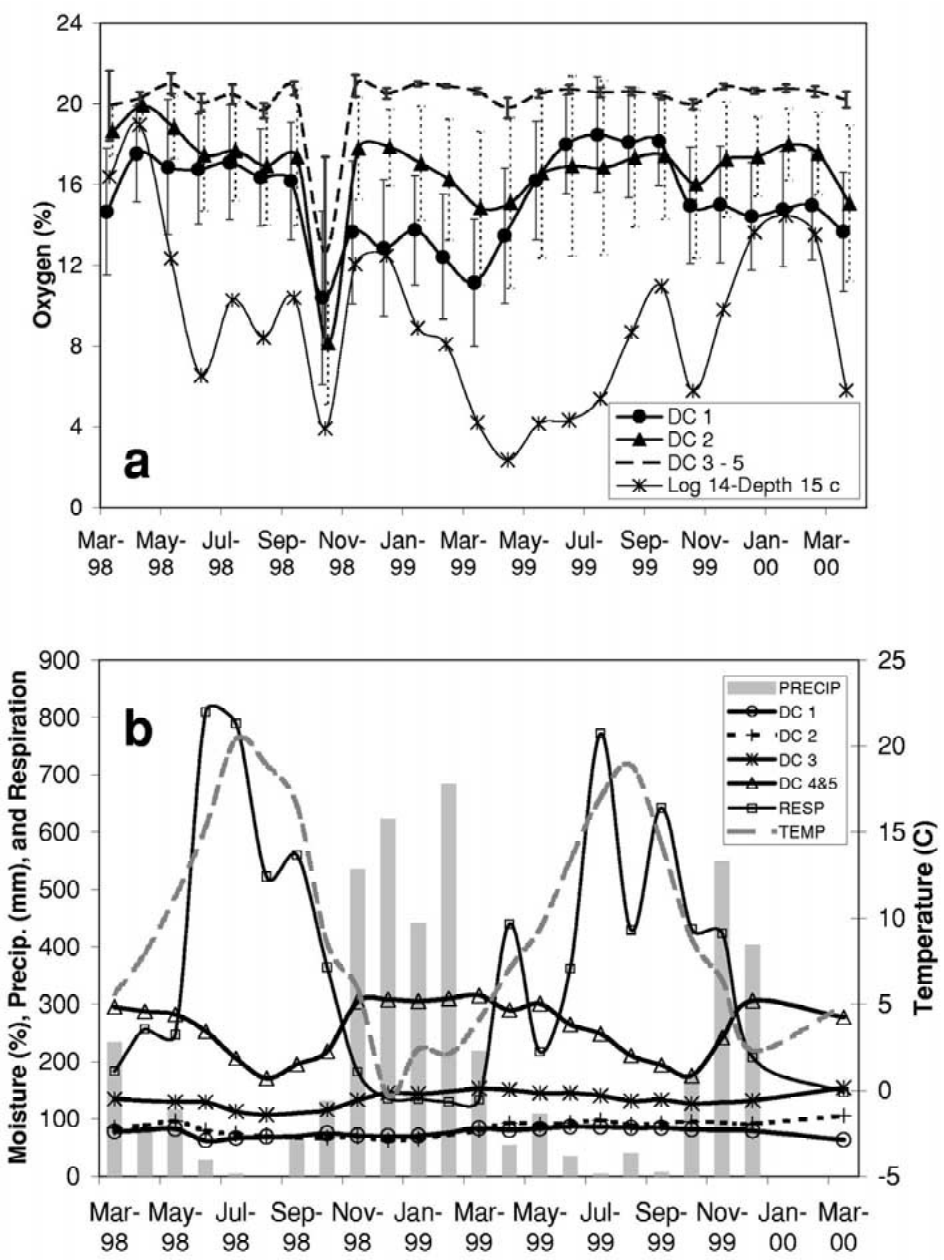

Figure 7. (a) Monthly mean O_2 concentrations and 95% confidence intervals for decay classes one, two, and three through five; and monthly O_2 levels at a radial depth of 15 cm in log 14 (*P. menziesii*, decay class two). (b) Average log moisture concentration determined by TDR in decay classes one, two, three, and four and five combined; mean monthly temperature, monthly precipitation, and respiration rate (mg CO_2 m^{-2} d^{-1}).

fect of this rewetting event. These rewetting events are likely transient, lasting for days to weeks; therefore, daily to weekly sampling is necessary to observe these hypothesized events.

