Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga heterophylla* forests on northern Vancouver Island

Andreas Brunner and J.P. Kimmins

Abstract: Asymbiotic nitrogenase activity in coarse woody debris was measured using the acetylene reduction assay under ambient conditions in three different stand ages (5, 53, and 88 years old) of an unmanaged second-growth *Tsuga heterophylla* (Raf.) Sarg. – *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes forest type and a *Thuja plicata* Donn. ex D. Don – *Tsuga heterophylla* old-growth forest on northern Vancouver Island, British Columbia, Canada. Four different decay classes of coarse woody debris, different species in the early decay stages, and sapwood and heartwood were sampled separately. Mean nitrogenase activity ranged between 1.3 and 19.5 nmol $C_2H_4 \cdot d^{-1} \cdot (\text{g dry mass})^{-1}$, with an overall mean of 5.7. High variability of the activity rates between logs and within logs was observed in all four stands. Mean activity rates were, in most cases, significantly different between decay classes, with generally increasing nitrogenase activity with the progress of decay. Moisture content of the samples was a good predictor of nitrogenase activity and could explain differences between decay classes. Only minor differences in nitrogenase activity were found between the different stands. Estimates of nitrogen fixation ranged from 1.0 to 2.1 kg $N \cdot ha^{-1} \cdot year^{-1}$, the magnitude of these values depending more on the mass of coarse woody debris substrate available for asymbiotic nitrogen-fixing bacteria (103–158 $t \cdot ha^{-1}$ in this study) than on differences in nitrogenase activity rates. The measured nitrogenase activity and the resultant estimates of nitrogen fixation are among the highest values reported in the literature.

Résumé : L'activité non symbiotique de la nitrogénase dans les débris ligneux grossiers a été mesurée à l'aide du test de réduction de l'acétylène en conditions ambiantes dans trois peuplements d'âge différent (5, 53 et 88 ans) situés dans une forêt de seconde venue non aménagée de *Tsuga heterophylla* (Raf.) Sarg. et de *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes ainsi que dans une forêt ancienne de *Thuja plicata* Donn. ex D. Don et de *Tsuga heterophylla* située au nord de l'île de Vancouver, en Colombie-Britannique, Canada. Quatre classes de décomposition des débris ligneux grossiers, différentes espèces aux stades initiaux de décomposition ainsi que le bois d'aubier et le bois de cœur ont été échantillonnés séparément. En moyenne, l'activité de la nitrogénase variait de 1,3 à 19,5 avec une moyenne globale de 5,7 nmol de $C_2H_4 \cdot j^{-1} \cdot (\text{g de masse sèche})^{-1}$. Le taux d'activité était très variable dans et entre les billes dans les quatre peuplements. Les taux moyens d'activité étaient dans la plupart des cas significativement différents entre les classes de décomposition et l'activité de la nitrogénase augmentait généralement avec le degré de décomposition. Le contenu en eau des échantillons était un bon prédicteur de l'activité de la nitrogénase et pouvait expliquer les différences entre les classes de décomposition. Seules des différences mineures dans l'activité de la nitrogénase ont été observées entre les différents peuplements. Les estimations de la fixation de l'azote variaient de 1,0 à 2,1 kg $N \cdot ha^{-1} \cdot an^{-1}$. L'ampleur de ces valeurs dépendait plus de la masse de substrat disponible dans les débris ligneux grossiers pour les bactéries qui fixent l'azote de façon non symbiotique (103–158 $t \cdot ha^{-1}$ dans cette étude) que des différences dans le taux d'activité de la nitrogénase. La mesure de l'activité de la nitrogénase et les estimations de la fixation de l'azote qui en résultent sont parmi les valeurs les plus élevées rapportées dans la littérature.

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Introduction

Coarse woody debris (CWD) is an important structural component of many unmanaged forests in western North America (Jurgensen et al. 1997; Caza 1993; Harmon et al. 1986). There are several different categories of aboveground CWD, but standing snags and boles on the ground in different decay stages make up the majority of this ecosystem component. Stumps and coarse roots make up a very significant but little studied additional contribution to the total ecosystem CWD. Coarse woody debris has a variety of different functions. It supplies an energy source for microbes, a habitat for animals and plants, a moisture and nutrient store for plants, and a location for nitrogen fixation. It plays an important role in maintaining soil structure by providing a long-term source of humus input to the soil.

Reported levels of CWD on the forest floor vary from 0 to 500 $t \cdot ha^{-1}$. CWD loads of between 100 and 200 $t \cdot ha^{-1}$ are common in old-growth conifer forests of the Pacific North-

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west (Caza 1993; Harmon et al. 1986). Removal of this important ecosystem component during timber harvesting or site preparation for regeneration and reduction in future inputs threatens the numerous functions of CWD. One consequence of significant reductions of CWD through timber harvesting would be a reduction of the ecosystem nitrogen inputs through fixation that occurs in this material, with as yet undetermined consequences for the long-term ecosystem nitrogen balance.

Asymbiotic nitrogen fixation has been reported for a variety of forest ecosystem components. The potentially important role of CWD in asymbiotic nitrogen fixation has received particular attention in the forests of the Pacific Northwest where CWD is an important component of the ecosystem (Hicks 2000; Cushon and Feller 1989; Sollins et al. 1987). Although species of nitrogen-fixing microbes have been isolated from forest CWD, it generally remains uncertain which species are responsible. Both anaerobic and microaerophyllic bacteria are believed to be involved (Silvester et al. 1982; Aho et al. 1974).

Two forest types representing two phases of the same ecosystem predominate on northern Vancouver Island, British Columbia: an old-growth type dominated by western redcedar (*Thuja plicata* Donn. ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (the CH phase), and a windstorm-derived type dominated by western hemlock and amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) (the HA phase). There are substantial differences in productivity and regeneration growth between these two forest types, and research has been conducted to find an explanation for these differences (the salal cedar hemlock integrated research program (SCHIRP); Prescott and Weetman 1994). The observed differences have been attributed to different availability of nitrogen and phosphorus in the two phases, but the causes of these nutritional deficiencies remain unclear. Several theories have been developed (Prescott and Weetman 1994). Research suggests that site differences between CH and HA stands are of minor importance and that the influence of redcedar and salal (*Gaultheria shallon* Pursh) on the nitrogen cycle of the site is probably the key to finding a satisfactory explanation (Prescott and Weetman 1994). Keenan (1993) investigated structure and function of mature stands in both phases, but did not investigate the possible role of nitrogen fixation in CWD as part of the explanation for differences in nitrogen cycles in the CH and HA phases.

This study addressed the hypothesis that a difference in nitrogen fixation in CWD between CH and HA stands is a significant long-term factor contributing to differences in nitrogen availability in the two stand types. According to this hypothesis, increased nitrogen fixation on the HA sites should result from both greater quantities of decomposable substrate added by major windthrow events and greater rates of fixation in the faster decomposing hemlock and amabilis fir logs than in the slower decomposing redcedar logs. This study was conducted to evaluate the amount and significance of nitrogen fixation in CWD in these two forest types on northern Vancouver Island. Differences between a time series of different aged HA phase stands and a CH phase stand were investigated. Measurements were made of nitrogenase activity in sapwood and heartwood of CWD of different species in different decay stages to investigate variation within the stands.

