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# Cone consumption by southeastern fox squirrels: a potential basis for clonal preferences in a loblolly and slash pine seed orchard

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## Abstract

Southeastern fox squirrels were observed feeding preferentially on seeds of certain clones of loblolly pine in a central Georgia seed orchard in the early 1990s and, similarly, on slash pine seed in an orchard in central Florida in the late 1990s. In each orchard, the degree of feeding preference and avoidance among selected clones was documented and quantified. We tested three hypotheses to explain this phenomenon: (1) seeds of preferred clones have greater nutritional quality or energy content; (2) cone armature differed between preferred and avoided clones; or (3) preferred clones have lower quantities of deterrent compounds present in cone tissue. Hypothesis 1 was tested using cones collected from three preferred and two avoided clones within a loblolly pine seed orchard. We found no consistent differences in total number of seeds per cone, viable seeds per cone, seed weight per cone, average weight per seed, energy content per seed, and energy content per cone between preferred and avoided cones. Hypotheses 2 and 3 were tested using cones collected from four preferred and four avoided clones within a slash pine seed orchard. We found a strong positive association between spine length and cone avoidance. Avoided cones had significantly higher concentrations of myrcene, α-phellandrene, β-phellandrene, β-caryophyllene, and α-humulene but lower concentrations of α-pinene. These physical and chemical cone defenses may increase handling time or reduce seed palatability and therefore act as significant deterrents to seed predation by fox squirrels when preferred feeding options are readily available, such as in a seed orchard.

*Keywords:* *Sciurus niger*; *Pinus taeda*; *Pinus elliotii*; Seed quality; Physical defense; Chemical defense; Terpenes; Sesquiterpenes

## 1. Introduction

Southeastern fox squirrels (*Sciurus niger*) are native to the pine and pine-hardwood forests of the Coastal Plain and Piedmont regions of the United States from Virginia to Mississippi (Loeb and Moncrief, 1993). Acorns of numerous oaks (*Quercus* sp.), pecans (*Carya illinoensis*) and other hickories are the main food resources of southeastern fox squirrels with fungi, fruits, insects, and staminate cones eaten as secondary foods (Moore, 1957; Ha, 1983; Weigl et al., 1989; Humphrey and Jodice, 1992). In addition, pine seeds may be a very important seasonal food resource, particularly during years of oak mast failure (Weigl et al., 1989; Kantola and Humphrey, 1990). While longleaf pine (*Pinus palustris*) is the most commonly

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utilized species, fox squirrels also forage on the seeds of loblolly (*Pinus taeda*) and slash pine (*Pinus elliotii*).

During late summer and early autumn, southeastern fox squirrels feed almost entirely on seeds within green cones of pines (Steele and Weigl, 1992). In longleaf pine, fox squirrels typically consume 20–30 cones per day during peak foraging activity in late August (Steele, 1988). Cone consumption occurs in the tree and cone cores are subsequently dropped to the ground, providing a direct record of food consumption (Steele and Weigl, 1992). Squirrels sample trees throughout their home ranges but usually restrict their feeding activity to a few preferred trees (Steele, 1988), thus maximizing their feeding efficiency (Smith, 1968; Elliot, 1974, 1988; Mollar, 1986). Steele and Weigl (1992) reported that fox squirrels in North Carolina select trees with cone crops having the greatest concentration of overall seed energy and often select "patches" (trees) of lower density but more profitable "prey" (cones).

During the early 1990s, fox squirrel consumption of loblolly pine cones was observed in the Briarpatch seed orchard in Putnam County, Georgia. Similarly, during the late 1990s, foresters from the Withlacoochee Forestry Center in Hernando County, Florida began to notice significant fox squirrel consumption of slash pine seeds in an orchard during late summer. In both cases, it was observed that the squirrels appeared to feed preferentially on certain clones that were randomly distributed throughout the orchard, while others were avoided.

To date, there are no studies that explain selective herbivory of pine seeds by fox squirrels in the southeast. Seed orchards are ideal for studying squirrel feeding preferences because they consist of cloned trees replicated over relatively large areas. Our objectives were to document loblolly and slash pine clonal seed preferences by fox squirrels and to provide an explanation for this behavior by examining differences in seed density and energy content, cone terpene composition and content, and cone armature among preferred and avoided cones. Two separate studies were undertaken, one in Putnam County, Georgia in 1993 and the other in Hernando County, Florida in 2001. The earlier study in a loblolly pine seed orchard explored an energetics/nutrition explanation for selective feeding. Because the energetic factors did not adequately explain cone selection by fox squirrels, we initiated another study in a slash pine orchard in Florida and focused on physical and chemical cone defenses as the significant factors influencing squirrel preference. Herein, we present data and observations from both studies to synthesize what we know regarding fox squirrel selection of pine cones in seed orchards.

