INTRODUCTION
In the past 20 years, the perceived role of fire in mixed-oak forests has changed from a solely destructive force to be prevented, to acceptance of its historical role in perpetuating mixed-oak forests, to active research on the effects and potential uses of prescribed fire as a regeneration tool. This research has produced a wide variety of results: sometimes fire is beneficial (Brown 1960, Carvell and Maxey 1969, Ward and Stephens 1989); sometimes it is detrimental (Johnson 1974, Loftis 1990, Wendel and Smith 1986); and sometimes it has no noticeable effect on oak regeneration (Merritt and Pope 1991, Teuke and Van Lear 1982). The studies differed from each other in many important aspects. For example, they were conducted in different regions and at different times of the year. Some were post-wildfire assessments, while others dealt with prescribed fires. Some were burned – unburned comparisons, while others were preburn versus postburn evaluations. Some occurred in the dense shade of stands that had been undisturbed for decades, while others took place in the high-light conditions of new or recently disturbed stands. They did share some similarities: nearly all of the studies used plots to inventory vegetation, focused on sprouts, assumed fire intensity was equal throughout the burn, and ignored root development differences among hardwood species. Consequently, they produced widely disparate findings and resulted in no definitive silvicultural technique involving fire as a predictable regeneration tool.

In 1993, the Virginia Department of Game and Inland Fisheries conducted a 1-year pilot study of prescribed fire effects on hardwood regeneration in oak-dominated shelterwood stands (Keyser and others 1996). The study revealed that oak reproduction was more resistant to summer fire than were competing hardwood species. This study led to a 4-year comprehensive fire project, which was intended to address some of the shortcomings of previous studies. The goal was twofold: (1) confirm the pilot study’s findings, and (2) elucidate why earlier fire/oak research had produced such different results. The fire project addressed some of the shortcomings of previous studies. For instance, responses of regeneration of major hardwood species were compared among varying fire severities within differing seasons-of-burn (Brose and others 1999a, Brose and Van Lear 1998). The spatial relationship between fuel loading and its proximity to a residual tree and subsequent fire damage were studied (Brose and Van Lear 1999). Also, a fire – silvicultural technique was developed (Brose and others 1999b). Like previous fire studies, this one relied heavily on plots to inventory hardwood regeneration and focused on what sprouted after the fires.

However, the study did not use plot-based inventory methods exclusively. Data also were collected on the fate of individual stems of the major hardwood species groups. The purpose of this paper is to present the findings gleaned from using the individual-stem approach to study fire effects in mixed-oak forests.

METHODS
Site Description
The study took place from 1994 to 1998 in three central Virginia mixed-oak stands. The stands were similar to each other. All were situated on the top and upper side slopes of gently rolling hills at elevations of 500-600 feet above sea level. Soil series for all three stands was a Cecil sandy loam with a white oak site index of 75 feet (base age 50). The stands originated in the late 1890s, were even-aged, and had been partially harvested about 1990, reducing basal area from 120 to 60 ft² per ac. The resultant shelterwood had about 50 percent canopy closure. The most abundant canopy species were the upland oaks (black oak (Quercus velutina), chestnut oak (Q. prinus), northern red oak (Q. rubra), scarlet oak (Q. coccinea), and white oak (Q. alba)). American beech (Fagus grandifolia), black gum (Nyssa sylvatica), flowering dogwood (Cornus florida), mockernut hickory (Carya tomentosa), pignut hickory (C. glabra), red maple (Acer rubrum), and yellow-poplar (Liriodendron tulipifera) also were present, especially in the midstory. The heavy partial cut resulted in abundant advance regeneration (> 20,000 stems per ac) with all canopy species represented though yellow-poplar was the most abundant.
species. Hickory and oak regeneration height averaged less than 2 feet while red maple and yellow-poplar reproduction averaged more than 4 feet.

