Abundance and Frequency of the Asiatic Oak Weevil (Coleoptera: Curculionidae) and Defoliation on American, Chinese, and Hybrid Chestnut (Castanea)

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Abstract

The Asiatic oak weevil, Cyrtepistomus castaneus Roelofs (Coleoptera: Curculionidae), is a nonnative defoliator of trees in the Fagaceae family in the United States but has not been studied on Castanea species in the southern Appalachian Mountains. Planted trees of Castanea dentata (Marsh.) Borkh. (Fagales: Fagaceae), Castanea mollissima Blume (Fagales: Fagaceae), and four hybrid breeding generations were evaluated in 2012 for insect defoliation and C. castaneus abundance and frequency. Defoliation was visually assessed throughout the growing season at two sites in the southern Appalachian Mountains (western North Carolina and eastern Tennessee). C. castaneus abundance and frequency were monitored on trees using beat sheets and emergence was recorded from ground traps. Asiatic oak weevils were more abundant and more frequently collected on American chestnut (Ca. dentata) and its most closely related BC3F3 hybrid generation than on the Asian species Ca. mollissima. In most months, C. castaneus colonization of hybrid generations was not significantly different than colonization of parental species. Frequency data for C. castaneus suggested that adults were distributed relatively evenly throughout the study sites rather than in dense clusters. Emergence of C. castaneus was significantly higher under a canopy dominated by Quercus species than under non-Quercus species or open sky. C. castaneus emergence began in May and peaked in late June and early July. These results may be useful for resource managers trying to restore blight-resistant chestnut to the Southern Appalachians while minimizing herbivory by insect pests.

Key words: defoliation, Castanea dentata, Castanea mollissima, Cyrtepistomus castaneus, hybrid chestnut

American chestnut, Castanea dentata (Marsh.) Borkh. (Fagales: Fagaceae), was once one of the most common and ecologically important trees throughout hardwood forests in the eastern United States. The range of Ca. dentata occupied over 200 million acres from Maine to Mississippi (Hough 1878, Sargent 1884). The species had multiple uses such as lumber, production of tannins used in tanning leather, and as a food source for humans, domesticated animals, and wildlife (Russell 1987, Minser et al. 1995, Lutts 2004, Anagnostakis 2012).

Two exotic pathogens have contributed to the removal of Ca. dentata as a mature component in eastern U.S. forests. Ink disease, caused by Phytophthora cinnamomi Rands, was noted in the late 1800s in the southeastern and central United States for causing mortality to Ca. dentata in wet and poorly drained soils (Hough 1878, 1882; Milburn and Gravatt 1932, Grandle et al. 1945; Anagnostakis 2012). Another Asian pathogen, Cryphonectria parasitica (Murrill) Barr, that causes chestnut blight, was introduced around the turn of the 20th century through importation of Japanese chestnut (Castanea crenata Siebold & Zucc.) (Merkel 1905, Anagnostakis 2012). C. parasitica quickly spread to affect the majority of Ca. dentata’s native range, functionally eliminating the species (Pyle 1985, Davis 2000). Some Ca. dentata trees have continued to stump-sprout, providing germplasm for resistance breeding programs (Griffin et al. 1983).

In response to chestnut blight, efforts to breed blight-resistant trees were initiated by various state and federal agencies and private foundations (Anagnostakis 2012). The American Chestnut Foundation has utilized a backcross breeding approach to transfer blight resistance from the Chinese chestnut (Castanea mollissima Blume) (Fagales: Fagaceae) into Ca. dentata (Burnham et al. 1986,
Hebard et al. 2014). American chestnut restoration studies using parental species and advanced breeding generations are currently being conducted in southern National Forests (Clark et al. 2014).

The Asiatic oak weevil, Cyrtediplostomus castaneus Roeloofs (Coleoptera: Curculionidae), is indigenous to Japan and was first recorded in North America in New Jersey in 1935 (Davis 1935). The insect has since been observed feeding on species in the Fagaceae family, primarily oaks (Quercus spp.), in many eastern states (Triplehorn 1955, Johnson 1956, Ferguson et al. 1992). C. castaneus larva feed on fine root hairs of trees and emerging radicals of acorns, while adults feed primarily on foliage, preferable in the Fagaceae family (Triplehorn 1955, Roling 1979). In autumn of 2011, the Asiatic oak weevil, C. castaneus was observed causing excessive herbivory to Castanea trees in plantations in eastern Tennessee (TEN) and western North Carolina (NOC) (Clark et al. 2014).