## 2. Methods

### 2.1. 1993 Georgia study

### 2.1.1. Study site

The study site was in the Briarpatch seed orchard, a commercial seed orchard operated by Mead Corporation located in the lower Piedmont Plateau physiographic region in Putnam County, Georgia. Seed orchards consist of trees cloned from parent trees by grafting cuttings onto seedlings planted for root stock. Clones are replicated throughout orchards to insure crossing occurs between clones, and a number of clones are included in each orchard for a variety of reasons (van Buijtenen et al., 1971). The study was conducted in a first generation orchard cloned from superior trees growing in coastal areas of the southeast. The "coastal" portion of the orchard contained >700 trees of various clones, which were replicated throughout the area. Squirrels had been observed feeding in the orchard since the 1970s (Debarr, US Forest Service, Southern Research Station, Athens, GA, personal communication).

### 2.1.2. Documenting clonal preference

We surveyed tree rows 1–44 of the orchard approximately every 2 weeks from 8 September to 28 October 1993. Each tree had a tag indicating clone number. Green cones fed upon by fox squirrels were generally completely stripped of scales, leaving only the inner fibrous cores, which could be found on the ground near the base of the trees. During each visit we examined the base of each tree for fresh cone cores and counted the number of damaged cones which were removed to avoid re-counting them in subsequent visits.

### 2.1.3. Cone collection and analysis

In mid-October 1993 we randomly selected six trees from each of two clones heavily used by squirrels and six trees from each of three clones that had very little predation. Ten cones collected from each tree with a hydraulic lift truck were dried in a drying oven so seeds could be extracted, counted, and X-rayed for viability (Debarr, 1970, 1978). A random sample of viable seeds from each clone were dried, weighed, and ground in a Wiley mill; energy content was determined by bomb calorimetry (Haufler and Servello, 1996a,b).

#### 2.1.4. Statistical analysis

Preference, avoidance, or no selection of clones was determined by the method of Neu et al. (1974), using a Bonferroni confidence interval of 0.003 ($\alpha = 0.05/15$). We used PROC GLM (SAS, 1989) to conduct nested one-way analyses of variance followed by LSD tests ($\alpha = 0.05$) to test for differences in cone and seed characteristics among clones.

### 2.2. 2001 Florida study

#### 2.2.1. Study site

The study site was located in Hernando County near Brooksville, Florida at the Withlacoochee Forestry Center, a seed orchard (primarily slash pine) operated by the Florida Department of Agriculture and Consumer Services, Division of Forestry. We selected a study block of 95 slash pine clones planted in 1964. The block initially consisted of 39 lines × 85 rows of trees (3315 total trees), but subsequent natural mortality, thinning and harvesting have reduced the number of remaining trees to 1917. The site was burned in 1997 and was mowed annually so that only short grass and scattered weeds occupied the site at the time of our study, which facilitated documentation of cone predation.

#### 2.2.2. Documenting clonal preference

We surveyed each tree in rows 22–39 (993 trees) of the orchard where most fox squirrel feeding was observed and which was adjacent to mature live oak habitat, thought to be an important refuge for the squirrels feeding within the orchard. For each tree, we noted the clone number and the number of damaged cones beneath the crown within a 1 m radius of the base on 22 August 2001. Of the 95 clones present in the orchard, some were represented by only one tree, while others had as many as 70 trees. From this survey we calculated the percentage of trees of each clone with apparent cone feeding and the average number of cones fed upon per tree within each clone. Clones were ranked from most to least preferred based on the above parameters. We selected the four most preferred and the four least preferred clones for further study. Squirrels avoided many clones completely or almost so, but we selected clones for which at least 10 representative ramets were surveyed to be certain we had an adequate sample size to evaluate feeding preference.

#### 2.2.3. Cone collection and analysis

On 23 August 2001, we collected six cones from each of three trees of eight selected clones using a hydraulic lift truck (18 cones per clone). Within each tree, three cones were selected from the lower crown and three from the upper crown when practical. Cones from each tree were sealed in polyethylene bags, kept on ice, and returned to the laboratory, where they were vacuum-sealed in Mylar bags and stored at minus 80 °C until analysis.

We measured spine length of five spines on each of the cones collected from two of the three trees sampled within each clone (12 cones per clone). The five spines were sampled from throughout the cone to obtain an average length per cone. We measured each spine from the terminal point of the spine to the base, where it articulated with the umbo of the cone scale, using a dissecting microscope and micrometer.

