Mass, nitrogen content, and decomposition of woody debris in forest stands affected by excreta deposited in nesting colonies of Great Cormorant

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Abstract

Great Cormorant (*Phalacrocorax carbo*), a piscivorous bird, has established breeding colonies in a coniferous forest near Lake Biwa in central Japan. This study investigated the possible effects of the colony's excreta on the mass, nitrogen (N) content, and decomposition of woody debris. Study plots were established in forest stands representing four stages from breeding colony establishment to post-abandonment. The mass of fallen branches (diameter 1–5 cm) and coarse woody debris (logs, snags, and stumps; diameter ≥ 10 cm) was greater in forest stands colonized by Cormorants than a control stand never colonized by Cormorants. This was primarily attributed to Cormorant activity that caused increased mortality of standing trees and by Cormorants breaking branches for nesting materials. Nitrogen content of branches and logs that had fallen to the forest floor was negatively correlated with the relative density of wood. Nitrogen content of branches was consistently higher (at a given value of relative density) in the colonized stands than in the control stand. The increase of branch N content was possibly caused by the incorporation of N into decomposing branches with excreta-derived N supplied as throughfall and/or soil solution. The mean value of 2-year mass loss of recently dead branches and logs was significantly greater for woody debris in the smallest diameter class but was not significantly different among the forest stands. This suggests that the excessive supply of excreta-derived N and concomitant enrichment of N in soil had negligible effects on the initial stages of decomposition of woody debris.

Keywords

Chamaecyparis obtusa • Coarse woody debris • Decomposition • Exogenous nitrogen • *Phalacrocorax carbo*

Introduction

Woody debris forms a dominant component of forest biomass and plays major roles in carbon (C) and nutrient cycling in forest soils (Harmon et al. 1986; Stokland et al. 2012). Woody debris characteristically has low nutrient content (Holub et al. 2001; Laiho and Prescott 2004) and high levels of cell wall polymers such as lignin and holocellulose (Eriksson et al. 1990); therefore, woody debris typically only slowly loses mass (Mackensen et al. 2001; Weedon et al. 2009). Woody debris can serve as a long-term reservoir of C as well as other nutrients such as nitrogen (N); colonization by decomposers and the decay decomposers induce causes woody debris to slowly accumulate N (Laiho and Prescott 2004; Fukasawa et al. 2009). Previous studies have produced varying results regarding how the decomposition of wood is affected by the addition of exogenous N, such as through fertilization and simulated atmospheric N deposition. That is, N addition can stimulate or retard the decomposition of woody debris (Fog 1988; Hobbie 2008; Allison et al. 2009; Bebber et al. 2011). This suggests that negative or positive feedback may occur when N is plentiful in terms of the sequestration of C and N in woody debris.

The population of Great Cormorant (*Phalacrocorax carbo* Kuroda), a piscivorous bird, has increased in size from 1992 to 2001 alongside Lake Biwa in central Japan (Ishida et al. 2003; Kameda et al. 2003). Cormorants feed on fish in the lake (Takahashi et al. 2006) and drop excreta in breeding colonies established in nearby forest stands, thus transferring N from aquatic to terrestrial ecosystems (Kameda et al. 2006). Nesting Cormorants break off branches and leaves in local forest stands of *Chamaecyparis obtusa* Endl. for nesting material, and often drop them on the forest floor. This results in a 7–22 times greater input of litterfall (2.6 Mg ha^{-1} $month^{-1}$ on mean) during the breeding season than occurs naturally in control forest stands (Hobara et al. 2001). In addition, the Cormorants excrete large amounts of N in their feces, increasing the N input by about 10,000 times that ordinarily received from precipitation (Kameda et al. 2000). This excessive supply of N has been shown to influence the species composition and physiological capabilities of decomposer fungi (Osono et al. 2002, 2006b). It also retards decomposition and enhances the immobilization of N in decomposing needles and twigs with diameters less than 5 mm (Osono et al. 2006a). These changes lead to changes in N cycling in the forest floor and mineral soils (Hobara et al. 2001, 2005). Fujiwara and Takayanagi (2001) documented increased tree mortality at sites with the greatest avian impact causing trees to exhibit symptoms of forest decline. In contrast, few studies have examined the mass, N content, and decomposition of woody debris [classified here as (1) branches and (2) coarse woody debris (CWD)] in forest stands that are receiving an excess supply of N of avian origin. We thus hypothesized that the colonization of forest stands by Great Cormorants and concomitant supply of excessive excreta-derived N (i) results in an increase in the mass and N content of CWD and (ii) retards the decomposition of woody debris on the forest floor.

