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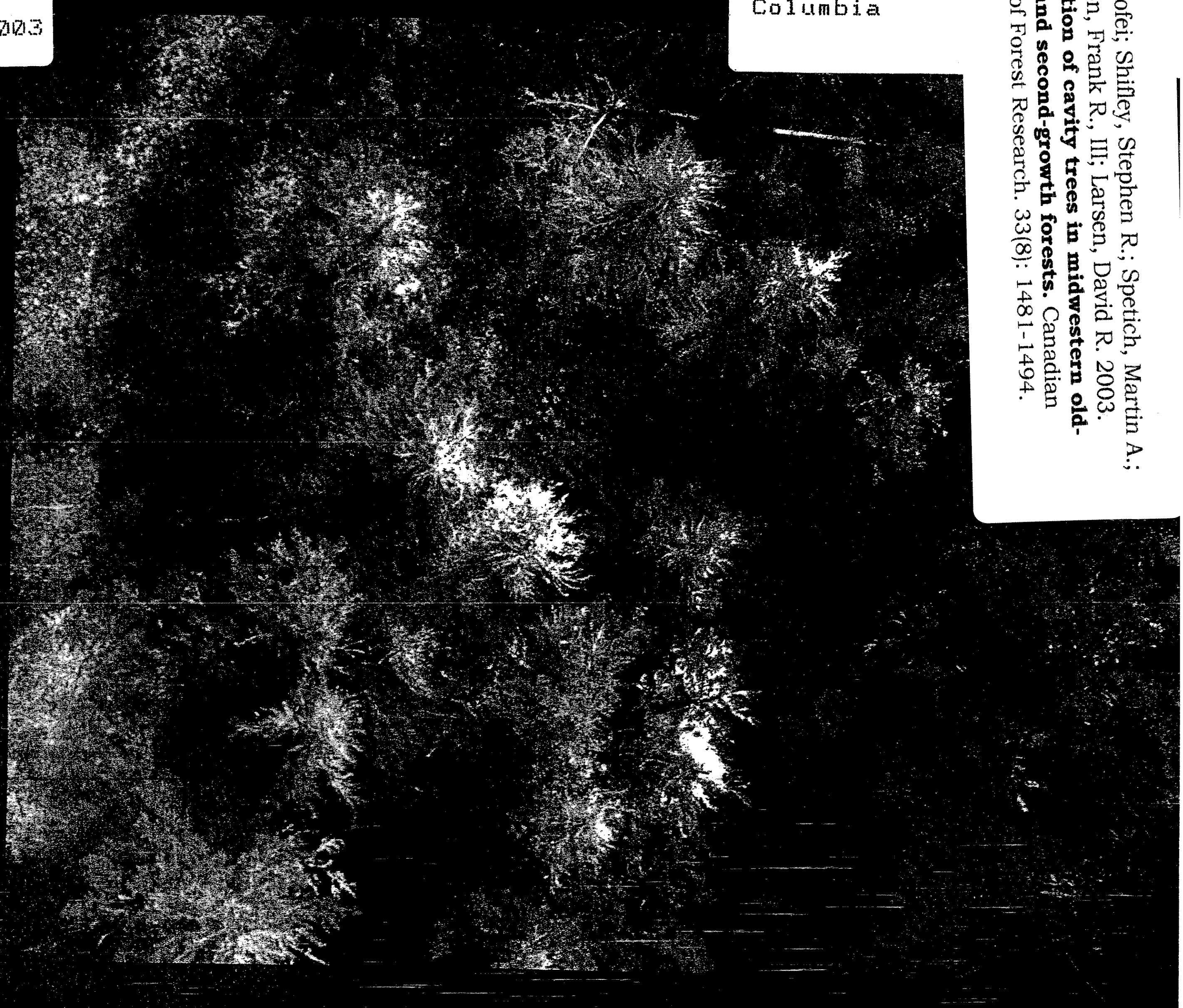

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Small Stream Channels and their Riparian Zones: Their Form, Function and Ecological Importance in a Watershed Context

[Les petits cours d'eau éphémères et intermittents et leurs zones riveraines : leur forme, leur fonction et leur importance écologique dans le contexte d'un bassin versant]

Continued on inside back cover / Suite au verso

Front cover: Jack pine (*Pinus banksiana*) stand in the Torch River Provincial Forest, Sask., 2 years after a jack pine budworm (*Choristoneura pinus*) outbreak. The presence of understory lichen (*Cladonia* spp., yellow patches) and bearberry (*Arctostaphylos uva-ursi*, dark green patches) is indicative of a relatively dry, poor-quality site that occurs on coarse, well-drained soils. Originating in the 1890s, the stand is undergoing horizontal and vertical diversification, as a result of budworm outbreaks, root disease, and the absence of major fires. Ecological legacy elements in this image include downed coarse woody debris, lichen-covered snags, long-dead trees, trees killed during the most recent outbreak, trees with dead tops, and live trees with crown damage. The photograph was taken on July 31, 1988. For more information see Hall et al. (1993, 1998) (Can. J. For. Res. **23**: 1337–1346, **28**: 1317–1327) or contact rhall@nrcan.gc.ca or jvolney@nrcan.gc.ca. (Photo by R. Hall.)

Page couverture : Peuplement de pins gris (*Pinus banksiana*) dans la forêt provinciale de Torch River (Saskatchewan) 2 ans après une infestation de la tordeuse de pin gris (*Choristoneura pinus*). La présence de lichens (*Cladonia* spp., étendues jaunes) et de l'arctostaphyle raison d'ours (*Arctostaphylos uva-ursi*, étendues vert foncé) dans le sous-étage donne une indication d'un site relativement sec et de mauvaise qualité sur un sol grossier et bien drainer. Le peuplement, datant des années 1890, subit une diversification horizontale et verticale à la suite d'infestations de la tordeuse de pins gris, de maladies des racines et de l'absence de feux de forêts importants. Parmi les éléments de l'héritage écologique retrouvés sur cette image figurent de gros débris ligneux, des chicots recouverts de lichen, de arbres morts (dont certains à la suite de la plus récente infestation), des arbres dont la cime est morte et des arbres dont la couronne est endommagée. La photo a été prise le 31 juillet 1988. Pour en savoir plus, consultez Hall et al. (1993, 1998) (Can. J. For. Res. **23** : 1337–1346, **28** : 1317–1327) ou communiquez avec rhall@nrcan.gc.ca ou jvolney@nrcan.gc.ca. (Photo de R. Hall.)

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Distribution of cavity trees in midwestern old-growth and second-growth forests

Zhaofei Fan, Stephen R. Shifley, Martin A. Spetich, Frank R. Thompson III, and David R. Larsen

Abstract: We used classification and regression tree analysis to determine the primary variables associated with the occurrence of cavity trees and the hierarchical structure among those variables. We applied that information to develop logistic models predicting cavity tree probability as a function of diameter, species group, and decay class. Inventories of cavity abundance in old-growth hardwood forests in Missouri, Illinois, and Indiana found that 8–11% of snags had at least one visible cavity (as visually detected from the ground; smallest opening ≥2 cm diameter), about twice the percentage for live trees. Five percent of live trees and snags had cavities on mature (≥110 years) second-growth plots on timberland in Missouri. Because snags accounted for typically no more than 10% of standing trees on any of these sites, 80–85% of cavity trees are living trees. Within the subset of mature and old-growth forests, the presence of cavities was strongly related to tree diameter. Classification and regression tree models indicated that 30 cm diameter at breast height (DBH) was a threshold size useful in distinguishing cavity trees from noncavity trees in the old-growth sample. There were two diameter thresholds in the mature second-growth sample: 18 and 44 cm DBH. Cavity tree probability differed by species group and increased with increasing decay class.