Cones were defrosted and 5–10 scales (with seeds) removed from the center of each were weighed and ground into small (1–5 mm) particles in a laboratory blender (Waring Products Division, Dynamics Corporation of America, New Hartford, Conn.). Ground-up scales from each tree (six cones) were homogenized into a single sample resulting in three replicates (trees) of each clone for chemical analysis. The inner fibrous cone core was not analyzed for terpenes since squirrels do not feed on that portion of the cone. A 1 g sub-sample was obtained from each ground-cone sample (representing six cones), placed in a 4 ml extraction vial and dissolved in 3 ml of pentane for 15 min. After gently compressing the solid cone tissue to the bottom of the extraction vial using a glass rod, 1 ml of supernatent was removed, filtered through plastic sterile filtered tips (Fisher Brand, Redi-Tip, Pittsburgh, PA) to remove particulate matter (Asaro et al., 2001) and placed into a 4 ml vial. We added 20 μl of a heptyl acetate solution (10,000 ng/μl of pentane) to each 1 ml sample extract as an internal standard in order to facilitate relative quantification of compounds among samples. Each 1 ml sample extract was subsequently diluted to 4 ml prior to analysis, resulting in 50 ng of internal standard per microliter of sample.

One microliter of each sample was injected into a Hewlett-Packard G1800C gas chromatograph–mass spectrometer with electron ionization detection and helium as the carrier gas. Following a splitless injection, the fused-silica column (HP-5MS, 30 mm × 0.25 mm, Hewlett-Packard, Palo Alto, CA), coated with cross-linked methyl polysiloxane (d.f. = 0.25 μm), was programmed to hold at 40 °C for 1 min, than rise at a rate of 8 °C per minute to hold at 100 °C for 1 min. Thereafter, the column temperature was ramped 15 °C per minute to 220 °C and held isothermal for 1 min, then ramped at the same rate to 240 °C and held isothermal for 1 min. Peaks for each terpene were identified by comparing sample mass spectra, recorded at 70 eV and intervals of 1.0 s, to the mass spectra and retention times of analytical standards. Standardization of peak areas between GC–MS runs was achieved by dividing the peak area of each compound by the associated peak area of the internal standard.

### 2.2.4. *Statistical analysis*

Preferred and avoided clones were distinguished based on differences in the degree of usage using $\chi^2$ analysis (SigmaStat 2.0, Jandel Corporation, 1995). Linear regression of the percentage of trees used per clone on spine (armature) length was performed with Sigmaplot 4.0 (SPSS, 1997). Peak areas for each compound within the preferred and avoided clones were averaged and compared with a *t*-test or Mann–Whitney rank sum test if ANOVA assumptions were not met (SigmaStat 2.0). A non-parametric test is preferred over parametric statistics on transformed data because no single transformation function produced normality and equal variance in all cases. In addition, non-parametric statistics are preferred when distributional assumptions cannot be reliably verified with relatively small data sets (Smith, 1995).

## 3. Results

### 3.1. *1993 Georgia study*

### 3.1.1. *Clonal preference*

Of the 15 clones examined, two (V15-70 and Y15-80) received heavy use, several received moderate use (CC15-91, F10-21, I10-28, P15-01) and the remainder received little use (Table 1). Based on percent use/availability data (Table 1), CC15-91, V15-70 and

Table 1
Number and percent of loblolly pine trees in each clone that had 0, low (1–5), medium (6–0), high (11–50) and very high (>50) complete cones eaten; percent of total trees ($n = 444$) represented by each clone (percent availability); and the percent of trees from each clone that received at least some use (percent usage) out of 105 total trees receiving some use (>1 complete or partial cone eaten)

| Clone | Total trees | Number of Trees (%) | | | | | Availability (%) | Usage (%) |
|---|---|---|---|---|---|---|---|---|
| | | 0 | Low (1–5) | Medium (6–10) | High (11–50) | Very high (>50) | | |
| BB15-90 | 12 | 10 (83.3) | 2 (16.7) | 0 | 0 | 0 | 2.7 | 1.9 |
| CC15-91 | 31 | 19 (61.2) | 8 (25.8) | 3 (9.7) | 1 (3.2) | 0 | 7.0 | 11.4 |
| DD15-96 | 7 | 6 (85.7) | 1 (14.3) | 0 | 0 | 0 | 1.6 | 0.9 |
| E10-27 | 48 | 41 (85.4) | 7 (14.6) | 0 | 0 | 0 | 10.8 | 6.7 |
| EE15-97 | 4 | 4 (100.0) | 0 (0.0) | 0 | 0 | 0 | 0.9 | 0.0 |
| F10-21 | 40 | 32 (80.0) | 6 (15.0) | 2 (5.0) | 0 | 0 | 9.0 | 7.6 |
| G10-41 | 36 | 31 (86.1) | 5 (13.9) | 0 | 0 | 0 | 8.1 | 4.8 |
| I10-28 | 34 | 28 (82.3) | 5 (14.7) | 1 (2.9) | 0 | 0 | 7.7 | 5.7 |
| J15-22 | 15 | 13 (86.7) | 2 (13.3) | 0 | 0 | 0 | 3.4 | 1.9 |
| M15-20 | 52 | 48 (92.3) | 4 (7.7) | 0 | 0 | 0 | 11.7 | 3.8 |
| N15-19 | 9 | 5 (55.5) | 3 (33.3) | 1 (11.1) | 0 | 0 | 2.0 | 3.8 |
| P15-01 | 56 | 48 (85.7) | 8 (14.3) | 0 | 0 | 0 | 12.6 | 7.6 |
| S15-66 | 22 | 18 (81.8) | 2 (9.1) | 1 (4.5) | 1 (4.5) | 0 | 5.0 | 3.8 |
| V15-70 | 48 | 29 (60.4) | 11 (22.9) | 1 (2.1) | 6 (12.5) | 1 (2.1) | 10.8 | 18.1 |
| Y15-80 | 30 | 7 (23.3) | 10 (33.3) | 2 (6.7) | 8 (26.7) | 3 (10.0) | 6.8 | 21.9 |