Materials and methods

Study sites

This study was conducted on or close to former research plots of Keenan et al. (1993), who provide a detailed description of the study area. It is a gently undulating coastal lowland, generally less than 300 m in elevation, situated on the east coast of northern Vancouver Island, British Columbia, between the towns of Port McNeill and Port Hardy, at a latitude of 50°60′N. The area is classified as the very wet maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1982). An ecological site classification was done by Lewis (1982), who described 60% of the tree-farm license as a *Thuja plicata – Tsuga heterophylla – Abies amabilis – Gaultheria shallon – Rhytidiadelphus loreus* (Hedw.) Warnst. ecosystem association (S1). Within this ecosystem association, a distinction between two phases is obvious: (*i*) CH, consisting of a relatively open-canopied old-growth stand type dominated by western redcedar and western hemlock with a dense understory of salal and (*ii*) HA, consisting of an even-aged, densely stocked hemlock and amabilis fir stand type originating from, and subject to, periodic major storm disturbances. The HA stands are dark and support little understory. A windstorm in 1906 destroyed large areas of these stands. The spatial transition between the two phases is very abrupt.

The surface geological material is a deep, unconsolidated morainal and fluvial outwash material overlaying sedimentary and volcanic bedrock. The soils of ecosystem association S1 are described as moderately well to somewhat imperfectly drained Duric Humo-Ferric Podzols in coarse to medium textured materials (Lewis 1982). Within the study area, the S1 ecosystem association represents a medium site quality (Lewis 1982).

Climatic data from the weather station at Port Hardy airport, 15 km from the study area, show a mean annual daily temperature of 8 °C (2.4 °C in January, 13.6 °C in July) and a mean annual precipitation of 1730 mm, with a distinct winter maximum but sufficient rainfall during the growing season (Lewis 1982).

Four different sampling plots were chosen for this investigation: one each in three different aged stands of the HA phase (five-year-old (HA5), fifty-three-year-old (HA53), and eighty-eight-year-old (HA88)) and one in an old-growth stand of the CH phase (CH). The HA88 and CH stands were part of the study reported in Keenan et al. (1993) (referred as SCHIRP sites). The HA5 plot was a patch of approximately 0.5 ha of the HA88 stand located adjacent to both the research plots of Keenan et al. (1993) and to a recent clearcut. This plot, at the exposed eastern edge of the HA88 stand, was disturbed by a storm about 5 years ago. About 80% of the stems were blown down and were, at the time of the study, mostly still suspended above the ground. Natural regeneration and salal were abundant in patches. Because of the small size of the patch and shelter from remaining trees and the adjacent HA88 stand, the micrometeorological conditions in this plot are regarded to be closer to a gap situa-

tion than to the adjacent clearcut sites. The HA53 stand, located 7 km northwest of the other three sites (close to the end of road Rupert 448 H2), originated from a storm event in about 1941 and is also unmanaged, such stands not being harvested or salvaged at that time. It is an even-aged, closed stand that is dominated by western hemlock. The proportion of amabilis fir in the stand had been reduced by recent stand self-thinning, as indicated by a high frequency of smaller diameter fir logs on the ground. The ground vegetation was sparse because of the dense, closed canopy.

Woody debris

The investigation focused on decaying woody material on the ground larger than 1 cm in diameter. The five-class scheme of Sollins (1982) was used to classify the different stages of decay. Structural integrity of heartwood and sapwood was the main criterion used. Decay classes I and II of Sollins (1982) were combined because of the generally minor contribution of this material to the total CWD biomass (Keenan et al. 1993) and only small differences in structural integrity between these two classes. Preliminary investigations showed differences in nitrogenase activity between woody debris of different species and differences in material from different positions within a given log. Species differences were only investigated for decay class I&II. Material from the outer part and the core of logs were sampled separately and are referred to hereafter as sapwood and heartwood, respectively. The incomplete combination of four decay classes, three species, and two positions (sapwood and heartwood) in the log resulted in a total of nine different substrates being sampled per stand (see Table 2).

Data on the mass of decaying fallen logs were available for CH and HA88 stands from Keenan et al. (1993). The HA5 patch was not measured for CWD mass because it was not regarded as a representative example of recently windthrown HA phase stands because of its small size; instead, an estimate of postwindthrow loading was derived from the average stem biomass of the adjacent HA88 stand. For the HA53 stand, the volume of the decaying wood on the ground was estimated using the line intersect method (Van Wagner 1982). For this purpose, three triangles of three lines of 30 m length were inventoried; for every piece of wood larger than 1 cm in diameter, the decay class and diameter at the point of intersection with the sample line were recorded. The volume was calculated as

$$V = \frac{\pi^2}{8L} \sum d^2$$

where L is the length of the sample line (m) (i.e., 30 m); d is the piece diameter at the intersection (cm); and V is the volume per unit area ($m^3 \cdot ha^{-1}$). The mass of wood on the ground was calculated from these volumes using estimates for densities of wood of different decay stages based on published results of Keenan et al. (1993) for HA stands in the same area. Application of these wood densities for conversion of wood water contents from percent of dry mass to $g \cdot cm^{-3}$ resulted in water contents of above 1.0 $g \cdot cm^{-3}$ for many samples of decay classes III to V. This suggests that the wood density of our material must have been lower. Additionally, Keenan et al. (1993) measured wood volume after transport of sample disks to the lab. Compression of the more decayed material during transport may have resulted in unnaturally high wood density estimates. We thus reduced wood densities for decay classes III to V by approximately 25%, which resulted in densities of 0.25, 0.17, and 0.14 $g \cdot cm^{-3}$, respectively. These adjusted values are comparable to values reported by Lambert et al. (1980), Graham and Cromack (1982), Sollins (1982), Harmon et al. (1987), Sollins et al. (1987), and Arthur and Fahey (1990). The CWD mass for the HA88 and CH stands of Keenan et al. (1993) was recalculated similarly.

Nitrogenase activity

To determine nitrogenase activity under ambient conditions, we used an adaptation of the acetylene reduction assay (Hardy et al. 1968, 1973; Turner and Gibson 1980; Knowles 1980) in the field incubations. Sampling was done between October 3rd and 7th, 1994. Disks from up to five randomly selected logs from each of the different decay classes and species were cut with a chain saw. Decay classification was based only on criteria visible on the surface of the logs, as was done in the inventory of Keenan et al. (1993), rather than on features of the sampled disks. The disks were immediately separated into heartwood and sapwood, cut into pieces with a maximum diameter of 5 cm to fit into jars, and transported to the location of further handling in plastic bags. Within 12 h, the wood samples were placed into 520-mL glass jars equipped with a plastic lid and a rubber septum for injection of gases. Preliminary tests with similar samples showed that even after storage of the samples in plastic bags in a refrigerator for 1 week, activity rates were not significantly different from those of incubations made directly after sampling. The jars were sealed with vacuum grease, and 24-h tests with a standard gas mixture in empty jars showed no leakage of gas. The sample jars were flushed with Argon for 30–60 s to reestablish anaerobic conditions in the wood samples prior to injection of acetylene. A purified sample (52 mL) of acetylene (C_2H_2) that had been scrubbed through a water trap (Hardy et al. 1973; Turner and Gibson 1980) was injected into the jars with a syringe after the same volume of the jar atmosphere had been removed to maintain normal air pressure. The amount of acetylene injected was equivalent to 10% of the total jar volume. Depending on the volume of the wood sample, the initial concentration of acetylene in the jar atmosphere was between 10 and 15%, which was assumed to be above saturation (Knowles 1980; Turner and Gibson 1980).