**Study Design and Implementation**

The basic design and implementation of the study are thoroughly described elsewhere (Brose and Van Lear 1998, Brose and Van Lear 1999, Brose and others 1999a), but are reviewed briefly here. The stands ranged from 15 to 50 acres; each was divided into four treatments (spring, summer, and winter burns, and an unburned control). In 1994, prior to the prescribed fires, fifteen 8-foot radius regeneration inventory plots were established systematically in each treatment to ensure uniform coverage. A linear transect to inventory fuels (Brown 1974) originated from each plot center and extended out 50 feet. Each plot transect was photographed before the fires. Along each fuels transect, three to five advance regeneration stems, visually judged to represent the range in height of surrounding reproduction, were tagged for long-term study. Species, root collar diameter (RCD), and root collar location (RCL) were recorded for each tagged stem. Root collar is defined as the transition point between stem and root and is identifiable by a ring of callous tissue and dormant buds. A total of 150 stems per treatment were measured, for a total of 600 stems (450 in burn treatments, 150 in controls).

Virginia Department of Game and Inland Fisheries personnel conducted the prescribed burns in February (winter), April (spring), and August (summer) 1995. Fire behavior was typical for the seasons: spring fires burned more intensely than summer and winter fires. Plots, transects, and tagged stems were re-inventoried for 3 years following the fires.

**Statistical Analysis**

In previous research (Brose and others 1999a, Brose and Van Lear 1998), fire severity (a continuous variable) was divided into discrete classes. This was accomplished by comparing the preburn photos to the appropriate plot immediately after the fire to visually assess fire effects. This evaluation subsequently was coupled with the initial postburn fuels inventory, leading to four severity classes (low, medium-low, medium-high, and high) within each season-of-burn (Brose and Van Lear 1998). The severity classes were defined as follows:

1. low - consumed only the most recently fallen leaf litter and 1-hour fuels, top-killed less than 75 percent of small reproduction (stems less than 4.5 feet tall) and small saplings [more than 4.5 feet tall but less than 2 in. in diameter at breast height (d.b.h.)]
2. medium-low - removed all leaf litter, 1-hour, and 10-hour fuels, top-killed more than 75 percent of small reproduction and small saplings but killed few, if any, stems greater than 2 in. in d.b.h.
3. medium-high – same as medium-low except stems 2-5 in. in d.b.h. were frequently top-killed
4. high – same as medium-high plus burned down into the duff layer, noticeably reduced 100-hour fuels, and top-killed stems greater than 5 in. in d.b.h.

The 12 combinations of fire severity and season-of-burn could be reduced to three groups of distinct impact (table 1). Minor impact indicated that only one species group was significantly reduced in density (number of stems per acre) and this response was found in the low-, medium-low and medium-high severity winter burns and the low-severity spring burn. Moderate impact indicated that densities of two species groups were reduced and this effect was noted in the high severity winter burn, medium-low severity spring burn, and the low and medium-low severity summer burn. Major impact indicated that densities of more than two species groups decreased in response to the prescribed fires and this result occurred in the medium-high and high severity spring and summer burns.

The tagged stems were sorted into four categories based on RCL: in litter, at litter/duff interface, in duff, and at or below the duff/soil interface. Four RCD classes (<0.25 in. diameter, 0.25-0.50 in. diameter, 0.51-0.75 in. diameter, and >0.75 in. diameter) were defined based on an approximate minimum number of 20-tagged stems per RCD class. This created a 4x4 RCD/RCL grouping table for each impact level.

The null hypothesis was that the stem mortality rate (the proportion of stems failing to sprout after fire) would not differ by RCD/RCL grouping. To test this hypothesis, Chi-square analysis (Ott 1993) was used on each impact level. The mortality rate in each impact level was calculated by dividing the number of dead stems by the total number of stems. The number of stems in each cell of the RCD/RCL grouping table was then multiplied by the mortality rate to obtain the expected number of dead stems per cell. The number of tagged stems failing to sprout in each RCD/RCL grouping was the observed value.

Also tested by chi-square analysis was species distribution of all tagged stems by RCD/RCL grouping. For this test, the null hypothesis was that there were no differences among species by RCD/RCL grouping. The expected value for each species was its proportional contribution to the entire sample size. For both tests, alpha was set at 0.05 to detect significant differences between expected and observed values.