Table 2

Mean (±S.D.) number of total and viable seeds per cone, mean weight of all viable seeds per cone, average weight of viable seeds, average seed energy content, and total energy content of seeds from loblolly pine

| Clone | Total number of seeds | Viable seeds | Total seed weight/cone (mg) | Average weight/seed (mg) | Energy content (cal/g) | Energy content/cone (cal) |
|---|---|---|---|---|---|---|
| E10-27 (A) | 97.7 (25.2) a | 13.3 (10.2) a | 424.3 (300.8) a | 32.6 (3.2) a | 5341 (131.4) a | 2266 |
| G10-41 (A) | 124.6 (24.0) c | 78.5 (23.8) b | 2766.7 (897.4) b | 35.1 (2.6) b | 5180 (72.6) b | 14331 |
| M15-20 (A) | 118.5 (31.8) c | 64.6 (29.0) c | 1860.7 (921.3) c | 28.1 (2.7) c | 5209 (83.6) b | 9692 |
| V15-70 (P) | 106.1 (36.4) ab | 52.8 (34.4) d | 1992.8 (1298.4) c | 37.8 (3.9) d | 5086 (73.2) c | 10136 |
| Y15-80 (P) | 115.8 (28.2) bc | 69.6 (25.1) bc | 2055.7 (755.4) c | 29.6 (2.3) c | 5203 (105.0) b | 10696 |

Means within a column followed by the same letter (a–d) do not differ significantly (LSD, $P \leq 0.05$). Strain numbers followed by an "A" denote avoided clones and those followed by a "P" denote preferred clones. Energy content per cone was calculated by multiplying total seed weight/cone (g) by energy content (cal/g).

Y15-8 were significantly preferred (i.e. percent usage was greater than percent availability), BB15-90, DD15-96, EE15-97, F10-21, I10-28, J15-22, N15-19, and S15-66 were neither preferred or avoided (i.e. usage and availability were approximately equal), and E10-27, G10-41, M15-20, and P15-01 were significantly avoided (percent usage was less than percent availability) ($\chi^2 = 59.37$, d.f. $= 14$, $P < 0.001$; Bonferroni confidence interval, $P < 0.003$).

### 3.1.2. Seed/cone characteristics in relation to clonal preference

No consistent relationship was found between clone selection and seed or cone characteristics (Table 2). For example, E10-27, one of the avoided clones, had the lowest number of total seeds per cone, viable seeds per cone, and total weight of seeds per cone. Although average seed weight was relatively high, it was significantly lower than average seed weight for G10-41

Table 3

Number and percent of slash pine trees in each clone that had 0, low (1–5), medium (6–10), high (11–50) and very high (>50) complete cones eaten; percent of total trees ($n = 326$) represented by each clone (percent availability); percent of trees that received at least some use (percent usage) out of 66 total trees receiving some use (>1 complete or partial cone eaten); and the average (±S.D.) spine length per cone for each of two trees per clone

| Clone | Total trees | Number of trees (%) | | | | | Availability (%) | Usage (%) | Average spine length (mm) |
|---|---|---|---|---|---|---|---|---|---|
| | | 0 | Low (1–5) | Medium (6–10) | High (11–50) | Very high (>50) | | | |
| 7 | 68 | 42 (61.8) | 21 (30.1) | 3 (4.4) | 2 (2.9) | 0 | 20.8 | 39.4 | 1.14 (0.16)<br>1.13 (0.20) |
| 26 | 11 | 4 (36.4) | 1 (9.1) | 2 (18.2) | 3 (27.3) | 1 (9.1) | 3.4 | 10.6 | 0.74 (0.16)<br>0.83 (0.17) |
| 304 | 36 | 22 (61.1) | 9 (25.0) | 4 (11.1) | 0 | 1 (2.8) | 11.0 | 21.2 | 1.19 (0.20)<br>1.33 (0.22) |
| 403 | 53 | 37 (69.8) | 12 (22.6) | 3 (5.7) | 1 (1.9) | 0 | 16.2 | 24.2 | 0.84 (0.15)<br>0.94 (0.16) |
| 11 | 44 | 42 (95.4.) | 2 (4.8) | 0 | 0 | 0 | 13.5 | 3.0 | 1.85 (0.25)<br>1.87 (0.31) |
| 201 | 34 | 34 (100.0) | 0 | 0 | 0 | 0 | 10.4 | 0 | 1.71 (0.34)<br>1.85 (0.39) |
| 202 | 22 | 21 (95.4) | 1 (4.8) | 0 | 0 | 0 | 6.7 | 1.5 | 1.56 (0.32)<br>1.77 (0.44) |
| 406 | 58 | 58 (100.0) | 0 | 0 | 0 | 0 | 17.8 | 0 | 1.47 (0.17)<br>1.78 (0.30) |