The purpose of the present study was to investigate the possible effects of avian colonization and excreta deposition on mass, N content, and mass loss rates of woody debris of *C. obtusa* in a temperate evergreen coniferous forest. First, we compared the mass and N content of woody debris consisting of both branches (diameter 1–5 cm) and CWD (logs, snags, and stumps; diameter $\geq$ 10 cm), among four forest stands that had very similar vegetation composition but were in different stages of breeding colony establishment. We then compared the 2-year mass loss of recently-dead woody debris in three diameter classes

(1, 3, and 10 cm) among the forest stands to demonstrate whether Cormorant colonization and excreta deposition affected the initial stages of decomposition on the forest floor.

Materials and Methods

Study site

The study was carried out at a 57 ha site known as the Isaki Headland (90 to 210 m a.s.l.; 35°12'N, 136°5'E), on the southeast side of Lake Biwa, Ohmihachiman City, Shiga Prefecture, Japan. The Hikone Weather Station reported a mean annual temperature of 14.6°C and annual precipitation of 1591.9 mm about 20 km northeast of the site from 1980 to 2005. The dominant tree species on the Isaki Headland was *Chamaecyparis obtusa* Sieb. et Zucc. (Fujiwara and Takayanagi 2001).

The population of Great Cormorant along Lake Biwa increased from about 3,000 birds in 1992 to about 16,450 in 2001 (Ishida et al. 2003). A colony of Cormorants was first discovered in the Isaki Headland in 1988, and the number of nests increased from 30–40 in 1989 to 5,300 in 1999 (Fujiwara and Takayanagi 2001).

Four study sites on Isaki Headland, coded as Sites NC (never colonized), AC (active colony during study; Cormorants abundant), A1 (abandoned after three years; no Cormorants in 2003–2005), and A2 (declined in 1997 to 2002 after 4 years of intensive colonization; no Cormorants in 2003–2005), had very similar vegetation composition but were in different stages of breeding colony establishment, use, and abandonment by the Cormorants (Table 1). Cormorants intensively colonized site AC and the birds were estimated to drop 2.2 Mg ha^{-1}

month^{-1} of excreta during the breeding season; this was estimated to be the equivalent of 240 kg ha^{-1} month^{-1} of excreta-derived N (Kameda et al. 2000).

Census of CWD and branches

In the present study, we established a single very long 2030 m × 4 m belt transect that included the four sites. We divided the belt transect into 202 grids (10 m × 4 m), and each of the 202 grids was allocated to Sites NC, AC, A1, or A2 and used for the measurement of CWD. CWD included logs (diameter ≥ 10 cm at the base), snags (height ≥ 120 cm, diameter ≥ 10 cm at breast height), and stumps (height < 120 cm, diameter ≥ 10 cm at the base). A total of 661 logs, snags, and stumps were marked in 2003, and each of them was assigned to one of the four tree species based on the remaining bark, branching characteristics, and/or the degree of bend of stem, when available. Each piece of CWD was also assigned to one of the five decay classes [least (I) to most decayed (V)] using visual criteria provided by Fukasawa et al. (2014). The volume of logs and snags was estimated using the method described in Fukasawa et al. (2014), and that of stumps was calculated from the height and diameter, with stumps considered to be cylinders.