Résumé : Nous avons utilisé la classification et l'analyse d'arbres de régression pour identifier les principales variables associées à l'occurrence d'arbres à cavité et la structure hiérarchique entre ces variables. Nous avons utilisé cette information pour développer des modèles de régression logistique visant à prédire la présence de cavités en fonction du diamètre, du groupe d'essences et de la classe de carie de l'arbre. Des inventaires d'abondance de cavités dans des forêts anciennes de feuillus au Missouri, en Illinois et en Indiana ont montré que 8–11 % des chicots ont au moins une cavité visible (détectée par examen visuel à partir du sol; diamètre de la plus petite ouverture ≥2 cm), soit le double du pourcentage correspondant pour les arbres vivants. Cinq pourcent des arbres vivants et des chicots avaient des cavités dans des placettes en forêt de seconde venue mature (≥110 ans) dans les régions boisées au Missouri. Étant donné que les chicots ne comptent typiquement pas pour plus de 10 % des arbres sur pied à chacun de ces sites, 80–85 % des arbres à cavités sont donc des arbres vivants. Si on prend en compte seulement les forêts matures et les forêts anciennes, la présence de cavités est fortement reliée au diamètre de l'arbre. Les modèles de classification et d'arbres de régression indiquent qu'un diamètre à hauteur de poitrine (DHP) de 30 cm constitue une taille seuil pour distinguer les arbres avec cavités de ceux sans cavités dans les forêts anciennes. Dans les forêts de seconde venue, il y a deux seuils : 18 et 44 cm DHP. La probabilité qu'un arbre ait une cavité varie selon les groupes d'essences et augmente avec la classe de carie.

[Traduit par la Rédaction]

Introduction

Cavity trees, whether living or snags (i.e., standing dead trees), are natural components of forests. Cavity trees provide wildlife with habitat for roosting, foraging, nesting, hiding, and hibernating. Snags are a focal point for wildlife management because they frequently contain cavities and they provide foraging sites and hunting perches (Conner et al. 1975; Scott et al. 1977; Evans and Conner 1979; Mannan et al. 1980; Brawn et al. 1982; Raphael and White 1984; Sedgwick and Knopf 1986; Rosenberg et al. 1988; McClelland and McClelland 1999). Scott et al. (1977) reported that snags provide essential habitat for 85 North American bird species that excavate cavities, use natural cavities, or use cavities excavated by other species. Bats roost in tree cavities and under exfoliating bark of snags

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(Menzel et al. 2002). In Missouri, more than 89 wildlife species require cavity trees or snags (Titus 1983). Densities and species richness of wildlife have been linked to forest structure and composition, including tree diameter and height, species composition, overstory basal area, density, and understory vegetation (Murphy 1970; Anderson and Shugart 1974; Smith 1977; Grier and Best 1980; Raphael and White 1984; Sedgwick and Knopf 1986). The availability of cavity trees is considered one of the most important factors to the success of populations of cavity-nesting birds and is of increasing concern because of removal of cavity trees and snags under intensive timber management (McClelland and Frissell 1975). Several studies revealed an adverse impact of timber management on cavity tree resources and thus on cavity-dependent birds and wildlife (Conner et al. 1975; Cline et al. 1980; McComb and Nobel 1980; Mannan and Meslow 1984; Zarnowitz and Manuwal 1985). Resource managers are often required to incorporate the habitat requirements of cavity-using wildlife into management plans and assess trade-offs between wildlife and timber resource goals (Loehle et al. 2002).

Because midwestern remnant old-growth forests have been relatively undisturbed, they serve as important points of contrast and comparison for the second-growth forests that make up the majority of the region's forest resources. In the central hardwood region, much of the research related to old-growth forests has focused on tree size structure, species composition, and woody biomass dynamics from living trees to snags to down wood (Schmelz and Lindsey 1965; McComb and Muller 1983; Parker et al. 1985; MacMillan 1988; Parker 1989; Muller and Liu 1991; Runkle 1991; Martin 1992; Shifley et al. 1997; Spetich et al. 1999). However, little has been done to describe the number and distribution of cavity trees in old-growth forests in this region. Information on the characteristics and distribution of cavity trees has been focused on second-growth forests (Carey 1983; Sedgwick and Knopf 1986; Allen and Corn 1990; Kowal and Husband 1996; Jensen et al. 2002).

We examined the abundance of cavity trees in old-growth forests and compared the findings in old-growth forests with those of mature second-growth forests in the central hardwood region. We also explored the factors associated with cavity tree abundance and developed models that can be used to predict the relative frequency of cavity trees based on tree size, species, and decay class. This information is useful in evaluating the potential impact of different management scenarios on cavity tree resources as the region's second-growth forests mature.

Materials and methods

Data sources

Data on tree cavities came from two sources. The first was an inventory of remnant old-growth tracts in Indiana, Illinois, and Missouri (Spetich 1995; Shifley et al. 1995, 1997; Spetich et al. 1999). From 1992 to 1994, 15 remnant old-growth tracts in Missouri, Illinois, and Indiana were inventoried for cavities in association with a general inventory of forest composition and structure (Table 1). Trees ≥10 cm diameter at breast height (DBH) were inventoried on 0.1-ha circular plots. Species, diameter, status (live or dead), and other characteristics were recorded for each tree. Cavities were observed from the ground, and natural and excavated openings at least 2 cm in size (smallest dimension) were recorded. Trees were considered cavity trees if they had at least one visible cavity, regardless of the cavity size or location. Tree crown class (2, dominant; 3, codominant; 4, intermediate; 5, overtopped) and crown ratio (by 10% classes) were also recorded for each tree. Decay classes based on a classification scheme described by Maser et al. (1979) were recorded for live trees (I, healthy; II, declining in vigor) and dead trees (III, recently dead with tight bark; IV, dead with loose bark; V, bole free of bark or nearly so; VI, broken top and clean of bark; VII, broken top and largely decomposed). Slope percent, slope position, and aspect were recorded for each plot. The number of inventory plots varied from 4 to 30 per tract, with a total of 294 plots with more than 8000 measured trees (Table 1). More information on tract locations, inventory procedures, and vegetation characteristics can be found in Spetich (1995), Spetich et al. (1999), and Shifley et al. (1995, 1997).

The second data source was part of the 1989 inventory of Missouri forests conducted by the Forest Inventory and Analysis (FIA) unit of the North Central Research Station, U.S. Department of Agriculture, Forest Service (Hahn and Spencer 1991; Spencer et al. 1992; Miles et al. 2001). Inventory plots were systematically spread across timberland in Missouri. Each inventory plot was composed of 10 subplots spread over approximately 0.4 ha. Trees ≥13 cm DBH were sampled with an 8.6-factor angle gauge (m^2/h) on each subplot, and subplots were combined to obtain estimates for the entire plot. Species, diameter, size of the largest cavity visible from the ground (narrow cavity dimension to the nearest 2.5 cm), and other characteristics were recorded for each sampled tree. With the exception of decay class, all variables recorded for trees on the old-growth sites were also recorded for the second-growth sites.

We focused attention on the subset of 125 plots (2781 sampled trees) in the FIA sample with an overstory age ≥110 years. We analyzed these data in detail and compared them with results from the old-growth sites. These older FIA plots were in second-growth forests subject to human disturbance and stand in contrast with the old-growth sites that historically have had little human disturbance.