and V15-70. Energy content per gram was high for E10-27 seeds but overall energy content per cone was very low (Table 2). G10-41, another avoided clone, had the highest total number of seeds per cone, the highest number of viable seeds per cone, the highest total seed weight per cone, the second highest average weight per seed, and the highest energy content per cone. M15-20, the third avoided clone, was intermediate in all characteristics except for average seed weight. This clone had the smallest seeds of any clone, but they were not significantly smaller than one of the preferred clones (Y15-80).

V15-70, a preferred clone, ranked low to intermediate for all of its seed and cone characteristics except for average seed weight, which was the highest of any clone. Seed and cone characteristics for Y15-80, the most preferred clone, were intermediate to high for all characteristics except average seed weight, which was

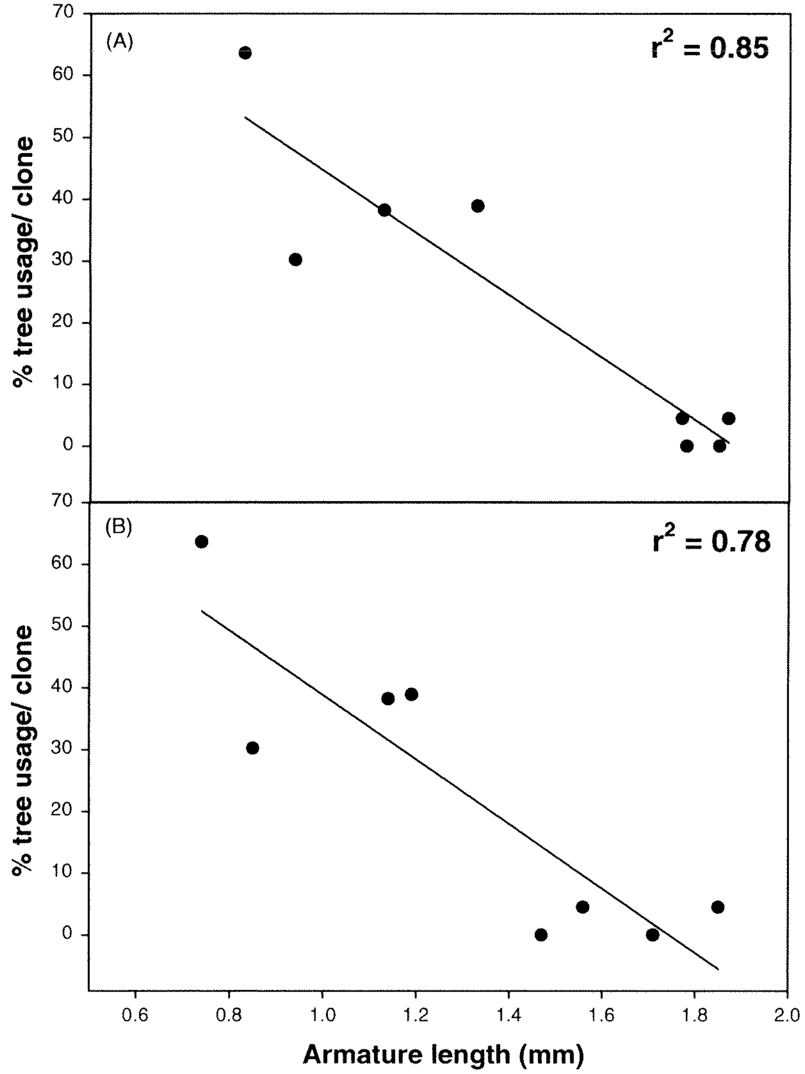

Fig. 1. Relationship between percentage of slash pine trees used per clone and the average armature (spine) length of cones sampled from two (A and B) of three trees of each clone ($n = 12$ cones/clone).

second lowest. Thus, no one characteristic explained preference or avoidance of loblolly pine clones by fox squirrels.

### *3.2. 2001 Florida study*

#### *3.2.1. Clonal preference*

Fox squirrels showed a strong feeding preference for clones 7, 26, 304, and 403 based on the number of cones eaten per tree and percent use/availability (i.e. percent usage was significantly greater than percent availability; Table 3). Similarly, clones 11, 201, 202, and 406 were strongly avoided based on the same criteria (percent usage was less than percent availability) ($\chi^2 = 70.9$, d.f. $= 7$, $P < 0.001$) (Table 3). Therefore, of the eight clones selected for study, four were clearly preferred by squirrels and four almost completely avoided.