One to ten CWD items were then chosen for each tree species, each form, and each decay class, and wood samples were collected using an electric drill to estimate the relative density of each piece of tested CWD. A drill bit (length 24 cm, diameter 9 mm) was used to drill into the CWD from the outer surface to the center; one to three drill holes were made per log, depending on log size, and all wood particles removed by drilling were harvested. The depth of each drill hole was measured. For well-decayed logs that were too fragile to be drilled, pieces of wood were collected and whittled into a rectangular parallelepiped to estimate wood volume. The samples were returned to the laboratory, oven-dried to constant weight at 40°C and weighed. The relative density (g cm^{-3}) of samples was then calculated as the dry weight divided by the volume of the drill hole or wood block. The mass of CWD was then calculated by multiplying the volume and the relative density measured for each category of debris.

We also established nine 1 × 1 m quadrats at each site and adjacent to the belt transect. The quadrats were used for the collection of branches and the decomposition experiment described below. We randomly chose five of the nine quadrats at each site and used them to describe the mass of branches (diameter 1 to 5 cm at the base) at Sites AC, A1, and NC. A total of 767 branch samples were collected in 2003, oven-dried at 40°C to a constant mass, and weighed. Each branch was assigned to one of the three tree species using the method described above. Each branch was then assigned to one of the three decay classes as defined above. Branches in decay class I had bark and intact wood; those in decay class II had loose bark and slightly rotten wood; and those in decay class III had detached bark and rotten wood.

Nitrogen content of woody debris

Samples of logs and branches of *C. obtusa* collected from the forest floor were used for N analysis. These included 74 logs (12 to 24 logs per site) in various decay classes and 90 branches (2 branches × 3 decay classes × 5 quadrats × 3 sites). The oven-dried samples were ground in a laboratory mill and passed through a 0.5-mm screen. Total N content (mg g^{-1} dry litter) was measured by automatic gas chromatography (NC analyzer SUMIGRAPH NC-900, Sumitomo Chemical Co., Osaka, Japan).

Mass loss rate of woody debris

Decomposition of woody debris was studied with 2-years of field incubation experiments. Wood samples in three diameter classes were prepared in May 2003 from a *C. obtusa* tree cut in a forest stand never affected by the Cormorants. These included 72 wood samples 1 cm in diameter and 4 cm long (D1), 72 samples 3 cm in diameter and 40 cm long (D3), and 12 samples 10 cm in diameter and 90 cm long (D10). Wood sub-samples were collected from D10 samples using an electric drill, three holes per sample, as described above, to calculate the relative density (g cm^{-3}) of the samples.

The decomposition study covered a 24-month period from June 2003 to June 2005. In June 2003, D1 and D3 samples were placed on the litter layer of nine quadrats at each site and tethered with metal wire to prevent movement. D10 samples were placed on the litter layer of three quadrats randomly chosen for each site. Sampling of these samples took place twice, at one (June 2004) and two years (June 2005) after the placement. On each sampling occasion, one D1 and one D3 sample was retrieved from each quadrat, making a total of 72 samples (9 quadrats × 4 sites × 2 collections) for each of D1 and D3. Wood sub-samples were collected from D10 samples only in June 2005 (after two years) using an electric drill as described above. D1 and D3 samples and the sub-sampled D10 wood particles were oven-dried to constant weight at 40°C and weighed, and the relative density of the D10 sub-samples was calculated as described above. The losses of dry mass (D1 and D3) and relative density (D10) were determined (as % of the original mass), and mean values of mass loss were calculated for each sampling and each site.

Statistical analyses

When comparing the N content of logs and branches between the study sites with different stages of Cormorant colonization, the effect of relative density of wood on the N content needs to be taken into account, because N content of woody residues generally increases with the loss of relative density during decomposition (Fukasawa et al. 2009, 2012, 2014). Therefore, linear relationships between the relative density and N content were examined for each study site according to the following equations:

$$\text{N content} = a + b \times (\text{relative density}). \qquad (1)$$

Intercepts (a) and slopes (b) of regression equations were calculated for the linear relationships using least-squares regression. Analysis of covariance (ANCOVA) was then used to evaluate the differences in regression equations among the study sites. The significance of the homogeneity of the slopes was evaluated, and when no significance was found, the interaction term was excluded from the analysis (Sokal and Rohlf 1995). When slope b differed between study sites, the regression with the greater b value showed a smaller decrease in the dependent variable y with respect to the unit increment of the independent variable x. This indicated a significant difference existed between the rates of changes in N content versus relative density. When b did not differ between study sites, but the intercept a

differed, the regression with the larger a value had a consistently greater y value at any given x value, indicating a significant difference in N content at given values of relative density between the study sites. The generalized linear model (GLM) was used to evaluate the difference in 1- and 2-year mass loss of woody debris using diameter class, study site, and the interaction of diameter class × study site as independent variables. These analyses were performed with JMP 6.0 software for Macintosh.