These two cavity tree inventories are unique in their size and spatial extent, but for some types of analyses they are limited. For example, the FIA inventory recorded only the largest cavity per tree. Although it can be used to estimate the number of cavity trees per hectare, it cannot be used to estimate the total number of cavities per hectare. For both inventories, cavities were determined by ground-based observation, which produces an imperfect inventory of the true number of cavities (Jensen et al. 2002). Nevertheless, the cavity tree estimates derived from these inventories serve as useful indicators of relative cavity abundance, and they can be used to assess the relationship of cavity trees to forest composition and size structure or changes thereof.

Data analysis

We employed classification and regression tree (CART) (Breiman et al. 1984) and logistic regression (SAS Institute Inc. 2000) to address the study objectives. Specifically, we

Table 1. Location, sample size, and overstory characteristics for sampled sites.

Site	No. plots	Tract size (ha)	Mean no. cavities in live trees (cavities/ha)	Mean no. cavities in dead trees (cavities/ha)	Mean no. cavities in live and dead trees (cavities/ha)	Live cavity trees (trees/ha)	Dead cavity trees (trees/ha)	All live trees (trees/ha)	All dead trees (trees/ha)	Canopy height[a] (m)	Dominant tree species[b]	Physiographic class[c]
Old-growth												
Illinois												
Funks Grove	4	57	68	28	95	45	8	273	28	25.2	Sugar maple, bur oak, green ash	Mesic, wet mesic
Starved Rock	4	15	60	13	73	40	10	340	33	20.9	Red oak, white oak, black oak	Mesic
Spitler Woods	30	65	96	17	113	49	8	406	39	21.5	White oak, sugar maple, red oak	Mesic
Mean	38	46	75	19	94	45	9	340	33	21.8	—	—
Indiana												
Bendix Woods	4	11	43	0	43	33	0	283	15	na	American beech, sugar maple, red elm	Mesic, wet mesic
Calvert-Porter Woods	4	16	10	8	18	10	5	270	25	na	Sugar maple, sycamore, yellow-poplar	Mesic, wet mesic
Davis-Purdue	30	21	106	51	158	47	11	308	30	31.7	White oak, red oak, sugar maple	Mesic, wet, wet mesic
Donaldson's Woods	30	27	123	37	159	59	9	239	16	32.5	White oak, yellow-poplar, American beech	Mesic, dry mesic
Hemmer Woods	30	17	41	13	54	32	4	258	23	23.3	White oak, black oak, red oak	Mesic
Hoot Woods	4	33	65	3	68	45	3	243	8	na	American beech, white oak, sugar maple	Mesic
Laughery Bluff	30	15	27	18	45	15	7	216	24	26.3	Yellow-poplar, sugar maple, American beech	Mesic
Lubbee Woods	4	14	53	8	60	33	3	248	10	na	American beech, white oak, sugar maple	Mesic
Pioneer Mothers	30	15	165	56	221	54	12	260	17	30.7	Sugar maple, American beech, white oak	Mesic, dry mesic
Mean	166	19	70	21	92	36	6	258	19	28.9	—	—
Missouri												
Big Spring	30	65	70	33	103	36	11	467	39	21.6	White oak, black oak, scarlet oak	Dry mesic, xeric
Dark Hollow	30	78	81	26	106	52	12	331	36	21.5	Red oak, white oak, American basswood	Dry mesic, mesic
Engelmann Woods	15	55	135	17	151	72	5	398	31	19.8	Sugar maple, red oak, chinkapin oak	Mesic, dry mesic
Roaring River	15	49	105	13	119	57	7	442	41	18.4	White oak, black oak, red oak	Xeric, dry mesic
Mean	90	62	98	22	120	54	9	410	37	20.7	—	—

Table 1 (*concluded*).

Site	No. plots	Tract size (ha)	Mean no. cavities in live trees (cavities/ha)	Mean no. cavities in dead trees (cavities/ha)	Mean no. cavities in live and dead trees (cavities/ha)	Live cavity trees (trees/ha)	Dead cavity trees (trees/ha)	All live trees (trees/ha)	All dead trees (trees/ha)	Canopy height[a] (m)	Dominant tree species[b]	Physiographic class[c]
Second-growth												
Missouri												
FIA inventory[d]	125[d]	various	—[e]	—[e]	—[e]	14	1	277	22	various	White oak, black oak, post oak	Predominantly dry mesic (62%) and mesic (31%)

Note: Data includes trees ≥13 cm diameter at breast height (DBH) for the Missouri Forest Inventory and Analysis (FIA) sample; ≥10 cm elsewhere. na, not available; —, not applicable.
[a]Mean height of dominant and codominant trees.
[b]By basal area. Scientific names are given in Table 2.
[c]As defined by White (1978).
[d]Includes plots with age ≥110 years old.
[e]Only the largest cavity per tree was recorded; total cavities per hectare cannot be estimated.

first used CART as an exploratory tool to uncover the factors and thresholds associated with the presence of cavity trees. Then we applied the factors identified by CART in logistic regression models describing the probability of cavity tree occurrence.

CART is a nonparametric, recursive partitioning technique developed by Breiman et al. (1984) for classification and (or) prediction purposes. Previous applications of CART in forestry included models to estimate tree mortality, insect infestation, and wood quality (e.g., LeMay et al. 1994; Dobbertin and Biging 1998; Gottschalk et al. 1998; Negron 1998). Dobbertin and Biging (1998) described the CART methodology in a forestry context where they intended to predict tree mortality. We were interested in identifying the factors that distinguish cavity trees ($y = 1$) from trees without cavities ($y = 0$). Generally, our CART analysis incorporates two processes: a recursive top-down partitioning process and a bottom-up pruning process. The recursive top-down partitioning starts from the whole population (also called the training data set). At each iteration, the data set is partitioned into two relatively homogeneous subsets (nodes), such that one node contains the highest possible proportion of cavity trees, and the other node contains the lowest possible proportion based on a cutoff value of one of the explanatory variables. We employed the gini index (Breiman et al. 1984) to evaluate the purity of each node and identify best partitions.

As indicated by Breiman et al. (1984), if no stopping rule (such as node size) is invoked, a fully grown tree will be generated. However, a fully grown tree, more often than not, overfits the data, is too complex to be useful, and is too large to be interpreted easily. To avoid these potential problems, we set the minimum terminal node size at 100 cases. We employed a pruning process to remove nonsignificant or superficial partitions for the best tree model (honest estimate) using the 10-fold cross-validation method. With this method, the data set was first randomly divided into 10 approximately equal-sized subsets. Nine subsets were then used to construct the tree model and the 10th subset was used to estimate the misclassification rate. We repeated this procedure 10 times until all subsets were used for CART model construction and for evaluation. The average misclassification rates for the fully grown regression tree and a set of subtrees were calculated, and the best model was defined as that which minimized the overall misclassification rates (Steinberg and Colla 1997).

For this best CART model, we bootstrapped (drew a sample of the same size as the original one with replacement) each internal node 1000 times (Efron and Tibshirdge 1993) and calculated the mean and 95% confidence interval (CI) of the proportion of cavity trees within each node. We also computed the ratio of the proportions for each split (the proportion of cavity trees in the right node divided by the proportion of cavity trees in the left node) as a measure of association for the observations in each node.

To increase the interpretability of the CART results, we combined tree species into eight groups based on their frequency of occurrence, genus, and growth form (Table 2). The old-growth forests spanned three states (Missouri, Indiana, and Illinois), which differ in species composition and forest productivity, but state was not a significant variable

Table 2. Species groups used for cavity tree analyses showing states where they occurred in the sample.