#### *3.2.2. Physical and chemical cone defenses in relation to clonal preference*

A strong negative association was found between percentage of trees used per clone and spine length (tree 1: $r^2 = 0.85$; $F = 34.69$; d.f. $= 1, 6$; $P = 0.001$; tree 2: $r^2 = 0.78$; $F = 20.91$; d.f. $= 1, 6$; $P = 0.004$) (Fig. 1A and B). Spine length for the four avoided clones ranged from 1.5 to 1.9 mm while those from the preferred clones ranged from 0.7 to 1.3 mm (Table 3). Clone 26 had the shortest spines and the largest percent usage to availability ratio as well as the largest percentage of trees in the high to very high feeding category (Table 3). Furthermore, longer spines were sharper, perhaps making the cones more difficult for the squirrels to handle compared to the shorter spines, which were generally more blunt (Fig. 2). However, these qualities were very difficult to measure.

Considerable differences in chemical composition of cones were apparent between preferred and avoided slash pine clones. In total, 27 compounds, primarily terpenes and sesquiterpenes, were identified collectively from all samples. Of these, relative quantities of six compounds differed significantly between preferred and avoided clones (Figs. 3–5). More than half of the 27 compounds were present in trace amounts (<1% of the peak area of the internal standard) (Figs. 3–5). Avoided clones had significantly higher concentrations of myrcene ($T = 102$, d.f. $= 22$, $P = 0.006$); α-phellandrene ($T = 102$, d.f. $= 22$, $P = 0.006$); β-phellandrene ($T = 111$, d.f. $= 22$, $P = 0.026$); β-caryophyllene ($T = 83$, d.f. $= 22$, $P < 0.001$); and α-humulene ($T = 81$, d.f. $= 22$, $P < 0.001$) (Figs. 3 and 4). Only α-pinene was found in significantly greater quantity from the preferred clones ($t = 2.69$, d.f. $= 22$, $P = 0.013$).

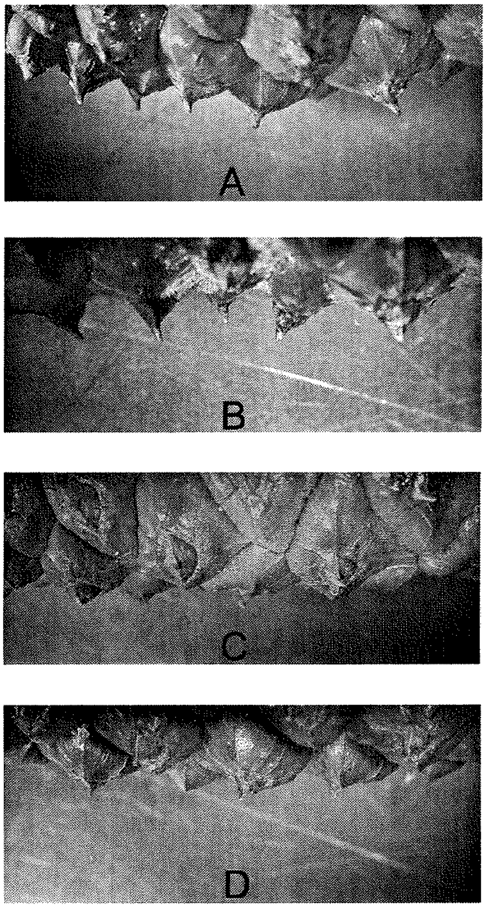

Fig. 2. A visual comparison of the armature (spine length and sharpness) of two avoided (A, B) and two preferred (C, D) slash pine clones.

## 4. Discussion

Explanations for selective herbivory by squirrels have been proposed based on research on Abert squirrels (*Sciurus aberti* Woodh.) in ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) habitat. Abert squirrels have an obligate relationship with ponderosa