Results

Mass of CWD and branches

The mass of CWD ranged from 7.72 to 42.05 Mg ha^{-1} and was greater at Sites AC, A1, and A2 than at Site NC (Table 2). *Pinus densiflora* accounted for 62.6% of CWD mass at Site NC and this was attributed to a previous outbreak of pine wilt disease; however, *C. obtusa* was a major component at Sites AC, A1, and A2 (32.6 to 74.4%). Snags were major components of CWD at Sites AC, A1, and A2 (67.5 to 87.4%). CWD in the decay class I was the dominant component at Site AC but its proportion decreased to Site A1 and again to Site A2, whereas the proportion of CWD in the decay class II increased as the age of the Cormorant colony increased from Sites AC to A1 to A2.

The mass of branches was greater at Sites AC and A1 than at Site NC (Table 2). Branches of *C. obtuse* in the decay class II were the dominant component at these three sites.

Nitrogen content

N content of logs and branches on the forest floor ranged from 0.33 to 7.13 mg g^{-1} and from 1.15 to 11.38 mg g^{-1}, respectively (Fig. 1). The linear relationships between N content and relative density were statistically significant for all sites (logs: $R = -0.59$ to -0.70, $P < 0.05$; branches: $R = -0.81$ to -0.85, $P < 0.001$), indicating that the N content of decomposing logs and branches increased as their relative density decreased (Fig. 1). Neither the slope nor the intercept of the regression equation for logs was significantly different among the study sites (ANCOVA, slope: $F = 1.23$, $P = 0.31$; intercept: $F = 0.30$, $P = 0.83$). The slope of the regression equation for branches was not significantly different among the sites (ANCOVA, $F = 1.75$, $P = 0.19$). Furthermore, the intercept of N content was significantly different in the order: Site AC > Site A1 > Site NC (ANCOVA, $F = 51.5$, $P < 0.001$), indicating that the N content of branches was consistently higher at Sites AC and A1 than at Site NC at a given value of relative density.

Mass loss

Mean values of mass loss of woody debris ranged from 1.2 to 9.9% for the first year and from 6.6 to 25.1% for the second year (Fig. 2). The 1-year mass loss was significantly affected by diameter class (GLM, deviance = 531.2, $P < 0.001$) but not by study site (GLM, deviance = 54.7, $P = 0.20$) or by the interaction of diameter class × study site (GLM, deviance = 25.9, $P = 0.53$). The same result was found for the 2-year mass loss; that is, the mass loss was significantly affected by diameter class (GLM, deviance = 2195.0, $P < 0.001$) but not by study site (GLM, deviance = 155.4, $P = 0.57$) or by the interaction of diameter class × study site (GLM, deviance = 518.4, *P* = 0.34). The mass loss was greatest for woody debris in the smallest diameter class.

Discussion

The mass of CWD at Site NC (control, never known to be colonized by Cormorants) in the present study (Table 2) was within the range previously reported for temperate coniferous forests (Siitonen et al. 2000; Ranius et al. 2003). However, those at the historic or present colony sites, Sites AC, A1, and A2, were at the upper end of or beyond the previous range, indicating that the activity of Cormorants caused increased mortality of standing trees (Fujiwara and Takayanagi 2001). Standing trees were being actively converted to snags in the decay class I in the forest stand presently colonized by Cormorants (Site AC) and then decomposed gradually to decay class II after the birds abandoned the colony and the forest stand declined (Table 2). Similarly, the Cormorants' active removal of branches for nesting materials, some of which they accidentally dropped, (Fujiwara and Takayanagi 2001), led to the greater mass of branches on the forest floor at Sites AC, A1, and A2 than at Site NC (Table 2).