The jars of all sample plots were incubated for 24 h on the ground (shaded with a plywood board) in a stand of similar density and species composition as the stands under investigation. Minimum and maximum temperatures under the shelter during incubation were recorded, respectively (HA5: 9 and 13 °C; HA53: 9 and 13 °C; HA88: 4 and 11 °C; CH: 9 and 14 °C). Gas samples of 11 mL were taken after 24 h following shaking of the jars to mix the jar atmosphere and were stored in sterilized and evacuated 10-mL vaccutainers for later analyses. Vaccutainers are not completely evacuated (cf. Turner and Gibson 1980), and laboratory tests showed that a dilution of the injected gases to a concentration of 77% occurred.

Impurity of even purified acetylene is a general problem in many assays using acetylene (Hardy et al. 1973; Turner and Gibson 1980; Silvester 1983). Scrubbing of acetylene in a water trap to remove acetone as a possible source of carbohydrate supply for microorganisms is necessary. More serious for measurements of nitrogenase activity are impurities of ethylene (C_2H_4). For the acetylene used here, an ethylene concentration of <0.5 ppm (below detection limit) in a 10% dilution of unscrubbed gas was found. These amounts were not accounted for with control jars, but the amounts of ethylene in the final gas phase of incubated jars originating from impurities were assumed to be negligible.

Oxygen concentrations in intact logs and in samples in incubation jars were assumed to have been comparable but are not known. They might have been different, leading to unnatural conditions during incubation. However, the argon-flushing technique is assumed to establish in situ oxygen levels in CWD rather than truly anaerobic conditions. It is uncertain if the organisms involved are aerobic or anaerobic; maximum activity at 2–5% oxygen concentration has been reported (Hicks 2000; Silvester et al. 1982).

The gas samples were analyzed with a Hewlett Packard 5830A gas chromatograph, equipped with two 1.8 m × 3 mm stainless steel columns packed with Porapak N (80/100) and a flame ionization detector. The carrier gas was nitrogen at a flow rate of 26 and 37 $mL \cdot min^{-1}$, respectively, for the different columns. The oven temperature was 50 °C, the injection temperature 105 °C, and the detector temperature 130 °C. Response of the detector and retention time were calibrated by standard gas mixtures of 105 ppm ethylene (C_2H_4) and 10% acetylene (C_2H_2) in air. Gas samples of 1 mL were run alternately on the two different columns.

The nitrogenase activity was calculated using the internal standard method (McNabb and Geist 1979). Conditions for the injection of acetylene were assumed to be normal air pressure and a temperature of 10 °C. Background ethylene production in the jars was measured using control jars that received the same treatment but were not incubated with acetylene. The average background concentration of ethylene was 0.75 ppm compared with an ethylene concentration of incubated samples of 2.5–40.9 ppm (concentrations in the vaccutainer stored gas). Most of this background concentration originated from ethylene within the sterilized vaccutainers (see Knowles 1980; Turner and Gibson 1980) of approximately 0.5 ppm (0–1.2 ppm). Background concentrations of ethylene in acetylene-incubated jars due to inhibition of ethylene oxidation by acetylene (as found by Hendrickson 1988, 1989; Weber et al. 1983; and Lindberg et al. 1979) were not accounted for; they may have been low as was reported by Jurgensen et al. (1992) for forest soils in the Pacific Northwest. The background concentration of acetylene in the vaccutainer-stored gas of control samples was 0–60 ppm, with a mean of 20 ppm. The background amounts of 1 ppm of ethylene (79% of all control samples had a concentration of <1 ppm) and 20 ppm of acetylene have been subtracted from the results. During the incubation, both acetylene and ethylene were dissolved in the water phase of the jar. These losses are accounted for with the internal standard method under the assumption of equal solubility of both gases in water, which is clearly not realistic (at 20 °C, 1 volume of water dissolves 1.05 volumes of acetylene but only 0.122 volumes of ethylene; Knowles 1980). During incubation time, the acetylene concentration in the jars decreased from over 10% to an average of 9.08%. The volume of water needed to dissolve these acetylene volumes is approximately 15 mL at 20 °C. The samples contained between 12 and 181 mL of water.

Water content

Dry mass and water content of the samples were determined by drying them at 70 °C for 3 days. For the interpretation of individual water contents, it is important to consider that water contents are not completely comparable among different decay stages because of differences in density and structure of the material (Boddy 1983). The same amount of water results in different water contents on a dry mass basis depending on the density of the material. Consequently, water content on a dry mass basis does not provide complete information about differences in the degree of water saturation between the different decay classes. Comparisons between decay classes should thus be made with caution. One way to partially overcome this restriction is to express water content as a mass per volume ($g \cdot cm^{-3}$). In this study, we used water content on a dry mass basis for presentation and statistical analysis because the wood density values necessary for conversion from dry mass to volume were only estimated. The same wood densities as reported above for the total amount of CWD biomass were used to convert mass to volume where water content was expressed on a volume basis.

Nitrogen fixation

For calculation of nitrogen fixation rates from measured nitrogenase activity, the following assumptions have been used:

(1) 240 days of nitrogenase activity per year, assuming a minimum temperature of 5 °C for significant activity (cf. Englund and Meyerson 1974). The monthly mean daily temperature at Port Hardy airport is >5 °C from April to November; the lowest monthly mean is 2.4 °C in January (Lewis 1982).

(2) Since measured nitrogenase activity did not represent a mean for the active period, long-term monthly mean daily temperatures (Lewis 1982) in combination with a Q_{10} relationship of 2 (based on the results of Hicks 2000; Sollins et al. 1987) was used to calculate the mean nitrogenase activity for the active period. The mean temperature measured during substrate incubation from the four stands was used as a reference temperature for the stand-specific Q_{10} relationship.

(3) A conversion factor from acetylene reduction to nitrogen fixation of 4 was used, corresponding to the theoretical conversion factor (Bergersen 1991) and close to the mean of empirical studies on CWD (Hicks 2000; Silvester et al. 1982).

Results

Amount of woody debris

CWD masses are given in Table 1 for stand HA53, to-

Table 1. Mass ($t \cdot ha^{-1}$) of coarse woody debris (CWD) in unmanaged second-growth western hemlock – amabilis fir forests (HA) of different age and a western redcedar – western hemlock old-growth stand (CH) on northern Vancouver Island.