Group	Included species	Missouri	Illinois	Indiana
(1) Sugar maple	Sugar maple (*Acer saccharum* Marsh.)	x	x	x
(2) White oak	Bur oak (*Quercus macrocarpa* Michx.)	x	x	x
	Chinkapin oak (*Quercus muehlenbergii* Engelm.)	x	x	x
	Post oak (*Quercus stellata* Wangenh.)	x		
	White oak (*Quercus alba* L.)	x	x	x
(3) Red oak	Black oak (*Quercus velutina* Lam.)	x	x	x
	Blackjack oak (*Quercus marilandica* Muenchh.)	x		
	Northern pin oak (*Quercus ellipsoidalis* E.J. Hill)	x		
	Northern red oak (*Quercus rubra* L.)	x	x	x
	Pin oak (*Quercus palustris* Muenchh.)	x		x
	Scarlet oak (*Quercus coccinea* Muenchh.)	x		
	Shingle oak (*Quercus imbricaria* Michx.)	x	x	
	Shumard oak (*Quercus shumardii* Buckl.)	x		x
	Southern red oak (*Quercus falcata* Michx.)	x		
(4) Hickory	Bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch)	x	x	x
	Black hickory (*Carya texana* Buckl.)	x		
	Mockernut hickory (*Carya tomentosa* Nutt.)	x	x	x
	Pignut hickory (*Carya glabra* (Mill.) Sweet var. *oderata* (Marsh.) Little)	x	x	x
	Shagbark hickory (*Carya ovata* (Mill.) K. Koch)	x	x	x
	Shellbark hickory (*Carya laciniosa* (Michx. f.))	x	x	x
(5) Elm	American elm (*Ulmus americana* L.)	x	x	x
	Slippery elm (*Ulmus rubra* Muhl.)	x	x	x
	Winged elm (*Ulmus alata* Michx.)	x	x	x
(6) Ash	Black ash (*Fraxinus nigra* Marsh.)			x
	Blue ash (*Fraxinus quadrangulata* Michx.)	x		
	Green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern.)	x	x	x
	White ash (*Fraxinus americana* L.)	x	x	x
(7) Beech	American beech (*Fagus grandifolia* Ehrh.)			x
(8) Other overstory	American basswood (*Tilia american*a L.)	x	x	x
	American sycamore (*Platanus occidentalis* L.)	x		x
	Bigtooth aspen (*Populus grandidentata* Michx.)	x		
	Black cherry (*Prunus serotina* Ehrh.)	x	x	x
	Blackgum (*Nyssa sylvatica* Marsh.)	x		x
	Black walnut (*Juglans nigra* L.)	x	x	x
	Black willow (*Salix nigra* Marsh.)	x		x
	Box-elder (*Acer negundo* L.)	x		x
	Butternut (*Juglans cinerea* L.)		x	
	Eastern redcedar (*Juniperus virginiana* L.)	x		x
	Hackberry, sugarberry (*Celtis* spp.)	x	x	x
	Honey-locust (*Gleditsia triacanthos* L.)	x	x	x
	Kentucky coffeetree (*Gymnocladus dioicus* (L.) K. Koch)	x		x
	Ohio buckeye (*Aesculus glabra* Willd.)	x	x	x
	Osage orange (*Maclura pomifera* (Raf.) C.K. Schneid.)	x	x	
	Persimmon (*Diospyros virginiana* L.)	x		x
	Red maple (*Acer rubrum* L.)	x		x
	Red mulberry (*Morus rubra* L.)	x		x
	Sassafras (*Sassafras albidum* (Nutt.) Nees)	x	x	x
	Silver maple (*Acer saccharinum* L.)			x
	Shortleaf pine (*Pinus echinata* Mill.)	x		
	White mulberry (*Morus alba* L.)	x		x
	Yellow-poplar (*Liriodendron tulipifera* L.)	x		

Note: Groups were designated based on number of observations, genus, and whether or not the species would achieve canopy dominance. The beech group (7) only occurred in Indiana, and the samples for the elm group (5) and the ash group (6) were too small to analyze separately in the Missouri Forest Inventory and Analysis (FIA) data set.

Table 3. The relative probability and 95% bootstrap confidence interval (CI) of cavity trees corresponding to each partitioning in the classification tree models.

Node	Variable	Cut-off value	Relative probability[a]	95% CI
Old-growth forests in Missouri, Illinois, and Indiana combined (Fig. 1)				
1	DBH	30 cm	3.4	3.0–3.8
2	Decay class	II–VII vs. I	2.3	1.9–2.7
3	Decay class	IV–VII vs. I–III	2.3	1.8–3.0
4	Species group	1, 7, 8 vs. 2, 3, 4, 5, 6	2.0	1.6–2.5
5	DBH	23 cm	2.2	1.6–3.1
6	DBH	56 cm	1.6	1.3–1.9
9	DBH	14 cm	2.0	1.5–2.5
10	Species group	7, 8 vs. 1, 2, 3, 4, 5, 6	2.1	1.5–2.9
13	Species group	1, 7 vs. 2, 3, 4, 5, 6, 8	2.1	1.4–3.1
Second-growth forests in Missouri (Fig. 2)				
1	DBH	44 cm	3.6	2.8–4.8
2	DBH	18 cm	6.8	2.2–21.5
3	Species group	2, 4 vs. 1, 3, 8	2.5	1.7–3.8
5	Crown ratio	25%	3.1	1.8–5.1

Note: DBH, diameter at breast height.
[a]Ratio of the probability of cavity trees in the two subsets formed at a given node. It is a measure of the ability of the variable and cut-off value to distinguish cavity trees.

during the initial CART analysis. Therefore, we combined the old-growth data from the three states in the CART analysis.

CART partitioned cavity trees based on DBH, species, and decay class categories, but the procedure did not describe the joint relationship of cavities by species and DBH or by decay class and DBH. We employed logistic regression to examine differences by DBH across species groups and decay classes. The lack of observations in certain species group by decay class combinations precluded the simultaneous analysis of effects through a multivariate, logistic regression model. We instead applied logistic regression by species groups and decay classes separately. The logistic model was of the form

$$[1] \quad \log\left(\frac{p_{ij}}{1-p_{ij}}\right) = b_{0j} + b_{1j}\mathrm{DBH}_{ij}$$

where p_{ij} is the probability that tree i of species group or decay class j is a cavity tree; DBH_{ij} is the diameter at breast height (cm) of tree i of species group or decay class j; and b_{0j} and b_{1j} are the estimated parameters for species group or decay class j. In the analysis of species group differences using eq. 1, we limited consideration to live, healthy trees (decay class = I) for the old-growth forests and all live trees for the second-growth forests. This eliminated the decay class effect, which was not measured in the second-growth (FIA) sample.

Results

The best CART models for both old-growth and second-growth forests (Figs. 1 and 2) showed that the distribution of cavities was related mainly to tree DBH, species group, decay class, and crown ratio. The significance of each factor and cut-off value was quantified by the relative probability

Fig. 1. Classification and regression tree (CART) partition of cavity trees for old-growth forests sampled in Missouri, Illinois, and Indiana. Nodes are numbered in bold type. Each node shows the percentage of trees that are cavity trees (top) and the total number of cavity trees within each node (bottom). Lines and their labels indicate classification variables and threshold values for successive nodes. DBH, diameter at breast height; sp-grp, species group.