C. castaneus is one of many insect species found on Castanea spp. in the United States (Packard 1890), but the potential importance of insect herbivory on Castanea in the United States is poorly understood. Opler (1979) identified Lepidoptera species known to feed on Ca. dentata and other Castanea spp. Other studies have examined effects of weevil herbivory on germination and seedling growth (Dalgleish et al. 2012). Other insects such as chestnut gall wasp (Dryococcus kurphilius) (Cooper and Rieske 2011) and chestnut sawfly (Cratesus castaneae) (Pincho et al. 2011) have recently been studied or documented on Ca. dentata.

As restoration plantings of putatively blight-resistant Castanea are planned in eastern U.S. forests, it is important to understand other potential problems that these trees may experience in addition to chestnut blight or ink disease. This study was a preliminary examination to evaluate insect defoliation, and C. castaneus abundance and frequency, among Castanea species and hybrids planted on chestnut restoration plots in the southern Appalachian Mountains. We utilized existing plantings of chestnut species and hybrids at two locations (Clark et al. 2014, 2015) and had three primary objectives:

1. Compare defoliation among Ca. dentata, Ca. mollissima, and four hybrid breeding generations at two widely separated sites.
2. Assess abundance and frequency of C. castaneus on Ca. dentata, Ca. mollissima, and hybrid chestnut.
3. Evaluate the emergence pattern of C. castaneus beneath oak and nonoak overstory in a chestnut planting.

Materials and Methods

Study Sites

This study was conducted May through October in 2012 at two plantings established in 2009 and 2010, located on National Forests in NOC and TEN, respectively (Clark et al. 2014, sites C and D; Knapp et al. 2014). The plantings were originally established to evaluate blight resistance, field performance, and phenology of the different breeding generations and parental species. Sites were chosen for planting based on the presence of Ca. dentata sprouts and small trees, indicating suitability for planting Castanea. To prepare sites, within a year prior to planting, each site was subjected to a commercial even-aged regeneration harvest, creating a shelterwood with reserve with approximately 10–20 square feet of basal area predominately consisting of chestnut oak, Quercus prinus, and eastern white pine, Pinus strobus, in the overstory at TEN and tulp poplar, Liriodendron tulipifera, and red maple, Acer rubrum, at NOC (Clark et al. 2015).

Experimental Material

All experimental materials were provided by The American Chestnut Foundation. Hybrid generations were produced through a series of backcrossing Ca. mollissima with Ca. dentata and intercrossing between selected backcrossed progeny. Three successive backcrosses and intercrosses created the BC$_3$F$_2$ generation (Griffin 2000, Hebard et al. 2014). The seedlings were grown for 1 yr at the Georgia Forestry Commission’s Flint River Nursery near Byromville, Georgia in 2008 (Clark et al. 2012). Each tree was tagged with an individual number to maintain pedigree throughout the study. The experimental material consisted of parental species Ca. dentata and Ca. mollissima and hybrid generations: BC$_1$F$_3$, BC$_2$F$_3$, and BC$_3$F$_3$ at both sites. An additional hybrid generation, BC$_3$F$_2$, was also evaluated at site TEN only. Twenty trees from each Castanea species and hybrid generation at each site were selected using a random number generator. The sample size totaled 120 trees from TEN and 100 trees from NOC. Trees had a mean height of 188 and 201 cm at site NOC and TEN, respectively, at the time of this study.

Defoliation Assessment

The degree of defoliation on each tree was visually estimated by two observers. Evaluations were conducted at three times during the growing season: early (May), mid (July), and late (September). Observers rated trees independently and then discussed to assign a final joint rating to ensure consistency among the defoliation assessments. Conceptually, each leaf on a tree was considered to occur in one of three severity classes, based on the percent of leaf area missing: 0–30, 31–60, and 61–100%. The proportion of all foliage occurring in each of these three classes was then estimated in 10% increments, following methodology similar to Hernández-Clemente et al. (2010) and Langstrom et al. (2001). To estimate average total defoliation for each tree, the proportion of foliage in each severity class was multiplied by the median missing leaf area represented by each class, and the three values were then averaged to give an estimated percent defoliation:

$$\text{Estimated percent defoliation} = \frac{\sum_{i=1}^{3} p \times (0.15 \times X_i + 0.45 \times X_i + 0.80 \times X_i)}{3}$$

where $j$ is the proportion of foliage in the 0–30% class, $j$ is the proportion of foliage in 31–60% class, and $k$ is the proportion of foliage in the 61–100% class.