	Decay class				
Stand	I&II	III	IV	V	Total
HA53	4.4	11.1	35.4	52.0	102.8
HA88*	11.8	35.5	67.2	43.6	158.0
CH*	17.7	63.0	30.1	18.2	129.1

*After Keenan et al. (1993), recalculated.

gether with the recalculated results of Keenan et al. (1993) for stands HA88 and CH. All three stands had large amounts of CWD, most of which was in advanced stages of decay (III–V). Only small amounts of early decay stages I&II were found, mostly originating from recently downed logs or branches. In stand HA53, the larger sized material originating from a blowdown in 1941 was mostly incorporated into the forest floor, but considerable quantities of smaller diameter material in decay classes I–IV originating from recent self-thinning were also found. Standing snags had mostly reached decay class III prior to falling over. Material in decay class I&II in stands HA53 and HA88 was mostly fir, with few hemlock logs found in this decay class. In the CH stand, decay class IV and V material was entirely hemlock, and many of the buried hemlock logs at this site were still in decay class IV. The most advanced decay class for redcedar logs was III. The older the stand, the greater the proportion of CWD found in earlier decay stages (cf. Spies et al. 1988).

Nitrogenase activity

The variation in rates of nitrogenase activity between replicates of the same substrate was high (Table 2). This variation reflects both a log to log variability and variability within logs. Preliminary investigations showed that even material from the same disk of one log had a high variation in nitrogenase activity rates.

Mean activity for the 36 different sampled substrates (Table 2) ranged from 1.3 to 19.5 nmol $C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$. Activity was found in all 180 individual samples. Water content (Table 3) and decay class have been used to explain variation in nitrogenase activity. The lowest activity rates were in most cases found in decay class I&II, and the highest in classes III or IV. Class V material generally showed lower activity than class III and IV. Only some of these differences were statistically significant (see Table 2).

Variation of water content between substrates (Table 3) was also high. Figure 1 presents the relationship between nitrogenase activity and water content. Water content is expressed as a percentage of dry mass in Fig. 1A and in $g \cdot cm^{-3}$ in Fig. 1B. A water content of >1.0 $g \cdot cm^{-3}$ in Fig. 1B only indicates an inappropriate wood density used for the conversion of that sample. The two variables for water content showed different explanatory power for nitrogenase activity, as can be seen from the scatter around the linear regression lines in Fig. 1 and the r^2 values. The relationships between nitrogenase activity and water content (percentage of dry mass) within the four decay classes are given in Fig. 2 and Table 4. The slopes of those linear regressions (parameter b_1 in Table 4) are significantly higher for decay classes I&II and III as compared with decay classes IV and V.

The four different stands showed no significant differences (ANOVA, $p = 0.05$) in nitrogenase activity. The somewhat higher activity in the overall mean for stand HA53 (Table 2) was due to much higher rates in decay class III material of this stand. The water content of this substrate was also noticeably higher than that of other stands and was comparable to class IV and V material (Table 3). Most of this class III material originated from recent self-thinning, and its wood structure was in a slightly more advanced decay stage than class III material in other stands.

Sapwood samples generally had a higher nitrogenase activity (Table 2) and water content (Table 3) than heartwood samples, but this was in most cases reversed in decay class IV. By definition, class IV material has rotten heartwood that is not supporting its own weight, and there is thus, in contrast to earlier decay stages, less difference in wood structure between sapwood and heartwood.

No differences in nitrogenase activity were found between the species in decay class I&II (Table 2). The only exception was a significantly higher activity in sapwood of redcedar in the CH stand.

Nitrogen fixation

The nitrogen fixation rates estimated for the three different stands with measured CWD mass varied between 1.0 and 2.1 $kg \cdot ha^{-1} \cdot year^{-1}$ (Table 5). Variation was mostly due to differences in mass of CWD because of similar nitrogenase activity in all stands. Most of the nitrogen was fixed by the medium and advanced decayed wood that contributed both the majority of mass and the highest activity rates.

Discussion

Nitrogenase activity rates per unit of CWD substrate were not significantly different between the HA and the CH phase stands investigated. The smaller mass of CWD, and consequently smaller nitrogen fixation, in the CH stand in this study is apparently atypical. Keenan et al. (1993) did not find significant differences in CWD mass between CH and HA stands based on means of three sites. Thus, nitrogen fixation in woody debris is unlikely to be responsible for the observed differences in nitrogen availability between the two phases (Prescott and Weetman 1994).

Nitrogenase activity rates and estimates of nitrogen fixation in our study are within the same range as other results from different conifer forest types in the Pacific Northwest (British Columbia, Washington, Oregon, Idaho, Montana) (Table 6). Mean nitrogenase activity rates generally varied between 2.5 and 16.8 nmol $C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$. Only Cushon and Feller (1989) found much lower values that are inconsistent with the other literature. Aerobic conditions during incubation in their assay might be responsible for this deviation. Nitrogenase activity rates in our study are amongst the highest reported in this region. Jurgensen et al. (1989) reported high values with an assay that included incubation of small pieces at 19 °C. The high rates in our study may be due to the moist and mild climatic conditions of our study area. Crawford et al. (1997) studied decay class IV and V material only and used significantly shorter incu-

Table 2. Nitrogenase activity (nmol $C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$) in samples of coarse woody debris (CWD) in unmanaged second-growth western hemlock – amabilis fir forests (HA) of different age and a western redcedar – western hemlock old-growth stand (CH) on northern Vancouver Island.

			Stand			
Decay class	Species	Wood	HA5	HA53	HA88	CH
I&II	Fir	Sap	3.50 (1.10)	3.01 (2.50)	5.25 (0.68)	
		Heart	1.52 (1.16)	2.22 (0.76)	3.88 (0.48)	
	Redcedar	Sap				10.9 (3.63)
		Heart				2.41 (0.43)
	Hemlock	Sap	5.33 (3.04)	1.96 (0.30)	4.70 (1.26)	3.10 (0.85)
		Heart	1.26 (0.43)	2.67 (0.89)	2.94 (0.29)	1.96 (0.49)
	Mean		2.90 (2.32)a	2.64 (1.34)a	4.19 (1.14)a	4.59 (4.14)
III	All	Sap	8.92 (8.00)	19.54 (10.56)	7.42 (3.54)	7.53 (1.91)
		Heart	4.94 (3.99)	13.54 (4.96)	3.18 (1.14)	3.82 (3.91)
	Mean		6.93 (6.32)ab	16.54 (8.40)c	4.30 (3.34)ab	5.68 (3.50)
IV	All	Sap	5.61 (2.03)	7.63 (5.89)	5.97 (1.58)	5.57 (1.11)
		Heart	11.12 (7.38)	8.95 (6.41)	6.94 (0.89)	6.51 (1.68)
	Mean		8.37 (5.87)b	8.29 (5.84)b	6.46 (1.32)b	6.04 (1.43)
V	All	All	2.15 (0.20)	4.77 (1.48)	7.91 (2.90)	5.77 (1.25)
	Mean		2.15 (0.20)a	4.77 (1.48)ab	7.91 (2.90)b	5.77 (1.25)
Mean			4.93 (4.89)	7.14 (7.30)	5.35 (2.36)	5.29 (3.30)
$p > F$			0.001	<0.001	0.002	0.161

Note: For each stand, means of the sampled substrates and overall means for the different decay classes are given. Values in parenthesis are standard deviations. The values for the nine different substrates per plot represent means of five samples each. The means for the different decay classes were tested with a one-way ANOVA and Bonferroni multiple comparison tests of the logarithm-transformed values. Probabilities of larger F values ($p > F$) for the ANOVA are given in the last row. Values for overall means of the decay classes that have the same letter within a column are not significantly different ($p = 0.05$). The mean at the bottom of the table is for all substrates (i.e., not for the overall means).