The N content of branches (diameter 1 to 5 cm) was higher in the order: Site AC > Site A1 > Site NC, regardless of their relative density, whereas similar differences among the study sites were not found for logs (diameter more than 10 cm; Fig. 1). Osono et al. (2006a) also found increased N content in decomposing twig litter (diameter less than 5 mm) at Site AC, which was the result of immobilization of excreta-derived N. Thus, the results of the present study demonstrated that the smaller woody debris served as a better N reservoir than the larger debris on a time scale of at least 7 years of Cormorant colonization (Table 1). The higher N content in branches in forest stands presently and previously colonized by Cormorants was probably caused by the incorporation of excreta-derived N into the branches. Excreta-derived N may be readily supplied to branch decomposers as ammonium ions in throughfall solution (Osono et al. 2006b) and/or ammonium ions and nitrates in soil solutions (Hobara et al. 2001), and became immobilized in decomposing branches at Sites AC and A1. The lack of N increase in log samples in the present study may be caused by their low surface area to volume ratio when compared to that of branches and/or the use of bulk samples for N analysis that included not only surface wood tissues but also inner tissues that had been less decomposed.

By combining the data of amount of branches on the forest floor at Sites AC, A1, and NC (Table 2) and the increased N content in branches at Sites AC and A1 relative to Site NC (Fig. 1), we were able to calculate a stand-level accumulation of N in fallen branches and its contribution to the total amount of N deposited as excreta. For each Site, specifically Sites AC, A1, and NC, we multiplied the mean values of N content of *C. obtusa* branches in three decay classes by the total weight of branches in these decay classes (kg ha^{-1}; Table 2). The total N amount in branches was found to be 15.96 kg ha^{-1} at Site AC, 13.76 kg ha^{-1} at Site A1, and 3.14 kg ha^{-1} at Site NC. Hence, Sites AC and A1 had 12.83 and 10.62 kg ha^{-1} more N found in branches relative to Site NC, respectively. These values of the amount of N found in branches accounted for 5.3% and 4.4% at Sites AC and A1, respectively, of monthly N input as excreta during the breeding season at Site AC (240 kg ha^{-1} month^{-1}; Kameda et al. 2000). This calculation is obviously tentative but implies the low contribution of N incorporated into branches to the total input of excreta-derived N. Similarly, Osono et al. (2006a) suggested needles and twigs of *C. obtusa* had a potential to immobilize only 7% of total excreta-derived N deposited on the forest floor at Site AC. Hobara et al. (2005) also reached the same conclusion, stating that the increased pool size of N in surface soil (forest floor plus mineral soil) at Site AC compared with Site NC was less than the amount of N transported by Cormorants. Leaching into deeper soil layers served as the major pathway of excreta-derived N cycling through the forest system (Hobara et al. 2005).

The 2-year decomposition field experiment showed that the mass loss of woody debris was not significantly different among forest stands that differed in their history of Cormorant colonization (Fig. 2). This finding suggests that the excessive supply of excreta-derived nutrients at Site AC and the concomitant enrichment in soil of nutrients at Site A1 had negligible effects on the initial stages of decomposition of woody debris. The mass loss rates found here were within the range reported for conifer woody debris in temperate regions (Brown et al. 1996; Frangi et al. 1997; Hyvönen et al. 2000; Inagaki and Fukata 2003). The low surface area to volume ratio of woody debris (Harmon et al. 1986) may partly account for the insensitivity of initial wood decomposition to Cormorant colonization. In contrast, Osono et al. (2006a) found slower mass loss of fine litter (needles and twigs less than 5 mm in diameter) of *C. obtusa* at Site AC than at Site NC, which was attributed to the reduction in lignin decomposition by fungal colonizers (Osono et al. 2006b; Osono 2007).