Frequency and Abundance of C. castaneus

Each sample tree was inspected for visible C. castaneus that were resting or directly feeding on the tree. If present, C. castaneus were collected by hand and placed in specimen containers labeled with the date, tree identification number, and site. Following hand collections, two 1-m$^2$ nylon beat sheets (Bioquip Products Inc., Rancho Dominguez, CA) were held opposite one another beneath the lowest branches. A stick was used to lightly strike the tree 10 times on each side to dislocate remaining insects (sensu Harris et al. 1972). C. castaneus were preserved in specimen containers with 95% ethanol. Specimen containers were brought to a laboratory where C. castaneus identity was confirmed. Frequency was recorded as presence or absence on each sampled tree, and abundance was recorded as the number of confirmed C. castaneus collected on each tree.
Emergence Patterns of *C. castaneus*

Temporal patterns in emergence of *C. castaneus* collected from traps at the TEN site was evaluated by date and overstory cover type (*Quercus* spp. vs. non-*Quercus* spp.). Emergence was monitored by using 18 conical wire mesh traps that were placed on the forest floor. The traps were constructed similar to pecan weevil traps (Lee 2013). To assemble the traps, a durable 0.16 cm steel wire mesh hardware screen was cut in to half circles at a diameter of 1.82 m and a 1.3 cm half circle was cut out of the middle of the straight edge. The straight edges were then brought together and stapled. Trap tops (Great Lakes IPM Inc., Vestaburg, MI) also used for boll weevils, pecan weevils, and citrus weevils were secured to the top of each trap. Traps were secured by placing three 10 lbs. bags of sand around the edges of each trap. Nine traps were placed in areas where the overstory tree canopy was dominated by *Quercus* spp. and nine traps were placed in areas where the overstory tree canopy was dominated by non-*Quercus* spp. The non-*Quercus* canopy consisted primarily of *Pinus* spp. or was open sky. We collected and counted *C. castaneus* from each trap approximately every 7 d from May 29 till October 1. Because of some variation in the days between collecting traps, the equation below was used to standardize the days between collections:

\[
\text{Weekly count} = \frac{A}{D + 0.1428}
\]

where *A* is the number of *C. castaneus* collected and *D* is the number of days that had passed between collections.

Statistical Analyses

Statistical analyses were carried out separately for sites TEN and NOC. All analyses were conducted using SAS 9.4 software (SAS Institute 2013). Mixed model analysis of variance was used to analyze fixed effects of chestnut species/breeding generation, month (May, July, and September), and their interaction on both of the following dependent variables by site: mean percent defoliation (calculated from defoliation ratings) and mean *C. castaneus* abundance (average number of *C. castaneus* collected per tree). Individual trees were analyzed as replicates and the random effect was tree within site. Fisher’s least significant difference was used for mean separation, and *P* values ≤ 0.05 were considered significant.

The glimmix procedure (PROC GLMM, SAS Institute 2013) was used to analyze frequency, which was preferable over linear models for binary response data to accommodate for violation of non-normality assumptions (Bolker et al. 2009, Stroup 2014, Clark et al. 2015). We specified a binary response distribution with (dist = binary), used LaPlace estimation methods, and GLMM were modeled on presence of *C. castaneus* (event = 1) on a tree. GLMMs were analyzed by site to find the fixed effects of month and generation excluding interactions, to simplify the model and to improve model fit (Bolker et al. 2009). Least significant difference mean separations were carried out using SAS macro %PDMIX800 provided by Saxton (1998). A paired *t*-test was used to analyze emergence of *C. castaneus* calculated from traps with *Quercus* and non-*Quercus* overstory.

Results

Defoliation of Chestnuts

At site TEN, mean percent defoliation on chestnut varied from 17 to 24% and did not differ among generations (Fig. 1, see Table 1 for all *F*, *df*, and *P* values). Significantly less defoliation was observed in September than in May and July (Fig. 2). There was no significant interaction between generations and month at site TEN (Fig. 3A).