Table 3. Water content (% of dry mass) in samples of coarse woody debris (CWD) in unmanaged second-growth western hemlock – amabilis fir forests (HA) of different age and a western redcedar – western hemlock old-growth stand (CH) on northern Vancouver Island.

			Stand			
Decay class	Species	Wood	HA5	HA53	HA88	CH
I&II	Fir	Sap	115.0	85.5	128.1	
		Heart	58.1	61.8	40.8	
	Redcedar	Sap				155.5
		Heart				53.6
	Hemlock	Sap	131.8	73.7	188.3	154.8
		Heart	48.1	88.2	72.1	72.8
	Mean		88.3	77.3	107.3	109.2
III	All	Sap	167.8	478.7	293.8	324.0
		Heart	148.5	322.5	118.8	149.0
	Mean		158.2	400.6	206.3	236.5
IV	All	Sap	527.3	462.5	266.2	406.8
		Heart	447.0	473.0	319.6	534.7
	Mean		487.2	467.8	292.9	470.8
V	All	All	469.4	429.6	478.5	476.0
Mean			300.7	343.8	271.3	323.1

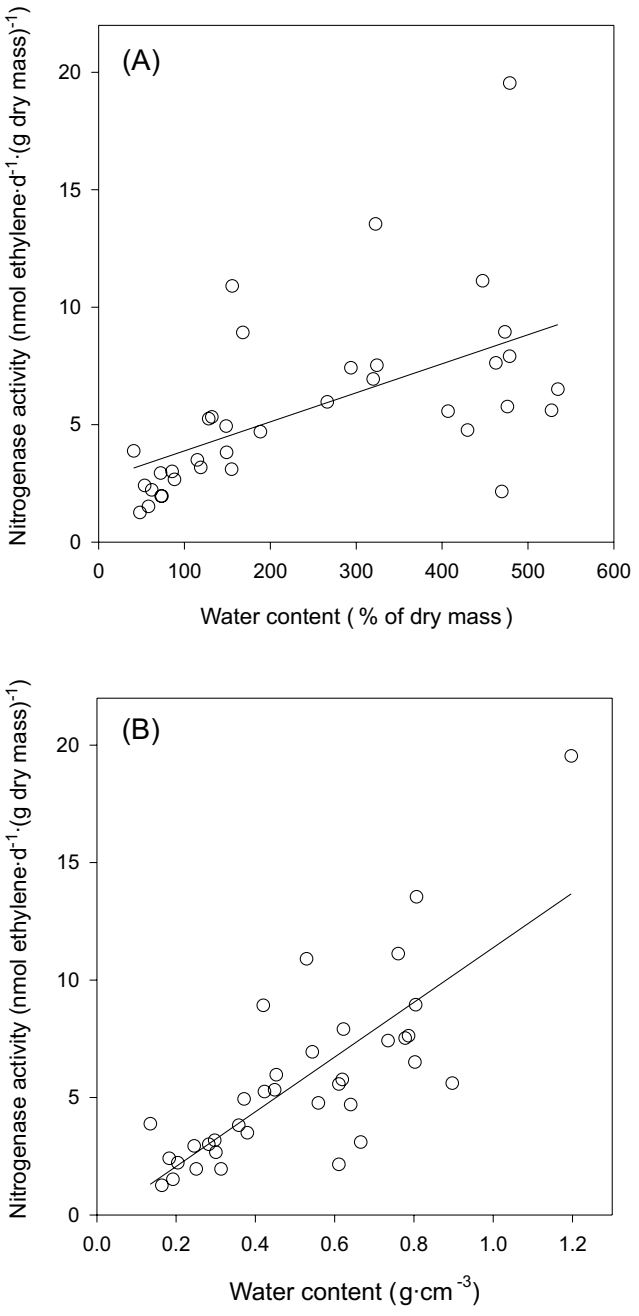
Note: For each stand, means of the sampled substrates (five samples per mean) and overall means for the different decay classes are given. The mean indicated in the bottom row is for the overall means.

bation periods than in our study, possibly explaining the differences with our results. Results from regions other than the Pacific Northwest are consistent with our results, with occasionally higher activity rates (Table 6).

Acetylene reduction in our assay was measured with a 24-h incubation, which seemed to be the standard at that time (e.g., Hicks 2000; Griffiths et al. 1993; Jurgensen et al. 1992; Hendrickson 1991). Subsequently, some studies have used shorter incubation times (Wei and Kimmins 1998; Crawford et al. 1997) because nitrogenase activity was significantly lower after 12 h in longer incubation periods (Hardy et al. 1968; Silvester et al. 1982). This was also noted in our own tests with different incubation times. Nevertheless, it remains uncertain whether the nonlinear time course of nitrogenase activity during incubation is due to stimulation at the beginning or due to suppression at the end of the incubation. The reported nitrogenase activity rates might thus underestimate real rates, and nitrogen fixation is thus conservatively estimated.

Estimates of nitrogen fixation for the Pacific Northwest range between 0.1 and 2.1 kg $N \cdot ha^{-1} \cdot year^{-1}$ (Table 6). The results of our study are among the highest reported, which is due to a combination of high nitrogenase activity rates and high amounts of CWD. Differences in nitrogen fixation between reported studies are mainly due to different amounts of CWD. It should be noted that most studies used the old theoretical conversion factor from acetylene reduction to nitrogen fixation of 3, which will overestimate nitrogen fixa-

Fig. 1. Relationship between nitrogenase activity and water content (expressed as percent of dry mass in A and g·cm^{-3} in B) for means of nine different substrates of coarse woody debris (CWD) in unmanaged second-growth western hemlock – amabilis fir forests of three different ages and a western redcedar – western hemlock old-growth stand on northern Vancouver Island.
The regression lines represent the following equations:
(A) activity = 2.650 + 0.012water, r^2 = 0.313.
(B) activity = –0.020 + 10.913water, r^2 = 0.558.



tion relative to the more likely higher conversion ratio (Hicks 2000). Other possible causes of differences are different activity periods and different representation of seasonal variation in nitrogenase activity. Results from regions other than the Pacific Northwest were either much lower, as was the case for the two pine studies, or in the same range, despite much higher activity rates reported for the eastern hardwood forests (Table 6). In both cases, CWD mass was much lower than in the Pacific Northwest.