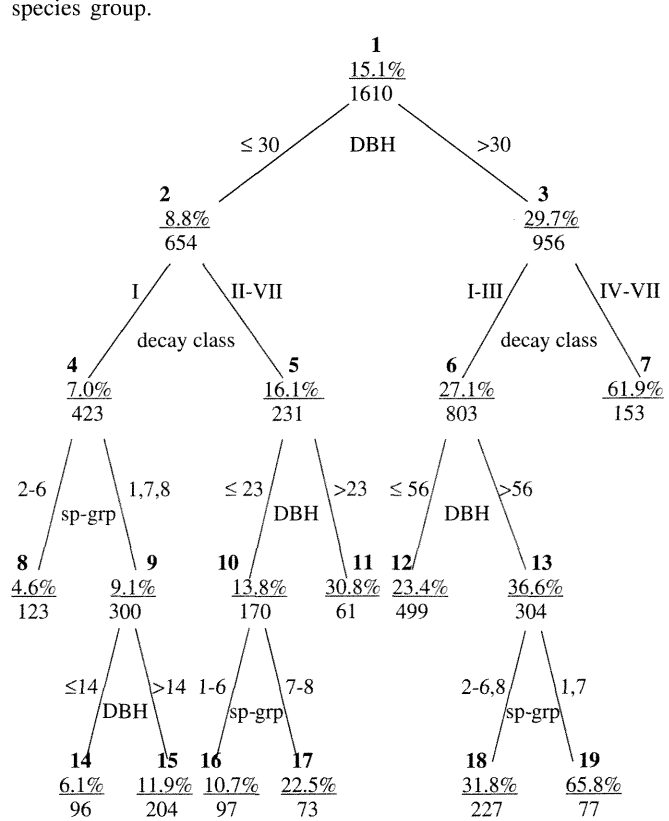
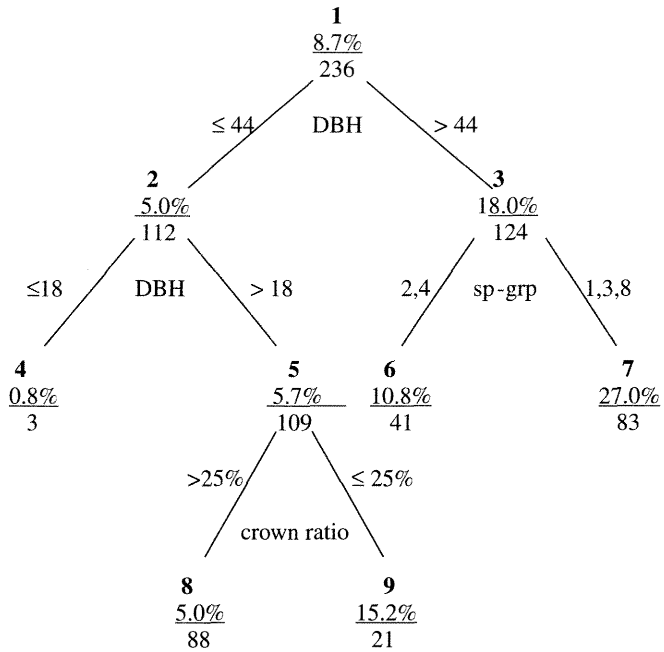


Fig. 2. Classification and regression tree (CART) partition of cavity trees in the mature, second-growth forest sample (plots ≥110 years old), Missouri. Nodes are numbered in bold type. Each node shows the percentage of trees that are cavity trees (top) and the total number of cavity trees within each node (bottom). Lines and their labels indicate classification variables and threshold values for successive nodes. DBH, diameter at breast height; sp-grp, species group.



(the probability of cavity trees in the right node divided by the probability of cavity trees in the left node) and 95% bootstrap CI (Table 3). The 95% CI for the partitions did not include 1, indicating that factors and cut-off values have a significant effect on the distribution of cavity trees.

The overall probability of cavity trees among trees >10 cm DBH in old-growth forests was 15.1% (Fig. 1, node 1), nearly two times (8.7%) that of the Missouri second-growth forests ≥110 years old (Fig. 2, node 1). However, the probability differed significantly with tree DBH, decay class, and species group. The likelihood for old-growth trees >30 cm DBH (Fig. 1, node 3) to be cavity trees averaged 29.7%, or 3.4 times (95% CI: 3.0–3.8) that of trees ≤30 cm DBH (8.8%) (Fig. 1 and Table 3). The probability of cavity trees was further differentiated by tree decay class. Trees ≤30 cm DBH (Fig. 1, node 2) were partitioned into healthy live trees with cavity tree probability of 7.0% (node 4) and unhealthy live trees plus dead trees with cavity tree probability of 16.1% (node 5). Trees >30 cm DBH (node 3) were partitioned into live trees plus recently dead trees (node 6) and other dead trees (node 7) with cavity tree probabilities of 27.1 and 61.9%, respectively. As indicated by nodes 4 through 7, the majority of cavity trees were live trees, but on a percent basis, dead trees were more likely to be cavity trees than live trees of the same size. The effect of species group on cavity tree distribution was determined to be significant between live trees plus recently dead trees (nodes 4 and 13) and small dead trees (node 10). Trees in old-growth forests were finally partitioned into 10 disjoint groups (nodes 7, 8, 11, 12, and 14–19), with cavity tree probability ranging from 4.6 to 65.8%.

In second-growth forests (110–155 years, Fig. 2), the CART model identified three tree size groups based on DBH: small (DBH ≤18 cm, node 4), medium (18 cm < DBH ≤ 44 cm, node 5), and large (DBH >44 cm, node 3) trees. Nearly all cavity trees were large or medium trees; cavity trees ≤18 cm were rare (3 out of 357). The large and the medium tree groups had approximately the same total number of cavity trees, but differed significantly in terms of cavity tree probability (5.7% for trees between 18 and 44 cm DBH, 18.0% for larger trees). Cavity tree probability was further differentiated by crown ratio and species group, respectively. Based on DBH, crown ratio, and species group, all trees in second-growth forests were classified into five groups (nodes 4, 6, 7, 8, and 9), with cavity tree probability ranging from 0.8 to 27.0%. Table 4 lists the 95% CI of the cavity tree probability of each node on the best CART models for old- and second-growth forests. Most CIs were narrow, fewer than 5 percentage points in width.

Tree species composition differed by state (Table 1), so we modeled species groups separately by state (Fig. 3 and Table 5). For most species groups, no significant lack of fit was found in the logistic models at the $\alpha = 0.05$ significance level. However, the generalized R^2 for all models was low (<0.2), even for the most significant relationships (Table 5). The effect of species group on cavity tree probability was evident when a tree reached a larger size (e.g., 30 cm DBH); we found little difference among species groups for small trees (Fig. 3). The predicted probability trajectory for each species group showed that shade-tolerant sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) were highly prone to cavity formation, although the species mix and exact species group order differred among Missouri, Illinois, and Indiana and between second- and old-growth in Missouri (Fig. 3).

The chance for a standing dead tree to have a cavity increased with its decay class. Snags in decay classes IV, V, and VI were far more likely to have cavities than living trees (decay classes I and II) (Fig. 4 and Table 6). The parameter estimates for most of these models were statistically significant (Table 6). No significant lack of fit was found at the $\alpha = 0.05$ significance level, except for decay class I. The generalized R^2 values for decay class models ranged from 0.01 to 0.29 and were relatively larger than for the species group models, indicating that DBH plus decay class explained more variation than DBH plus species group in the cavity tree probability modeling. The logistic model for decay class IV, in terms of the generalized R^2, captured more variation than the models for other decay classes.

Discussion

Factors related to cavity tree abundance

The CART models for both old- and second-growth forests (Figs. 1 and 2) showed the distribution of cavities was related mainly to individual tree characteristics (DBH, species, decay class, and crown ratio) and had little association with environmental factors and stand-level attributes. Stand

Table 4. The 95% bootstrap confidence interval (CI) of the probability (%) of cavity trees within each node in the classification and regression tree (CART) models.