At site NOC, mean percent defoliation varied between 15 and 21% and differed by generation. *Ca. mollissima* sustained more defoliation than all other generations, whereas defoliation of the BC2F3 generation was greater than *Ca. dentata* and BC3F3 generations but did not differ from BC1F3 (Fig. 1). The greatest defoliation at site NOC was observed in July followed by May and then September (Fig. 2). There was a significant interaction of mean defoliation by generation and month (Fig. 3B). In May, defoliation on BC2F3 and *Ca. mollissima* was higher than other generations, however, did not statistically differ from BC1F3. Defoliation on *Ca. mollissima* in July (mean = 21.1) was significantly greater than all other generations and months. In September, there were no significant differences in estimated percent defoliation among generations (Fig. 3B).

*C. castaneus* Abundance

For both sites, abundance of adult *C. castaneus* was lowest in May (Fig. 4). At NOC, the mean number *C. castaneus* collected per tree was statistically similar in July (mean = 1.5) and September. At TEN, more *C. castaneus* per tree were collected in July (mean = 3.8) than in September (Fig. 4).

At site TEN, there was an interaction in *C. castaneus* abundance by chestnut generation and month predominantly due to *Ca. dentata* showing an increase in *C. castaneus* abundance between July and September, while all other generations show a decrease. There was no significant difference in the number of *C. castaneus* collected per tree among the species/generations in May, but in July, fewer *C. castaneus* were collected from *Ca. mollissima* than from BC1F3 and BC2F3 hybrids (Fig. 5A). This general trend continued in September, with fewer weevils collected on *Ca. mollissima* than *Ca. dentata*, BC3F3, BC2F2 and BC2F3, none of which differed from abundance on BC1F3 (Fig. 5A).

At site NOC, there was also an interaction in *C. castaneus* abundance by generation and month due to the increased abundance of *C. castaneus* on *Ca. dentata* and BC1F3 while *Ca. mollissima* and all other generations show a decrease. There was no significant difference among species/generations at NOC in May or July. In September, however, there were more *C. castaneus* collected on *Ca. dentata* and the BC3F3 than on *Ca. mollissima* (Fig. 5B).

*C. castaneus* Frequency

The frequency of *C. castaneus* (proportion of trees from which weevils were collected) varied by month at site at TEN and NOC. At both locations, *C. castaneus* was collected less frequently in May than in July and September (Fig. 6). At site TEN, *C. castaneus* was collected less frequently on *Ca. mollissima* than all other species/generations and more frequently on the BC1F3 generation compared to the two parental species (Fig. 7). At site NOC, *C. castaneus* was collected less frequently on *Ca. mollissima* and BC1F3 than on *Ca. dentata* and BC2F3 (Fig. 7).

*C. castaneus* Emergence

Emergence of adult *C. castaneus* at site TEN began in late May, peaked between mid-June and early July, and continued to decrease into late September (Fig. 8). Significantly more *C. castaneus* per trap emerged from traps located directly beneath the *Quercus* canopy (1.49 ± 0.23) than beneath non-*Quercus* species or open sky (0.51 ± 0.15).
In this study, we compared the abundance and frequency of Asiatic oak weevils (C. castaneus) at three times during the growing season on American chestnut, Chinese chestnut, and various hybrid generations with varying genetic similarity to the parental species. Frequency of C. castaneus was relatively high at both sites, with adults collected from 40% or more of Ca. dentata and most Castanea hybrid generations, suggesting that C. castaneus were found uniformly throughout sites rather than on a few trees in high numbers. At both of our southern Appalachian study sites, Asiatic oak weevils were more abundant and more frequently collected on American chestnut (Ca. dentata) and its most closely related BC 3F3 hybrid generation than on the Asian species Ca. mollissima (Figs. 5 and 7). While the GLMMs did not include the interaction term of month by generation when analyzing C. castaneus frequency, we examined the raw means that showed a possible interaction. Weevil collection frequency on American and most hybrid chestnuts generally increased in July and September, whereas collection frequency on Chinese and BC 3F3 were lower than on other species and decreased in September. One possible explanation for this pattern is that Ca. mollissima, which may have co-evolved with C. castaneus in Asia, may possess physical or chemical defensive traits (e.g., heavier leaf pubescence, secondary metabolites) that Ca. dentata and BC 3F3 lack, making the latter more preferred hosts. At least one study has examined differences in foliar chemistry (e.g., carbohydrates and tannins) between Ca. dentata and American-Chinese hybrids with possible implications for susceptibility to generalist insect herbivores (Rieske et al. 2003). We did not investigate the mechanisms behind a potential host preference for Ca. dentata and hybrids over Ca. mollissima, but if C. castaneus becomes an economically important pest in the effort to restore blight-resistant chestnut in North America, such investigations may be worthwhile.