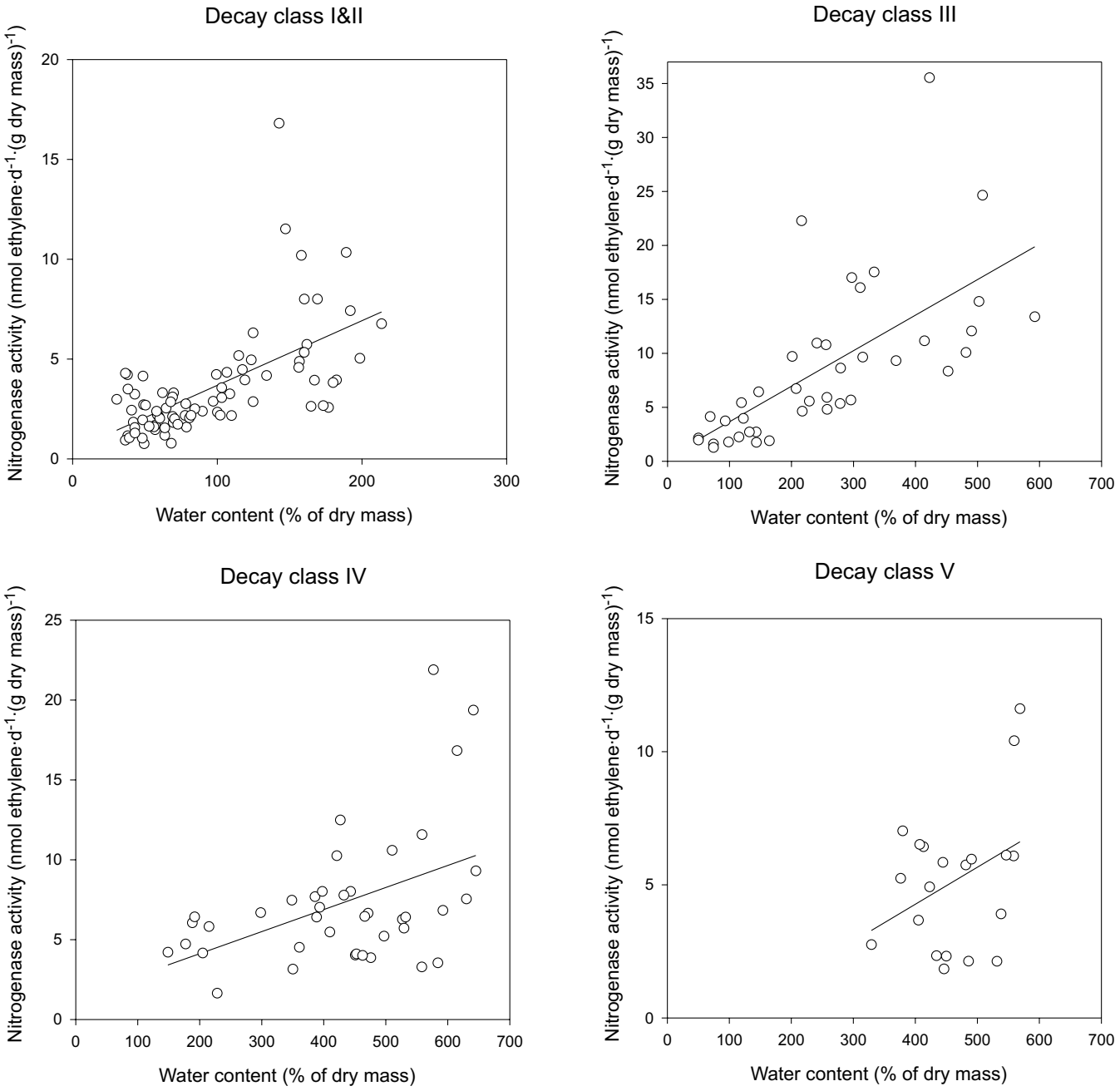
Estimates of nitrogen fixation are highly sensitive to the underlying assumptions. Our choice of assumptions is considered to yield a conservative estimate of nitrogen fixation. We used a period of 240 days with nitrogenase activity, which is a conservative assumption for this area based on the long-term average climate data (Lewis 1982). Some activity might even occur during the mild winters at temperatures between 0 and 5 °C, although nontemperature limitations (e.g., because of carbohydrate supply) might reduce it to insignificance. Based on bimonthly measurements, Cushon and Feller (1989) estimated significant nitrogenase activity to occur for between 180 and 240 days per year in a mature stand of Douglas-fir, western redcedar, and western hemlock in the dry subzone of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1982). However, the winter in the study area of Cushon and Feller (1989) is significantly colder than at our site on northern Vancouver Island. Our estimates of nitrogen fixation was based on a single observation of nitrogenase activity within the active period. Variation of nitrogenase activity within the year was assumed to be mostly dependent on variation in temperature. Under the climatic conditions of our study sites and in the closed stands studied, it is unlikely that drought is limiting nitrogenase activity in the summer. The acetylene reduction method of estimating nitrogen fixation (Hardy et al. 1968) has been widely used because it is relatively simple. However, this method only measures nitrogenase activity, and direct comparisons between acetylene reduction and the ^{15}N technique for estimating nitrogen fixation rates are rare and have yielded conflicting results for CWD (Hicks 2000; Silvester et al. 1982; Roskoski 1980; Aho et al. 1974). The conversion ratio from acetylene reduction to nitrogen fixed of 4 that we applied gives a more conservative estimate of nitrogen fixation than the conversion rate of 3 applied by many other studies (Table 6). However, given the considerable variation in the conversion ratio with temperature and substrate (Hicks 2000; Silvester et al. 1982), it is desirable to apply ^{15}N techniques to the same substrates for calibration of acteylene reduction estimates, which we were not able to do.

Influence of environmental conditions

Nitrogenase activity in CWD under natural conditions depends on a number of environmental factors. Only moisture and decay stage have been investigated in our study.

Moisture of decaying woody substrate has frequently been reported as one of the most important factors for nitrogenase activity (e.g., Hicks 2000; Wei and Kimmins 1998; Baines and Millbank 1978). The positive correlation between nitrogenase activity and water content in our study is in agreement with other results. The choice of a suitable variable to express levels of moisture in different substrates seems to be critical in an analysis of the importance of this factor (Fig. 1). Water content on a dry mass basis alone could not provide a complete explanation of the variation in nitrogenase activity rates across all decay classes (Fig. 1A). However, water content provided a satisfactory explanation for the variation in nitrogenase activity within a particular decay class (Fig. 2, Table 4). The steeper slopes of regression lines in decay classes I&II and III in contrast with IV

Fig. 2. Relationship between nitrogenase activity and water content for coarse woody debris (CWD) in unmanaged second-growth western hemlock – amabilis fir forests of three different ages and a western redcedar – western hemlock old-growth stand on northern Vancouver Island. Regression lines for different decay classes represent the equations given in Table 4.



and V, together with the lower water content and the lower nitrogenase activity in the early decay classes, suggest that low water content is more limiting to nitrogenase activity in earlier than in more advanced decaying material. Wood moisture regulates oxygen diffusion and thus influences nitrogenase activity. The importance of oxygen concentration for nitrogenase activity is well known (e.g., Hicks 2000; Silvester et al. 1982; Granhall 1981). However, because anaerobic and microaerophilic bacteria are responsible for asymbiotic nitrogen fixation (Silvester et al. 1982; Aho et al. 1974), a variation in response to oxygen is likely.