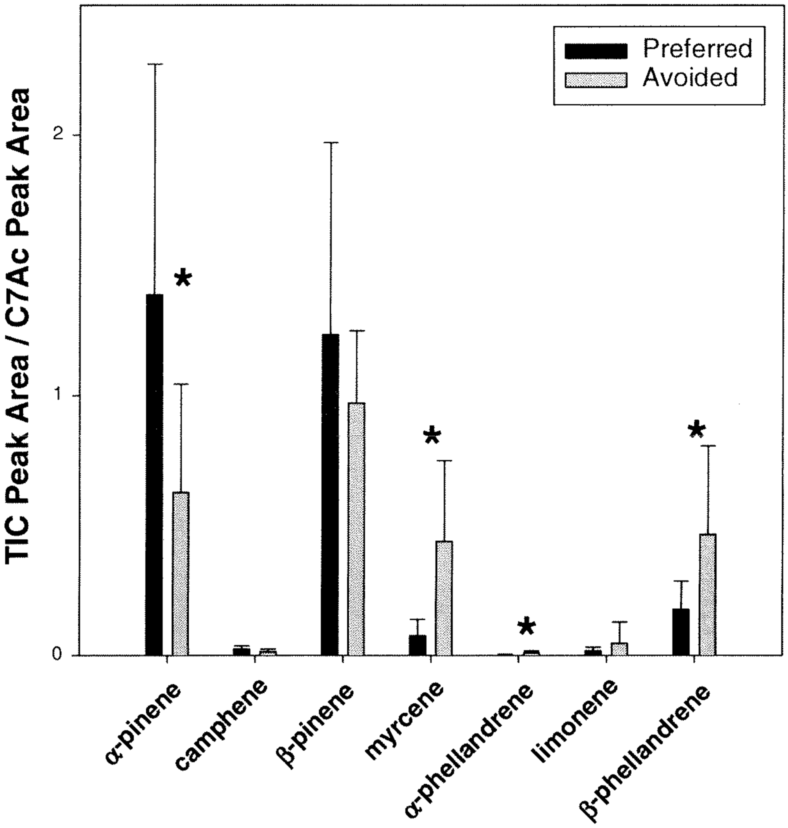

Fig. 3. A comparison of average (±S.D.), standardized peak areas for seven terpenes found in extracts of preferred and avoided slash pine cones. Pairs of bars denoted by an asterisks are significantly different (*t*-test or Mann–Whitney rank sum test, $\alpha = 0.05$).

pine, feeding on the seeds, inner bark (phelloderm, phloem, and cambium), terminal buds, fruiting bodies of fungi that grow in ponderosa pine duff, and mistletoe berries (Pederson and Welch, 1985). During winter, Abert squirrels feed almost exclusively on the cortical tissue from the inner bark of small twigs of certain ponderosa pine trees (Farentinos et al., 1981). Within a specific area, pronounced selection of particular feed trees by Abert squirrels and avoidance of others has been well documented (Coughlin, 1938; Pederson et al., 1976; Hall, 1981).

Farentinos et al. (1981) found that twigs collected from trees used by *S. aberti* as sources of cortical tissue for food contained smaller amounts of monoterpenes than twigs from similar trees not used by the squirrels. Of 18 monoterpenes isolated from twig samples, α-pinene was the best single predictor of food source trees. In experiments with captive squirrels, consumption of a preferred food was inversely correlated with the concentration of α-pinene added to the food (Farentinos et al., 1981), in contrast to our results (Fig. 3). However, Pederson and Welch (1985) found no significant difference in the level of monoterpenes in the inner or outer bark of feed and non-feed trees. In addition, proteins and other nutrients from the inner bark did not differ significantly between feed and non-feed trees. The use of certain trees over others was attributed to the ease of peeling and separating outer from inner bark tissue. Zhang and States (1991) reported that squirrel recognition of non-feed trees was related to higher total terpene concentration, a greater diversity of terpenes, and the presence and concentration of myrcene, sabinene, and terpinolene. There was no correlation found in sugar and moisture content of the feed/non-feed pairs. A comparison of the composition of terpenes in resins of Arizona

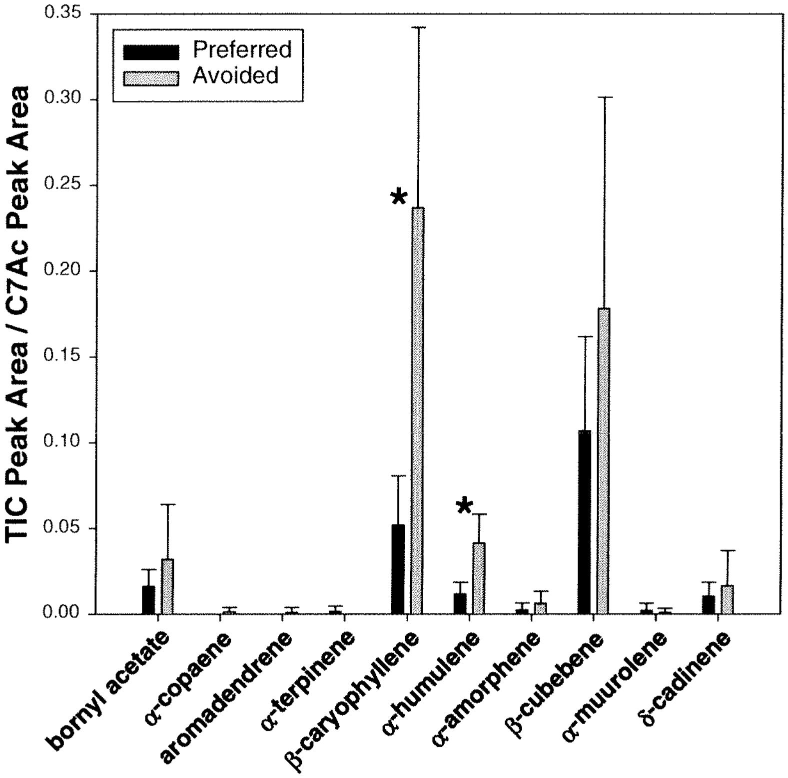

Fig. 4. A comparison of average (±S.D.), standardized peak areas for 10 compounds, mostly sesquiterpenes, found in extracts of preferred and avoided slash pine cones. Pairs of bars denoted by an asterisks are significantly different (*t*-test or Mann–Whitney rank sum test, $\alpha = 0.05$).