The present study demonstrates that (i) the mass of CWD and branches increased and (ii) the branch N content increased in forest stands presently and previously colonized by Cormorants, and that (iii) Cormorant colonization had no significant effects on the 2-year mass loss of woody debris. Further long-term studies are needed to evaluate the effects of excreta deposition on the decomposition of CWD (larger than 10 cm in diameter) and the roles of CWD as a long-term reservoir of C and N in Cormorant-colonized forests. CWD was four to six times more abundant than branches in the present study sites (Table 2), and more importantly, most CWD was present as snags in the colonized forests and persisted as standing-dead snags for 10 years after Cormorant colonization (e.g., at Site A2); of course, this gradually shifted to more advanced decay classes (Table 2). Particular attention should be paid to the rates of fragmentation of these snags to fallen logs and the processes of decomposition and N dynamics of these logs; this will allow us to better understand C and N accumulation and turnover in CWD in forest stands affected by the excreta of Cormorants.

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Figure legends

Fig. 1 Relationship between nitrogen content and relative density of (a) logs and (b) branches of *Chamaecyparis obtusa* on the forest floor of Sites NC, AC, A1, and A2 at different stages of Cormorant colonization. Logs and branches had diameters ≥ 10 cm and 1 to 5 cm, respectively. Squares and a black line indicate Site NC; gray circles and a gray line, site AC; black triangles and a broken line, site A1; black diamonds and a dotted line, site A2. No data were available for branches at Site A2. Analysis of covariance (ANCOVA) was then used to evaluate the differences in the regression equations among the study sites. *** $P < 0.001$, ns, not significant.

Fig. 2 One- (a) and 2-year (b) mass loss (% original mass) of woody debris of *Chamaecyparis obtusa* of three diameter classes incubated on the forest floor of the four sites (Sites NC, AC, A1, and A2) at different stages of Cormorant colonization. D1, 1 cm diameter; D3, 3 cm diameter; D10, 10 cm diameter. Values indicate means ± standard errors. No data were available for the first-year mass loss of D10. A generalized linear model (GLM) was used to evaluate the difference in 1- and 2-year mass loss of woody debris using diameter class, study site, and the interaction of diameter class × study site as independent variables. *** $P < 0.001$, ns, not significant.

Fig. 1

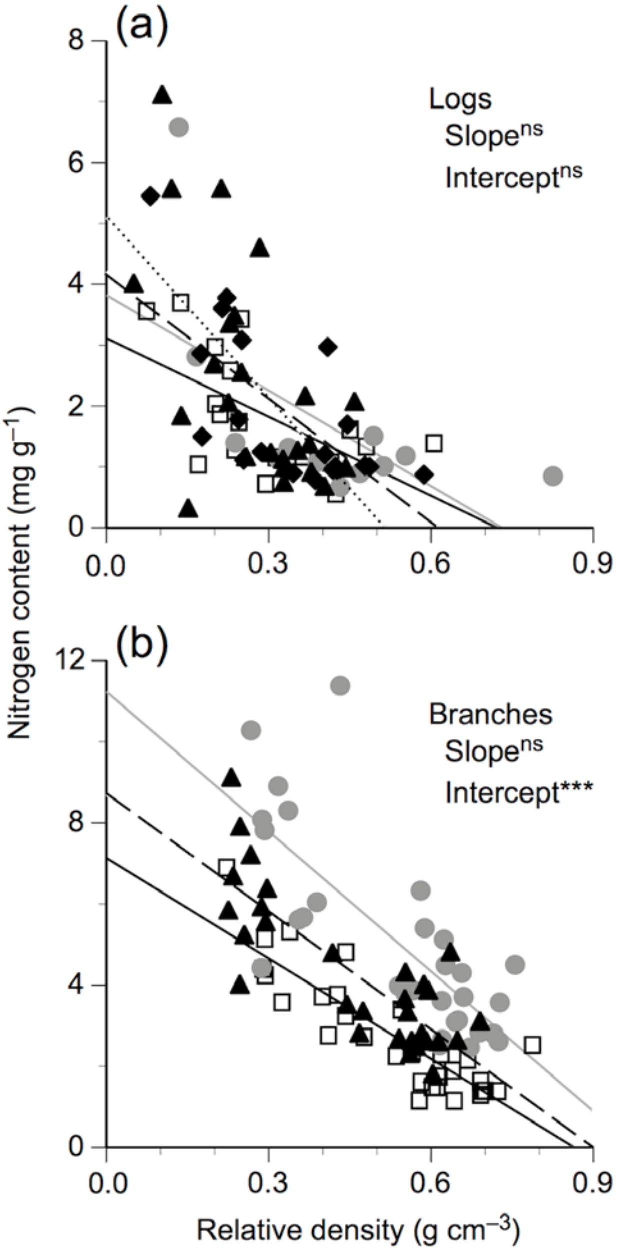
(a)
Logs
Slope^{ns}
Intercept^{ns}
8
6
4
2
0
0.0
0.3
0.6
0.9
(b)
Branches
Slope^{ns}
Intercept***
12
8
4
0
0.0
0.3
0.6
0.9
Nitrogen content (mg g^{-1})
Relative density (g cm^{-3})