Nitrogenase activity generally increases as decay of wood progresses (Hicks 2000; Cushon and Feller 1989; Jurgensen et al. 1984). Differences in moisture among material of different decay stages seem to be the main cause of different activity rates. In our study, we found an exception in the most advanced decay stages, where nitrogenase activity was lower than in medium decay stages. This difference may be due to greater detail in the classification of advanced decay stages in our study than in other studies. Hicks (2000) reported similar results. Lower activity rates in the most advanced material that was already buried in the forest floor may be partially explained by the lower water content of this material compared with decay class IV material when expressed as a mass of water per volume of material. A decline in the supply of carbohydrate as decay progresses (Preston

Table 4. Relationship between nitrogenase activity and water content in different subsamples of coarse woody debris (CWD) in unmanaged, second-growth western hemlock – amabilis fir forests (HA) of different age and a western redcedar – western hemlock old-growth stand (CH) on northern Vancouver Island.

Decay class	b_0	b_1	SE b_1*	Adjusted r^2	$p > F$†	n
I&II	0.4465	0.0324	0.0048	0.363	<0.0001	80
III	0.3693	0.0329	0.0061	0.421	<0.0001	40
IV	1.3554	0.0138	0.0044	0.186	0.0032	40
V	–1.2927	0.0139	0.0083	0.086	0.1127	20

Note: The table gives parameters of the linear regression equation nitrogenase activity (nmol $C_2H_4 \cdot d^{-1} \cdot$(g dry mass)$^{-1}$) = $b_0 + b_1$water content (percent of dry mass).

*Standard error of the parameter estimate.

†Probability of larger F value for the regression.

et al. 1990) cannot on its own explain the observed decrease in nitrogenase activity in decay class V, because low carbohydrate rates are also common for decay classes III and IV (Preston et al. 1990). However, low concentrations of easily accessible carbohydrates that provide an energy supply for bacteria (Jurgensen et al. 1984; Means et al. 1992) may contribute to the phenomenon. The positive effect of carbohydrate supply on nitrogenase activity in decaying wood was demonstrated by Hendrickson (1991). Decay class III material in stand HA53 had a much higher nitrogenase activity than all other substrates (Table 2). Higher water content alone did not explain activity rates that are higher than all the decay class IV means. Special conditions in standing snags that favor decomposition and nitrogenase activity and result in a more advanced state of decay when the CWD reaches the ground might provide an explanation for these observed high activity rates. The advanced decay of the many standing snags in this stand, which originated from recent self-thinning, are in contrast with observations from lodgepole pine stands in which little decay occurred before snags fell to the ground (Fahey 1983).

Reported relationships between seasonal air temperature and nitrogenase activity in CWD vary from strongly linear (Jurgensen et al. 1984; Roskoski 1980) to weak (Hicks 2000; Heath et al. 1988; Granhall and Lindberg 1978), depending on the influence of other environmental factors. Reported differences in nitrogenase activity between different seasons (e.g., Wei and Kimmins 1998; Cushon and Feller 1989; O'Connell and Grove 1987) or between different years (Jurgensen et al. 1992) can often be explained by changes in temperature or moisture. The uncertainty of the influence of weather and climate on nitrogenase activity has significant consequences for estimates of nitrogen fixation (Hicks 2000).

Influence of stand conditions

Nitrogenase activity was not significantly different between tree species in early decay classes in our study. Investigations of species effects have been limited to early decay stages because of wood species identification problems in advanced decay classes. In contrast with our results, Larsen et al. (1978) and Sharp (1975) reported differences in nitrogenase activity among tree species caused by differences in substrate. Nitrogenase activity in heartwood samples of western redcedar was not lower than that of other species in our study. An inhibitory effect of thujaplicins on nitrogenase activity was not apparent. Jin (1987) and Jin et al. (1988) found that thujaplicins are inactivated by early decay fungi.

Nitrogenase activity varied greatly within decaying logs in our study. Significant differences between sapwood (outer parts) and heartwood (inner parts) have also been reported by Silvester et al. (1982). Local differences in water content and decay stage within the log (cf. Pyle and Brown 1999) may be responsible for both effects.

The chronosequence of the three different HA phase stands suggests a cyclic development in CWD and nitrogen fixation. Stand-replacing wind events can add 400–800 t·ha^{-1} of CWD to forest floors that already have high loadings of CWD (Keenan 1993). Even if the recent material has a much lower nitrogenase activity, it should add a significant amount to the total amount of nitrogen fixed. As stand development proceeds, the supply of new CWD is close to zero until self-thinning starts, but initially this only contributes small amounts of CWD. Consequently, the 53-year-old stand had a much lower CWD mass and total amount of nitrogen fixation than the other two stands. Conditions in young stands after blowdowns are also favorable for decay because of the moist conditions so that large amounts of the blowndown material are decomposed rapidly. With further stand development, more and larger self-thinning material is produced and accumulates in CWD, increasing the amount of nitrogen fixation. If mature stands of the HA phase become subject to further windthrow events, the cycle starts again.

Roskoski (1980) found differences in nitrogen fixation in CWD between stands of different ages, which was mainly due to differences in CWD mass, as was the case in our study. The chronosequence was similar in both studies, with high loads of CWD in young stands, minimum values in medium-age stands, and increases as stand development continues (cf. Spies et al. 1988; Harmon et al. 1986).

Significance of nitrogen fixation in coarse woody debris

The significance of asymbiotic nitrogen fixation in CWD for the total nitrogen balance of forest ecosystems is highly variable and is mostly dependent on the amount of CWD, which varies more than the reported rates of nitrogen fixation per unit of CWD. Reported estimates of up to 2.1 kg N·ha^{-1}·year^{-1} (Table 6) are low, but may be important if they are sustained annually for many years.

Little is known about the fate of nitrogen fixed in CWD (Jones 1978). The relative proportions of fixed nitrogen lost by denitrification, immobilized by soil microbes, or taken up by vegetation have not been quantified. The accumulation of nitrogen that has been reported in decaying woody material as decay progresses is only partly due to nitrogen fixation. Other inputs by roots, fungi, and leaching from vegetation canopies, as well as apparent accumulation caused by the loss of carbohydrates during decomposition, mask inputs by asymbiotic nitrogen fixation. Denitrification at the same location as nitrogen fixation is likely due to anaerobic conditions (Jones 1978), but only one investigation is known that looked at both processes in CWD (Cushon and Feller 1989).

Table 5. Nitrogen fixation in coarse woody debris (CWD) of unmanaged second-growth western hemlock – amabilis fir forests (HA) of different age and a western redcedar– western hemlock old-growth stand (CH) on northern Vancouver Island.