Node	Description	95% CI
Old-growth CART model (Fig. 1)		
1	All trees	14.5–15.7
2	Trees with 10 cm < DBH ≤ 30 cm	8.3–9.3
3	Trees with DBH >30 cm	28.4–31.0
4	Healthy live trees with 10 cm < DBH ≤ 30 cm	6.6–7.6
5	Vigor-declining live trees and snags with 10 cm < DBH ≤ 30 cm	14.6–17.8
6	Live trees and recently dead trees (with tight bark) with DBH >30 cm	25.7–28.4
7	Snags except recently dead trees (with tight bark) with DBH >30 cm	56.7–67.2
8	Healthy live oaks, hickories, elm, and ash with 10 cm < DBH ≤ 30 cm	3.9–5.2
9	Healthy live maple, beech, and other species with 10 cm < DBH ≤ 30 cm	8.3–9.9
10	Vigor-declining live trees and snags with 10 cm < DBH ≤ 23 cm	12.2–15.4
11	Vigor-declining live trees and snags with 23 cm < DBH ≤ 30 cm	25.1–35.5
12	Live trees and recently dead trees (with tight bark) with 30 cm < DBH ≤ 56 cm	21.8–24.9
13	Live trees and recently dead trees (with tight bark) with DBH >56 cm	33.9–39.3
14	Healthy live maple, beech, and other species with 10 cm < DBH ≤ 14 cm	5.1–7.1
15	Healthy live maple, beech, and other species with 14 cm < DBH ≤ 30 cm	10.6–13.2
16	Vigor-declining live trees and snags of maple, oaks, hickories, elm, and ash with 10 cm < DBH ≤ 23 cm	9.1–12.4
17	Vigor-declining live trees and snags of beech and other species with 10 cm < DBH ≤ 23 cm	18.5–26.2
18	Live and recently dead (with tight bark) oaks, hickories, elm, ash, and other species with DBH >56 cm	29.0–34.6
19	Live and recently dead (with tight bark) maple and beech with DBH >56 cm	58.1–73.5
Second-growth CART model (Fig. 2)		
1	All trees	7.2–8.9
2	Trees with DBH ≤44 cm	4.2–5.7
3	Trees with DBH >44 cm	15.8–20.3
4	Trees with 10 cm < DBH ≤ 18 cm	0.3–1.7
5	Trees with 18 cm < DBH ≤ 44 cm	4.8–6.6
6	White oaks and hickories with DBH >44 cm	8.1–13.4
7	Maple, red oaks, and other species with DBH >44 cm	23.1–31.3
8	Trees with crown ratio >25%	4.2–5.9
9	Trees with crown ratio ≤25%	9.6–19.9

Note: Diameter at breast height (DBH).

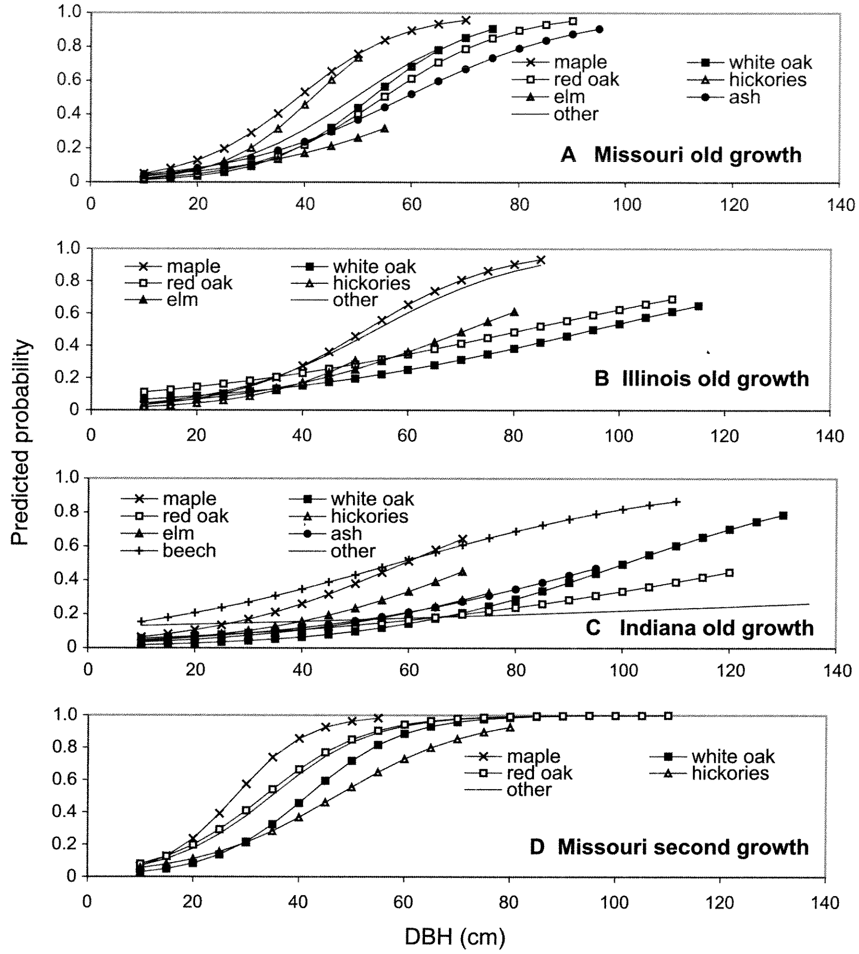
age is clearly associated with cavity tree abundance (e.g., Carey 1983; Fan et al. 2003), but age was limited to a narrow range for the comparison of mature second-growth forests (≥110 years) and old-growth forest (uneven aged, with overstory trees >120 years old).

The mature second-growth forests (Fig. 2) had a smaller proportion of cavity trees (8.7%) relative to the old-growth tracts (15.1%, Fig. 1), but for both populations, diameter was a primary determinant of relative cavity tree abundance. Our results were comparable with findings for mature oak–hickory (*Quercus* spp. – *Carya* spp.)forests in the Missouri Ozark Forest Ecosystem Project (Brookshire and Shifley 1997; Shifley and Brookshire 2000). The relatively undisturbed forests in that study were predominantly mature sawtimber, with ages of overstory trees typically between 40 and 110 years. Five percent of more than 50 000 inventoried trees (live trees ≥11 cm DBH and snags >15 cm DBH) had at least one cavity with an opening of at least 2.5 cm in diameter (smallest dimension) Sites averaged 18 cavity trees per hectare for live and dead trees combined, and the probability of a tree having a cavity increased exponentially with tree diameter (Jensen et al. 2002).

Species and decay class were the other principal determinants of cavity tree abundance. Some tree species are prone to decay and cavity formation (McClelland et al. 1979; McComb et al. 1986; Franklin et al. 1987). These differences have been observed by many investigators and are well known to timber buyers. Kowal and Husband (1996) ascribed the abundance of red maple (*Acer rubrum*) and American elm (*Ulmus americana*) cavity trees to their poor resistance to ice damage, which opens avenues to decay, and to their lack of resistance to heartwood decay, which is a precursor to cavity formation and creates a suitable excavating substrate for cavity-dependent wildlife (McClelland and Frissell 1975).

The CART models (Figs. 1 and 2) indicate that species differences in cavity formation were usually subordinate to the effects of tree size and decay class. Consequently, simple

Fig. 3. The estimated probability of cavity tree occurrence by diameter at breast height (DBH) and species group, based on the logistic model and coefficients in Table 4.



summaries of the number of cavity trees by species (Table 5) tell only part of the story. The population structure (number of trees by size, decay class, and species) also affects the observed percentage of cavities by species. For example, 14.8% of sugar maple trees in the Missouri old-growth sample had cavities, but only 2.3% of sugar maples in the mature second-growth sample had cavities. This is due to a preponderance of small sugar maples in the second-growth sample. Small maples rarely have cavities, but larger sugar maples are more likely to have cavities than most other species groups (Figs. 3 and 4). There are regional differences as well. From Missouri through Illinois to Indiana, sugar maple becomes more important and hickories become less important in terms of total and relative cavity tree abundance within the old-growth forests.