ponderosa pine with those of feed trees in Colorado indicated that Abert squirrels may have adapted to resins of feed trees characteristic of their respective regions (Zhang and States, 1991).

In our study, seed characteristics of preferred and avoided cones did not differ in any consistent manner. In contrast, *Tamiasciurus* sp. in British Columbia selected feed trees based on the number of seeds per cone (Smith, 1970), and fox squirrels in North Carolina selected trees with the greatest concentration of overall energy (Steele and Weigl, 1992). However, as Steele and Weigl (1992) point out, tree selection is probably based on multiple factors, and it is possible that we did not measure one of the important factors. For example, we did not estimate the number of cones per tree, which may be an important component of overall tree quality. Physical and chemical characteristics may have also been important (see later), and energetic considerations may have been mitigated by their impacts.

More heavily armed cones may require longer handling times and therefore may be avoided by fox squirrels in order to optimize foraging behavior. Although it is unlikely that heavy cone armature would prevent squirrels from breaking open the cones, even a slight delay in reaching the seeds might induce the squirrels to choose other, less heavily armed cones when given a choice. For example, handling time also appears to be an important determinant of tree selection by Abert's squirrels foraging on *P. ponderosa* twigs (Pederson and Welch, 1985). A seed orchard with many different clones presents an ideal environment for squirrels to be very choosy about their food selection.

Collectively, avoided slash pine cones had longer, sharper scale armature and two to five times the relative concentration of five terpenes or sesquiterpenes. These physical and chemical cone defenses may increase handling time or reduce seed palatability, resulting in significant reductions in seed predation

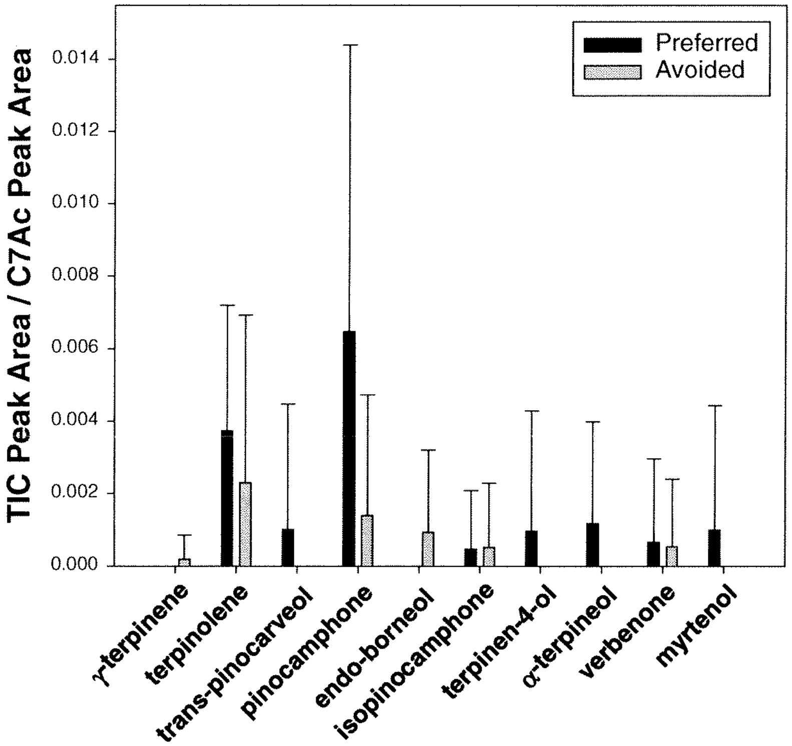

Fig. 5. A comparison of average (±S.D.), standardized peak areas for 10 compounds found in trace quantities in extracts of preferred and avoided slash pine cones. No significant differences were found (*t*-test or Mann–Whitney rank sum test, $\alpha = 0.05$).

by fox squirrels when preferred feeding options are readily available. Further experimentation is needed to determine which of these factors, if any, has the most important influence on squirrel cone selection. Although nutritional variation among cones (seed density, seed weight, energy content) may be a significant selection factor in a more natural setting, it does not seem to play a major role in cone selection within seed orchards. In areas where fox squirrel predation is significant, seed orchard managers might consider physical and chemical cone characteristics when selecting the best clones, provided they do not conflict significantly with other desirable traits such as growth rate, tree form, and wood properties.

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