Fig. 2

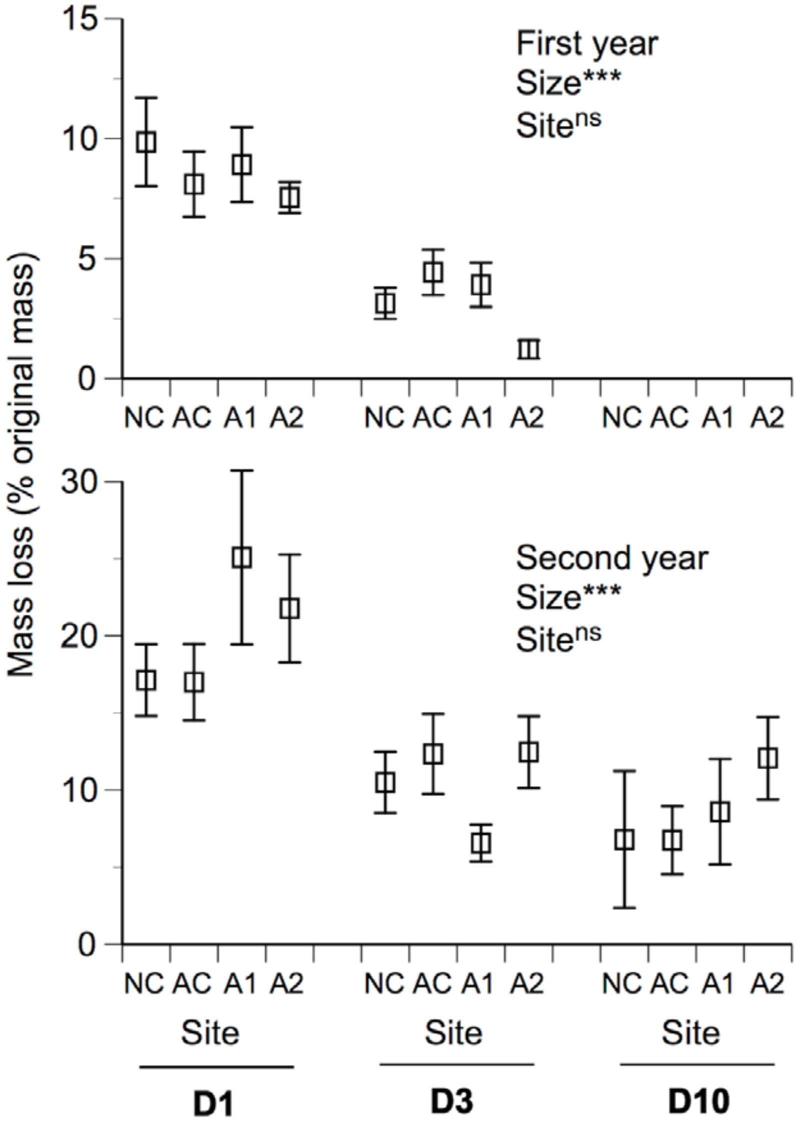
Mass loss (% original mass)
15
10
5
0
First year
Size***
Site^{ns}
NC AC A1 A2
NC AC A1 A2
NC AC A1 A2
30
20
10
0
Second year
Size***
Site^{ns}
NC AC A1 A2
NC AC A1 A2
NC AC A1 A2
Site
Site
Site
D1
D3
D10

Table 1 Study sites and descriptions of Cormorant breeding colonies (Fujiwara and Takayanagi 2001; Kameda et al. 2006).