Stand	Decay class	Species	Wood	Nitrogenase activity (nmol $C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$)	Wood ratio	Species ratio	Mean nitrogenase activity (nmol $C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$)	Mass ($t \cdot ha^{-1}$)	N-fixation ($kg \cdot ha^{-1} \cdot year^{-1}$)
HA5	I&II	Fir	Sap	3.50	0.33				
			Heart	1.52	0.67	0.6			
		Hemlock	Sap	5.33	0.33				
			Heart	1.26	0.67	0.4	2.35	150.0*	0.56*
	III	All	Sap	8.92	0.33				
			Heart	4.94	0.67		6.25	35.5	0.35
	IV	All	Sap	5.61	0.33				
			Heart	11.12	0.67		9.30	67.2	0.99
	V	All	All	2.15	1.00		2.15	43.6	0.15
	Total							296.2*	2.04*
HA53	I&II	Fir	Sap	3.01	0.33				
			Heart	2.22	0.67	0.9			
		Hemlock	Sap	1.96	0.33				
			Heart	2.67	0.67	0.1	2.48	4.4	0.02
	III	All	Sap	19.54	0.33				
			Heart	13.54	0.67		15.52	11.1	0.31
	IV	All	Sap	7.63	0.33				
			Heart	8.95	0.67		8.51	35.4	0.54
	V	All	All	4.77	1.00		4.77	52.0	0.44
	Total							102.8	1.30
HA88	I&II	Fir	Sap	5.25	0.33				
			Heart	3.88	0.67	0.9			
		Hemlock	Sap	4.70	0.33				
			Heart	2.94	0.67	0.1	4.25	11.8	0.10
	III	All	Sap	7.42	0.33				
			Heart	3.18	0.67		4.58	35.5	0.34
	IV	All	Sap	5.97	0.33				
			Heart	6.94	0.67		6.62	67.2	0.93
	V	all	All	7.91	1.00		7.91	43.6	0.72
	Total							158.0	2.09
CH	I&II	Redcedar	Sap	10.90	0.14				
			Heart	2.41	0.86	0.5			
		Hemlock	Sap	3.10	0.33				
			Heart	1.96	0.67	0.5	2.97	17.7	0.08
	III	All	Sap	7.53	0.20				
			Heart	3.82	0.80		4.56	63.0	0.46
	IV	All	Sap	5.57	0.33				
			Heart	6.51	0.67		6.20	30.1	0.30
	V	All	All	5.77	1.00		5.77	18.2	0.17
	Total							129.1	1.01

*Values for stand HA5 are uncertain because of estimated mass data. For decay classes III–V, mass values of the adjacent stand HA88 were used, whereas for decay class I&II, only an estimate of the recently blown down material was available.

Asymbiotic nitrogen fixation in CWD is likely to be an important contribution to the total nitrogen balance over long time scales in ecosystems where symbiotic nitrogen fixation and atmospheric inputs are low. It is highly affected by forest management practices that remove tree stems and may reduce the future production of new CWD by stand self-thinning (Jurgensen et al. 1997, 1992, 1980). In the Pacific Northwest where high loads of CWD exist in unmanaged forests, timber harvesting will significantly reduce the contribution of CWD to nitrogen fixation.

Because of the dynamic nature of CWD loadings and the accompanying changes in decay class and N fixation rates, ecosystem management models that incorporate key ecosystem processes have to be used to assess the total contribution of CWD to the nitrogen economy of unmanaged forests and the consequences of reducing CWD loadings through timber harvest (e.g., Kimmins et al. 1999).

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Table 6. Rates of nitrogenase activity (acetylene reduction) and estimated nitrogen fixation in coarse woody debris (CWD).

Forest and (or) substrate type	Location	Nitrogenase activity ($nmol\ C_2H_4 \cdot d^{-1} \cdot (g\ dry\ mass)^{-1}$) Min.–Max.	Mean	Mass ($t \cdot ha^{-1}$)	Conversion ratio	Nitrogen fixation ($kg\ N \cdot ha^{-1} \cdot year^{-1}$)	Reference
Tsuga heterophylla, Abies amabilis, Thuja plicata	B.C., CWH* very wet	1.3–19.5	5.7	103–158	4	1.0–2.1	This study
Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata	B.C., CWH* dry	0.03–0.8	0.2	144	3	0.06	Cushon and Feller 1989
Tsuga heterophylla, Thuja plicata, Pseudotsuga menziesii	Oregon, Washington	0.7–8.4	3.0	143	3.5	1.0	Sollins et al. 1987
Pseudotsuga menziesii, Larix occidentalis, Tsuga heterophylla, Thuja plicata, Abies lasiocarpa, Picea engelmannii, Abies grandis	Montana, Idaho	0.7–7.3	2.5	45–154	3	0.2–1.4	Jurgensen et al. 1987
Pseudotsuga menziesii	Montana	1.0–10.4	4.1	49–114	3	0.3–0.7	Jurgensen et al. 1984
Pseudotsuga menziesii, Abies lasiocarpa, Tsuga heterophylla	Montana	1.5–10.6	3.0	113	3	0.7	Larsen et al. 1978
Pseudotsuga menziesii	Oregon	0.2–16.3	3.8	100	3.5	1.4	Silvester et al. 1982
Abies lasiocarpa, Tsuga heterophylla, Thuja plicata, Abies grandis, Pseudotsuga menziesii	Idaho	0.6–46.7	8.7				Jurgensen et al. 1989
Pseudotsuga menziesii	Montana	1.3–8.2	4.1				Spano et al. 1982
Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata	Oregon	5.3–34.8	16.8				Crawford et al. 1997
Tsuga heterophylla, Thuja plicata, Pseudotsuga menziesii, Abies amabilis, early decay	Oregon	0–3.5					Griffiths et al. 1993
Tsuga heterophylla, Thuja plicata, Abies lasiocarpa, soil wood	Montana, Idaho	1.3–4.8	2.1	22–52	3	0.05 – 0.4	Jurgensen et al. 1992
Thuja plicata, Tsuga heterophylla, soil wood	Washington	1.4–6.6	3.0	49	3	0.3	Larsen et al. 1982
Thuja plicata, Tsuga heterophylla, Larix occidentalis, Pinus monticola, decay of living trees	Idaho	1.1–1.9	1.4	4–100	3	0.01–1.0	Harvey et al. 1989
Pinus contorta	Wyoming	0.5–32.7	12.1	20	3	0.2	Fahey et al. 1985
Pinus sylvestris	Sweden	0.02–1.1	0.4	0.2–3.1	3	0.001–0.03	Granhall and Lindberg 1980
Prunus pensylvanica, Betula alleghaniensis, Acer pensylvanicum, Fagus grandifolia, Acer saccharum	New Hampshire	0–78		7–39	8.5	0.1–2.1	Roskoski 1980
Castanea dentata	North Carolina	24.8–36.8	30.5	12	3	0.9	Cornaby and Waide 1973
Cornus florida, Acer rubrum, Quercus alba	North Carolina				3	1.7	Todd et al. 1978
Pinus contorta	B.C.	0–12.5					Wei and Kimmins 1998
Pinus resinosa, Populus tremoloides, Pinus strobus, Acer rubrum, Picea glauca, Betula papyrifera, logging slash	Ontario	0.3–51.8	8.8				Hendrickson 1988
Populus trichocarpa, living sapwood	B.C.	0.1–3.1	1.6				Van der Kamp 1986

*Coastal Western Hemlock biogeographic zone.

mous reviewer on an earlier version of this paper are much appreciated.

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