The interaction of species and decay class with tree diameter was best illustrated by the logistic regression models shown in Figs. 3 and 4. For all species, the probability of a tree being a cavity tree increased with increasing DBH, but maple and beech (where it occurred) were consistently the species most likely to have cavities. Nevertheless, cavity tree occurrence was highly variable by diameter class even within a given decay class or species group. Consequently, although most logistic models were statistically significant (Figs. 3 and 4; Tables 5 and 6), R^2 and goodness-of-fit statistics tended to be low.

In general, the Indiana old-growth sample had a lower proportion of cavity trees at a given DBH, and the range of data for Indiana included larger trees than the other sites. The Missouri sites had a rapid rise in cavity tree probability between 20 and 40 cm DBH. A similar increase occurred between 40 and 60 cm DBH for the Illinois sites, and >60 cm DBH for the Indiana sites. This is at least partially related to the gradient of increasing site productivity from western Missouri to eastern Indiana (e.g., Spetich et al. 1999). Trees in Indiana tended to achieve a greater overall size and had a lower cavity probability at a given DBH than the other sites. A similar response occurred by decay class (Fig. 4, old-growth sites only).

Importance of snags to cavity tree abundance

On the old-growth sites in Indiana, Illinois, and Missouri, we found that the percentages of snags having at least one cavity were 14, 11, and 8%, respectively. The corresponding percentages of live trees with cavities were 6, 5, and 4%, respectively. Thus, snags were twice as likely to be cavity

Table 5. Summary of cavity tree abundance by species groups and the maximum-likelihood estimates (MLE) of parameters in eq. 1 for predicting cavity tree probability using diameter at breast height (DBH).

Species group	No. of trees sampled[a]	No. of cavity trees[a]	% of cavity trees	MLE of parameters in eq. 1: β_0 (SE)	β_1 (SE)	Generalized R^2	Hosmer–Lemeshow goodness-of-fit test (Pr $>\chi^2$)[b]
Old-growth							
Missouri							
(1) Sugar maple	313	54	17.3	–3.94 (0.43)	0.10 (0.02)	0.16	0.09
(2) White oak	1096	107	9.8	–5.30 (0.34)	0.10 (0.01)	0.13	0.86
(3) Red oak	662	115	17.4	–4.71 (0.38)	0.09 (0.01)	0.18	0.71
(4) Hickory	491	48	9.8	–4.96 (0.47)	0.12 (0.02)	0.11	0.32
(5) Elm	94	7	7.4	–3.76 (0.84)	0.05 (0.03)	0.03	0.14
(6) Ash	69	10	14.5	–3.66 (0.76)	0.06 (0.02)	0.19	0.25
(8) Other	485	44	9.1	–4.18 (0.37)	0.08 (0.01)	0.09	0.22
Illinois							
(1) Sugar maple	488	44	9.0	–4.18 (0.35)	0.08 (0.01)	0.11	0.93
(2) White oak	148	28	18.9	–2.96 (0.64)	0.03 (0.01)	0.05	0.44
(3) Red oak	46	15	32.6	–2.35 (1.10)	0.03 (0.01)	0.06	0.24
(4) Hickory	103	8	7.8	–4.67 (1.19)	0.08 (0.04)	0.05	0.05
(5) Elm	288	23	8.0	–3.65 (0.41)	0.05 (0.01)	0.05	0.01
(8) Other	223	36	16.1	–3.83 (0.47)	0.07 (0.01)	0.17	0.39
Indiana							
(1) Sugar maple	1388	177	12.8	–3.21 (0.18)	0.05 (0.01)	0.05	0.36
(2) White oak	298	56	18.8	–4.42 (0.61)	0.04 (0.01)	0.11	0.89
(3) Red oak	156	29	18.6	–3.05 (0.85)	0.02 (0.01)	0.03	0.66
(4) Hickory	298	25	8.4	–3.73 (0.51)	0.04 (0.01)	0.03	0.40
(5) Elm	378	27	7.1	–3.65 (0.39)	0.05 (0.01)	0.03	0.09
(6) Ash	146	16	11.0	–3.37 (0.58)	0.03 (0.01)	0.05	0.07
(7) Beech	348	110	31.6	–2.06 (0.25)	0.04 (0.01)	0.12	0.05
(8) Other	811	121	14.9	–1.95 (0.16)	0.01 (0.00)	<0.01	0.03
Second-growth							
Missouri							
(1) Sugar maple	88	2	2.3	–4.14 (0.17)	0.15 (0.09)	0.03	0.85
(2) White oak	1613	83	5.1	–4.62 (0.36)	0.11 (0.02)	0.02	0.88
(3) Red oak	542	91	16.8	–3.50 (0.37)	0.10 (0.02)	0.06	0.61
(4) Hickory	231	14	6.1	–3.62 (0.65)	0.08 (0.05)	0.01	0.01
(8) Other	307	28	9.1	–3.65 (0.42)	0.11 (0.02)	0.05	0.13

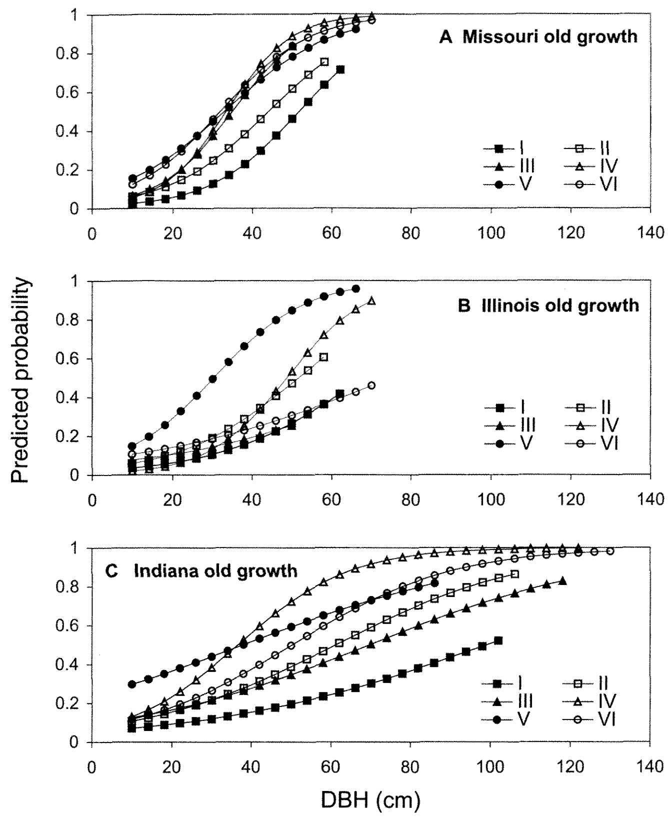
[a]Values refer to the count of sample trees.
[b]Pr, predicted probability. Small values indicate a lack of fit of the model.

trees as were living trees. However, there were approximately 10 times as many live trees as snags per hectare on the old-growth sites. Consequently, live trees accounted for about 80% of the cavities and 85% of the cavity trees per hectare at the old-growth sites (Table 1).

Our findings of oak-dominated forests were striking in their similarity to results reported by Goodburn and Lorimer (1998) for managed and old-growth northern hardwood and hardwood–hemlock forests. They evaluated only cavities that appeared to have been used by wildlife and found an average of only 12.4 cavity trees per hectare, but the percentage of cavities in live trees (85%) and snags (15%) was similar to the ratio we observed (80% vs. 20%). As on our sites, they reported that the proportion of snags that were cavities trees was approximately twice the proportion for live trees.