**Table 1—Impact of fire severity and season-of-burn interaction on mortality of hardwood regeneration**

<table>
<thead>
<tr>
<th>Fire severity classification</th>
<th>Spring</th>
<th>Summer</th>
<th>Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>Minor</td>
<td>Moderate</td>
<td>Minor</td>
</tr>
<tr>
<td>Medium-low</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Minor</td>
</tr>
<tr>
<td>Medium-high</td>
<td>Major</td>
<td>Major</td>
<td>Minor</td>
</tr>
<tr>
<td>High</td>
<td>Major</td>
<td>Major</td>
<td>Moderate</td>
</tr>
</tbody>
</table>

* Minor, moderate, and major signify that one, two, and more than two species groups were reduced in density, respectfully.
RESULTS
The 450 tagged stems in the burn treatments were distributed by species as follows: 228 oak, 55 hickory (combined with oak for analysis purposes), 80 red maple, and 87 yellow-poplar. All species were found in all RCD/RCL groupings, but definite species-specific trends were detected (table 2).

Yellow-poplar dominated the smallest/shallowest RCD/RCL classes, while oak and hickory comprised the vast majority of the stems in the largest/deepest RCD/RCL classes, and red maple was predominated in the middle groupings.

Of the 450 tagged stems in the burn treatments, 37 were not top-killed by the fires and were dropped from the analysis. The remaining 413 were distributed among the three impact levels as follows: minor–121, moderate–135, and major–157. Within each impact level, the tagged stems were fairly evenly distributed among the 16 RCD/RCL groupings with about 5 to 15 stems per each combination. Of these, 183 failed to sprout by the end of the study and were distributed among the three impact levels as follows: minor–34, moderate–62, and major–87 (table 3).

Chi-square analysis rejected the null hypothesis, dead stems were not evenly distributed in any three impact categories (table 3). The distribution of the 183 dead stems by RCD/RCL class was skewed toward the smallest/shallowest classes, regardless of impact level. At minor impact, 34 of the 121 (28.1 percent) tagged stems never sprouted and two-thirds of these dead stems were found in the two smallest RCD/RCL classes (<0.25/in. litter and <0.25/in. litter-duff). However, neither of these had 100 percent mortality of all stems.

Table 2—Distribution of 450 hardwood stems in the burn treatments by RCD/RCL grouping

<table>
<thead>
<tr>
<th>Root collar location</th>
<th>Root collar diameter</th>
<th>&lt;0.25</th>
<th>0.25–0.50</th>
<th>0.51–0.75</th>
<th>&gt;0.75</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter</td>
<td></td>
<td>11, 8, 28</td>
<td>9, 8, 21</td>
<td>10, 3, 13</td>
<td>7, 6, 8</td>
</tr>
<tr>
<td>Litter/duff</td>
<td></td>
<td>35, 7, 6</td>
<td>16, 10, 6</td>
<td>12, 5, 0</td>
<td>12, 4, 1</td>
</tr>
<tr>
<td>Duff</td>
<td></td>
<td>32, 5, 2</td>
<td>22, 8, 0</td>
<td>17, 7, 1</td>
<td>14, 2, 0</td>
</tr>
<tr>
<td>Duff/soil</td>
<td></td>
<td>23, 3, 1</td>
<td>26, 1, 1</td>
<td>24, 2, 0</td>
<td>13, 1, 0</td>
</tr>
</tbody>
</table>

Chi-square: 181.65, Critical Value: 34.76 (alpha = 0.05, df = 47).

* Each three-number sequence in each column represents, from left, numbers of hickory/mixed oak, red maple, and yellow-poplar, respectively.