Site	Colonization period	Description
NC	No colonization	Never known to be colonized by Cormorants (control)
AC	1997–2005	Active colony during study; Cormorants abundant
A1	1996–1999	Abandoned after 3 years of colonization; no Cormorants in 2003–2005
A2	1992–1996	Declined in 1997 to 2002 after 4 years of intensive colonization; no Cormorants in 2003–2005

Sites NC, AC, A1, and A2 correspond to sites C, 1, 2, and 3, respectively, in Osono et al. (2006a, 2006b).

Table 2. Mass (Mg ha^{-1}) and compositions of coarse woody debris (CWD; diameter ≥ 10 cm) and branches (diameter 1–5 cm) in four forest stands (Sites NC, AC, A1 and A2 of Table 1). Numbers in parentheses indicate the proportions relative to the total mass. Measurement of branches was not performed at Site A2. nd, not determined. Cypress, *Chamaecyparis obtusa*; pine, *Pinus densiflora*.

	NC		AC		A1		A2	
Coarse woody debris								
Total	7.72	(100.0)	25.28	(100.0)	15.54	(100.0)	42.05	(100.0)
Tree species								
Cypress	1.78	(23.1)	16.21	(64.1)	5.07	(32.6)	31.31	(74.4)
Pine	4.83	(62.6)	7.27	(28.8)	4.66	(30.0)	2.72	(6.5)
Broad-leaved	0.95	(12.4)	1.67	(6.6)	4.07	(26.2)	6.93	(16.5)
Unknown	0.16	(2.0)	0.13	(0.5)	1.73	(11.1)	1.10	(2.6)
Form								
Log	2.85	(37.0)	6.05	(23.9)	4.04	(26.0)	3.90	(9.3)
Snag	3.30	(42.7)	17.38	(68.7)	10.49	(67.5)	36.77	(87.4)
Stump	1.57	(20.3)	1.86	(7.3)	1.00	(6.4)	1.38	(3.3)
Decay class[a]								
I	2.69	(34.8)	17.54	(69.4)	7.95	(51.2)	5.30	(12.6)
II	2.13	(27.5)	0.27	(1.1)	6.13	(39.5)	30.47	(72.4)
III	1.65	(21.4)	1.72	(6.8)	0.67	(4.3)	5.05	(12.0)
IV	1.23	(15.9)	5.68	(22.4)	0.78	(5.0)	1.24	(3.0)
V	0.03	(0.4)	0.08	(0.3)	0.00	(0.0)	0.00	(0.0)
Branch								
Total	1.27	(100.0)	3.85	(100.0)	3.59	(100.0)	nd	Nd
Tree species								
Cypress	0.99	(78.1)	2.24	(58.1)	3.10	(86.4)	nd	nd
Pine	0.00	(0.0)	0.79	(20.4)	0.00	(0.0)	nd	nd
Broad-leaved	0.28	(21.9)	0.83	(21.5)	0.49	(13.6)	nd	nd
Decay class[b]								
I	0.17	(13.7)	0.78	(20.3)	0.47	(13.0)	nd	nd
II	0.81	(64.0)	2.86	(74.1)	2.33	(64.9)	nd	nd
III	0.28	(22.3)	0.22	(5.6)	0.79	(22.1)	nd	nd

[a] Decay class of CWD followed Fukasawa et al. (2014). Decay class I, bark is intact, structural integrity sound, small twigs present, invading root absent; decay class II, bark is mostly intact, sapwood somewhat decayed, larger twigs present, invading roots absent; decay class III, bark is sloughing or absent, heart wood mostly sound and supports own weight, large branches present, invading roots present only in sapwood; decay class IV, bark is detached or absent, heart wood rotten and does not support own weight, branch stub present,

invading roots throughout; decay class V, bark is detached or absent, no structural integrity, branches absent, invading roots throughout.

[b] Branches in decay class I had bark and intact wood; those in decay class II had loose bark and slightly rotten wood; and those in decay class III had detached bark and rotten wood.