The number of snags alone does not accurately indicate the extent of the cavity resource in hardwood forests (Sedgwick and Knopf 1986; Carey 1983; Healy et al. 1989; Allen and Corn 1990; Kowal and Husband 1996) as well as it would in coniferous forests where cavities in live trees are rare (McClelland and Frissell 1975, Cline et al. 1980, Mannan et al. 1980). Snags in the advanced stages of decomposition (e.g., classes IV, V, and VI) were far more likely to have cavities (Figs. 1 and 4; Table 5) than living trees or trees that recently died. Although the general trend was one of an increasing probability of cavities with increasing decay class, there was considerable variation in that

Fig. 4. The estimated probability of cavity tree occurrence by diameter at breast height (DBH) by decay classes (I–VI), based on logistic model and coefficients in Table 5. Decay class VII was not modeled because of lack of observations. Decay classes were recorded only for the old-growth sites.



trend. This is at least partially due to the difficulty of defining discrete decay classes and securing a reasonable sample size within each class.

Comparison of old-growth and second-growth forests

The proportion of cavity trees in Missouri old-growth forests was approximately twice the proportion for second-growth forests ≥110 years old. The old-growth sites had more large-diameter trees prone to cavity formation (such as sugar maple and hickories) than did the second-growth forests. For example, sugar maple accounted for only 1.5% of the basal area in the second-growth sample compared with 6.7% in the old-growth sample. Longevity is probably also a factor; in these forests, cavity trees per hectare have been shown to increase with stand age (Fan et al. 2003). The old-growth sites are technically uneven aged, but many individual overstory trees are older than those found on the second-growth sites, and they have experienced more opportunities for damage, decay, and (or) cavity formation.

Limitations of the data

The data used in this study are extensive in geographic coverage, and collectively, they constitute a large sample size. However, the number of cavity trees is a surrogate for the actual number of cavities per hectare, a measure of even greater interest. The number of cavity trees is a good index of the relative abundance of cavities, but the actual number of cavities can only be inferred. For the old-growth sites, we found an average of 1.9 cavities per cavity tree (range 1.2–3.3, based on data in Table 1). Live trees averaged 1.9 cavities per cavity tree (range 1.0–2.1); dead trees averaged 2.8 cavities per cavity tree (range 1.0–4.7).

Cavities are difficult to observe from the ground, so a full, accurate inventory of cavities presents logistical difficulties. Ground-based cavity inventories overlook some cavities and misclassify some bole defects as cavities when they are not actually useable as such. A recent Missouri study where cavities were inventoried from the ground found that when the trees were felled and dissected, the actual number of usable cavities was 70% of the ground-based estimate (Jensen et al. 2002).

Management implications

Resource managers should be cognizant of the dynamic nature of the cavity resource and the role of live hardwood trees in supplying the majority of cavities on an area basis. Cavity trees, particularly snags, are subject to blowdown and provide cavity habitat for only a finite period. Thinning and selection harvests repeated over several decades have the potential to reduce the cavity tree population over the long term, but over a single harvest cycle, they may have little net effect on the number of cavity trees (Jensen et al. 2002). We agree with Adams and Morrison (1993) that from a wildlife perspective, effective habitat management should include maintenance of a diverse stand structure and species composition and retention of both snags and live trees with signs of stem rot.

Trees in advanced stages of decomposition are more often cavity trees than are live trees of the same species or diameter, so retaining standing dead trees is a good way to increase the number of current and future cavities. Moreover, snags do not compete with other trees for growing space, which may be a concern when timber production is an objective.

Conclusions

The CART analysis highlighted the major variables (DBH, decay class, species group, and crown ratio) and threshold values associated with cavity trees. The subsequent logistic models showed the interaction of tree diameter with species group and decay class. Beech, sugar maple, post oak (*Quercus stellata*), and trees in the red oak and elm groups had a relatively high probability of being cavity trees; shortleaf pine (*Pinus echinata*) had the lowest probability. The logistic models are useful for estimating (or predicting) cavity abundance for stands that differ in size structure and species composition.

Based on the classification models, trees with diameters less than 30 cm are unlikely to have cavities, and the larger the diameter, the more likely a tree is to contain at least one cavity. Dead trees were about twice as likely to be cavity trees than were live trees, and on old-growth sites, a typical dead cavity tree had about 1.5 times as many cavities as a typical live cavity tree. Despite the high relative probability

Table 6. Summary of cavity tree abundance in old-growth forests by decay classes and the maximum-likelihood estimates (MLE) of parameters in eq. 1 for predicting cavity tree probability using diameter at breast height (DBH).

				MLE of parameters in eq. 1			
Decay class	No. of trees[a]	No. of cavity trees[a]	% of cavity trees	β_0 (SE)	β_1 (SE)	Generalized R^2	Hosmer–Lemeshow goodness-of-fit test (Pr $>\chi^2$)[b]
Missouri							
I	3210	385	12.0	–4.37 (0.16)	0.08 (0.00)	0.13	0.01
II	416	72	17.3	–3.16 (0.30)	0.07 (0.01)	0.11	0.11
III	90	19	21.1	–3.18 (0.67)	0.09 (0.03)	0.13	0.39
IV	62	14	22.6	–3.56 (0.85)	0.10 (0.03)	0.23	0.37
V	44	15	34.1	–1.80 (0.72)	0.05 (0.03)	0.08	0.38
VI	75	25	33.3	–2.50 (0.61)	0.08 (0.02)	0.18	0.26
Illinois							
I	1360	158	11.6	–3.68 (0.19)	0.05 (0.00)	0.11	0.00
II	100	23	23.0	–3.39 (0.57)	0.07 (0.01)	0.28	0.10
III	45	6	13.3	–3.23 (1.06)	0.04 (0.03)	0.05	0.65
IV	37	6	16.2	–4.78 (1.38)	0.10 (0.03)	0.29	0.34
V	21	9	42.9	–2.32 (1.29)	0.08 (0.05)	0.15	0.11
VI	27	6	22.2	–2.38 (0.96)	0.03 (0.02)	0.08	0.28
Indiana							
I	3823	561	14.7	–2.54 (0.08)	0.02 (0.00)	0.04	0.03
II	450	94	20.9	–2.17 (0.20)	0.03 (0.01)	0.07	0.29
III	64	18	28.1	–1.13 (0.41)	0.01 (0.01)	0.01	0.17
IV	98	37	37.8	–2.25 (0.46)	0.07 (0.02)	0.26	0.53
V	28	13	46.4	–1.31 (0.82)	0.03 (0.02)	0.11	0.68
VI	244	93	38.1	–2.24 (0.30)	0.05 (0.01)	0.22	0.53

Note: Decay class VII is not evaluated because of the small sample size.
[a]Values refer to the count of sample trees, not trees per hectare.
[b]Pr, predicted probability. Small values indicate a lack of fit of the model.

of cavity occurrence in snags, in healthy midwestern hardwood forests, the majority of the cavity resource per unit area is in the live trees that typically constitute about 90% of all standing trees. Management of the cavity resource must give appropriate weight to the live trees that provide the majority of the cavity resource in these ecosystems.

The old-growth sites analyzed in this study were unique in their lack of prior timber harvest and their limited exposure to other anthropogenic disturbances. The old-growth sample had nearly five times as many cavity trees per hectare as the mature (≥110 years old), second-growth sites. This difference is related to both greater tree size and greater abundance of cavity-prone species on the old-growth sites.

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