Table 3—Distribution of total and dead stems by RCD/RCL grouping within each impact level

<table>
<thead>
<tr>
<th>Root collar location</th>
<th>Root collar diameter</th>
<th>&lt;0.25 in.</th>
<th>0.25–0.50 in.</th>
<th>0.51–0.75 in.</th>
<th>&gt;0.75 in.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minor impact (121 total stems, 34 dead, 28.1%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter</td>
<td>14, 12, 86%</td>
<td>9, 4, 44%</td>
<td>8, 1, 13%</td>
<td>4, 0, 0%</td>
<td></td>
</tr>
<tr>
<td>Litter/duff</td>
<td>15, 11, 73%</td>
<td>7, 3, 43%</td>
<td>5, 0, 0%</td>
<td>3, 0, 0%</td>
<td></td>
</tr>
<tr>
<td>Duff</td>
<td>9, 3, 33%</td>
<td>8, 0, 0%</td>
<td>7, 0, 0%</td>
<td>5, 0, 0%</td>
<td></td>
</tr>
<tr>
<td>Duff/soil</td>
<td>8, 0, 0%</td>
<td>10, 0, 0%</td>
<td>5, 0, 0%</td>
<td>4, 0, 0%</td>
<td></td>
</tr>
</tbody>
</table>

Chi-square: 46.23, critical value: 7.26 (alpha = 0.05, df = 15).

| Moderate impact (135 total stems, 62 dead, 45.9%) | | | | | |
| Litter              | 17, 15, 88%         | 11, 7, 64% | 6, 4, 67%     | 6, 2, 33%     |
| Litter/duff         | 15, 13, 87%         | 8, 5, 63%  | 3, 1, 33%     | 4, 0, 0%      |
| Duff                | 13, 9, 69%          | 10, 3, 30% | 7, 0, 0%      | 4, 0, 0%      |
| Duff/soil           | 8, 2, 25%           | 8, 1, 13%  | 9, 0, 0%      | 6, 0, 0%      |

Chi-square: 32.74, critical value: 7.26 (alpha = 0.05, df = 15).

| Major impact (157 total stems, 87 dead, 55.4%) | | | | | |
| Litter              | 16, 13, 81%         | 14, 13, 93%| 12, 5, 42%    | 5, 2, 40%     |
| Litter/duff         | 18, 16, 89%         | 11, 8, 73%| 9, 5, 56%     | 7, 1, 14%     |
| Duff                | 14, 11, 79%         | 7, 5, 71% | 5, 2, 40%     | 5, 0, 0%      |
| Duff/soil           | 8, 4, 50%           | 10, 2, 20%| 12, 0, 0%     | 4, 0, 0%      |

Chi-square: 26.72, critical value: 7.26 (alpha = 0.05, df = 15).

* The first number in each column is the total number of stems before the prescribed fires, the second number is the number of dead stems after the prescribed fires, and the third is the proportion of stems killed.
Four other classes, occupying the upper-middle range of RCD/RCL classes, also contained some dead stems, but not to the same extent as the two smallest classes. The lower-middle and largest/deepest RCD/RCL classes contained no dead stems. Also, the dead stems were primarily yellow-poplar. Only a few red maple, hickory, and oak seedlings failed to sprout.

In the moderate-impact level, 62 of the 135 (45.9 percent) tagged stems never sprouted (table 3). Again, these were concentrated in the two smallest/shallowest RCD/RCL cells (<0.25/litter and <0.25/litter-duff) which had nearly 100 percent mortality, and the three adjacent intermediate RCD/RCL classes, which had mortality greater than 50 percent. As RCD and RCL increased, mortality decreased and no mortality occurred to stems in the largest/deepest RCD/RCL classes. Yellow-poplar and red maple constituted the majority of dead stems, but oak and hickory also were killed, especially in the smallest/shallowest RCD/RCL classes.

In the major impact group, 87 of the 157 (55.4 percent) tagged stems never sprouted (table 3). Only the largest/deepest RCD/RCL groups (0.51-0.75/duff-soil, >0.75/duff, and >0.75/duff-soil) had no mortality, while the smallest/shallowest groupings (<0.25/litter, <0.25/litter-duff, <0.25/duff, 0.25-0.50/litter, and 0.25-0.50/litter-duff) had almost 100 percent mortality. The remaining eight groups were split between four having greater than 50 percent mortality and four with less than 50 percent mortality. Nearly all yellow-poplar died in this impact grouping as did approximately 50 percent of hickory, oak, and red maple.