Other than the response in November 1998, the lack of a consistent seasonal pattern of log O_2 concentrations is unexpected. The relatively close relationship between temperature and respiration would presumably create a seasonal pattern of O_2 concentration. Paim and Beckel (1963) found average CO_2 concentrations in *Fagus grandifolia* logs to rise and fall with temperature from May to October in Ontario; however, their oxygen levels did not consistently relate to temperature or CO_2. In our case, the Mediterranean climate of the Pacific Northwest may contribute to the lack of a seasonal pattern of O_2 concentrations in logs (Figure 7b). The warm, dry summers and cool, wet winters create a pattern where low precipitation levels and log moisture in summer may increase O_2 diffusion rates when respiration is high, while high log moisture in the winter would decrease O_2 diffusion rates when respiration is low. This combination of high O_2 diffusion rates with high respiration and low O_2 diffusion rates with low respiration would obscure a seasonal pattern.

Individual logs often had unique responses that are difficult to discern from average values. For example, O_2 concentrations in log 14, a decay class two log, at a depth of 15 cm varied greatly from near atmospheric levels to 2.4% in April 1999 (Figure 7a). O_2 concentrations below 5% occurred in 5 of the 18 logs, but primarily in decay classes one and two. In addition, O_2 levels in log 14 varied more than the average seasonal response. This suggests that logs, particularly in decay class one and two, probably have unique patterns of wetting and decay that appear random at the scale we measured.

Model comparison

The comparison of the results from our model of O_2 diffusion in the radial direction and field data indicate that *in vivo* measurements of radial O_2 diffusion do not adequately explain field data (Table 3). Large cracks and passages in decay class five logs that were specifically avoided when cutting wood cores for diffusion measurements probably contribute to the generally higher field O_2 concentrations. In decay class one logs, which do not generally have cracks and passages, O_2 diffusion in the longitudinal direction may be accounting for the underprediction of field O_2 levels when using model parameters solely calculated from radial O_2 diffusion data. Our model also tended to overestimate decay class one log moisture in spring and underestimate log moisture in summer in comparison to the TDR data. Model overestimates of log moisture will produce lower O_2 levels, whereas underestimates of log moisture will produce overestimates of log O_2 concentrations. The addition of longitudinal diffusion in the model, improvements in the moisture dynamics portion of the model, and better estimates of *in situ* oxygen diffusion rates should improve the seasonal estimates for decay class one logs.

Conclusions

Physiological processes in dead wood such as respiration and nitrogen fixation are influenced by O_2 concentration, but do the O_2 levels we observed limit either of these processes? Fungal respiration does not seem to be inhibited much above 5% O_2 (Scheffer, 1985), while nitrogen fixation is optimum at concentrations from 2 to 5% O_2 (Hicks et al., 2002b; Silvester et al., 1982). Therefore, respiration is probably not greatly inhibited by the O_2 concentrations found in our logs. We did not take into account CO_2, which rises as oxygen declines and can also inhibit respiration. Nitrogen fixation rates are likely to be limited by the generally high O_2 levels found in our logs. However, our methods examine large-scale patterns of O_2 relative to the size of microorganisms. Microscale patterns of depleted O_2 may be occurring in the vicinity of nitrogen fixing organisms in the wood. Nitrogen fixing organisms often have mechanisms for regulating the O_2 levels around them (Sprent, 1979). Still these mechanisms do not seem to compensate completely for high O_2 concentrations, because the microorganisms are inhibited in laboratory studies when incubated at O_2 concentrations above 5% (Hicks et al., 2002b; Silvester et al., 1982). Therefore, nitrogen fixation may be inhibited by the O_2 levels we observed, while respiration is probably not.

We were somewhat surprised that low oxygen levels were not more common in logs. Other investigations have demonstrated anaerobic conditions in wood or found oxygen levels below 1% in wood (Huang et al., 1977; Paim and Beckel, 1973). However, these investigations dealt with wood that was partially or completely submerged in water, indicating that anaerobic conditions in terrestrial woody debris may not be as common as we previously thought. Oxygen

limitations on decomposition may occur in relatively sound and/or water soaked wood, but probably not in decayed logs in a terrestrial setting.

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