**DISCUSSION**

Previous research has shown the importance of season-of-burn and fire severity as factors influencing the response of hardwood regeneration to fire (Brose and others 1999a, Brose and Van Lear 1998). This study adds root collar diameter and root collar location as significant explanatory factors. The stems with the shallowest and smallest roots sprouted in far fewer numbers after the fires than stems with deeper and larger roots (table 3). Species seemed inconsequential as hickory and oak seedlings with shallow and small roots were as susceptible to fires as comparable red maple and yellow-poplar. The reverse also was true as large, deep-rooted maples and poplars sprouted after the fires, as well as similar oaks and hickories.

Species differed in distribution among the RCD/RCL classes (table 2). While generally all species were found in all cells, yellow-poplar dominated the smallest/shallowest ones, while oak and hickory dominated the largest/deepest classes. Red maples occurred most often in the intermediate RCD/RCL cells. Consequently, there were differing species responses to the fires and this was a function of at least four factors: season-of-burn, fire severity, root collar diameter, and root collar location.

This study also provides insight into the disparate results among many of the early fire/hardwood studies. Root collar location and diameter of the regeneration usually were not determined and fire severity often was ignored or considered equal throughout the burn area. Without knowing these factors, predicting or understanding the outcome of a fire is virtually impossible. One can imagine a high-severity, growing-season fire annihilating a newly established cohort of oak seedlings arising from unburied acorns (shallow/small roots) while older, well-established red maple regeneration (somewhat deep/large roots) is able to sprout. A comparable fire in well-established oak reproduction (deep/large roots) and new red maple seedlings (shallow/small roots) would probably produce opposite results. Thus, fire studies that do not account for these important root characteristics could reach opposite conclusions about fire effects on oak and red maple regeneration.

The root collar diameter and location differences between oak/hickory and red maple/yellow-poplar (table 2) are a result of their silvics. Hickory nuts and acorns have hypogeal germination, i.e., cotyledons remain in the shell and serve as a belowground energy source for seedling development. Red maple and yellow-poplar seeds have epigeal germination, i.e., cotyledons emerge and rise above the shell to form the first photosynthetic leaves. This difference in germination strategy places hickory and oak seedlings' root collar, and the accompanying dormant buds, lower than that of red maple and yellow-poplar.

This basic difference in germination strategy is accentuated by wildlife. Hickory nuts and acorns are routinely buried an inch or more into the forest floor by birds and small mammals while seeds from red maple and yellow-poplar typically are not cached. Thus, a hickory or oak seedling generally will have a deeper root collar than a red maple or yellow-poplar seedling because of seed burial and hypogeal germination.

Another important silvical difference between hickory/oak and red maple/yellow-poplar reproduction is the developmental rate of the root system. Upon germinating, oaks and hickories send a strong radicle deep into the soil to establish a taproot and emphasize root development over stem growth (Kelty 1988, Kolb and others 1990). Red maple and yellow-poplar take the opposite approach; root development is sacrificed to promote rapid stem growth. Thus, hickory and oak regeneration usually are shorter than their competitors, but have larger root systems. It is these two silvical characteristics, hypogeal germination and emphasis on root development, and seed burial by wildlife that allows hickory and oak regeneration to be favored over reproduction of their competitors in a periodic fire regime.

An important management consideration evident from this study is the need to withhold fire, and possibly harvesting, too, when advanced reproduction is relatively small. Seedlings with root collars less than 0.25 in. diameter exhibit significantly greater mortality after a prescribed fire than reproduction with larger root collars. Treatment should be delayed a couple of years to allow newly established oak seedlings to grow large enough roots to survive a fire or other forest-floor disturbance.

**ACKNOWLEDGMENTS**

The authors acknowledge all the support provided by the Virginia Department of Game and Inland Fisheries, especially Patrick Keyser, without which this project would not have been possible. The authors also thank Gary Miller,
Steve Horsley, Thomas Schuler, and Susan Stout for their efforts in reviewing earlier drafts of this manuscript.

LITERATURE CITED