Although C. castaneus abundance and frequency were higher on American chestnut relative to Chinese chestnut, we did not observe a consistent corresponding pattern in percent defoliation (Figs. 1 and 3). In fact, we observed slightly more defoliation on Chinese and BC 3F3 were lower than on other species and decreased in September. One possible explanation for this pattern is that Ca. mollissima, which may have co-evolved with C. castaneus in Asia, may possess physical or chemical defensive traits (e.g., heavier leaf pubescence, secondary metabolites) that Ca. dentata and BC 3F3 lack, making the latter more preferred hosts. At least one study has examined differences in foliar chemistry (e.g., carbohydrates and tannins) between Ca. dentata and American-Chinese hybrids with possible implications for susceptibility to generalist insect herbivores (Rieske et al. 2003). We did not investigate the mechanisms behind a potential host preference for Ca. dentata and hybrids over Ca. mollissima, but if C. castaneus becomes an economically important pest in the effort to restore blight-resistant chestnut in North America, such investigations may be worthwhile.

Table 1. MMANOVA statistics by site for estimated percent defoliation (EPD), mean number of C. castaneus (MNC), and mean frequency of C. castaneus (MFC) by fixed effects: generation (Gen), month, and Gen × month

| Comparison          | Site | F     | df    | P        |
|---------------------|------|-------|-------|----------|
| EPD by Gen          | TEN  | 1.31  | 5, 113| 0.2635   |
|                     | NOC  | 6.98  | 4, 89.91| <0.0001  |
| EPD by month        | TEN  | 7.12  | 2, 189.6| 0.0011   |
|                     | NOC  | 24.27 | 2, 118.4| <0.0001  |
| EPD by Gen × month  | TEN  | 1.60  | 10, 189.6| 0.1078   |
|                     | NOC  | 2.21  | 8, 147.2| 0.0301   |
| MNC by month        | TEN  | 64.03 | 2, 251.9| <0.0001  |
|                     | NOC  | 15.27 | 2, 195.4| <0.0001  |
| MNC by Gen × month  | TEN  | 2.35  | 10, 204.9| 0.0197   |
|                     | NOC  | 3.20  | 8, 251.9| 0.0007   |
| MFC by month        | TEN  | 52.66 | 2, 237 | <0.0001  |
|                     | NOC  | 17.57 | 2, 198 | <0.0001  |
| MFC by Gen          | TEN  | 5.95  | 5, 114 | <0.0001  |
|                     | NOC  | 3.33  | 4, 95  | 0.0099   |
| MNC emergence rate  | TEN  | 2.42  | 1, 142 | <0.0001  |

MMANOVA, mixed model analysis of variance. Not all fixed effects were tested for each variable.

Fig. 1. Mean estimated percent defoliation by generation at site TEN and NOC in 2012. Error bars indicate standard error. Within sites, means labeled with the same letter are not significantly different alpha < 0.05. Bars without labels did not statistically differ.

Fig. 2. Mean estimated percent defoliation by month at site TEN and NOC in 2012. Error bars indicate standard error. Within site, means labeled with the same letter are not significantly different alpha < 0.05.
NOC. Depending on variability in host nutritional quality and the propensity of weevils to switch hosts (neither of which were examined in this study), there might also have been an aspect of compensatory feeding, where a lack of nutrients was compensated by more leaf consumption (Yang and Joern 1994, Berner et al. 2005). At site TEN, where weevil populations were higher (Fig. 4), there were no significant differences in percent defoliation among chestnut species and generations (Fig. 3A). These patterns may have been inconsistent due to possible interference between herbivores, if trees with low numbers of *C. castaneus* harbored higher numbers of other primary defoliators. The broad defoliation severity classes used also may have made it more difficult to detect differences between species and generations that more narrow categories may have been able to detect. The observed patterns in *C. castaneus* defoliation among chestnut species and generations represent a snapshot within the longer-term population variability at these southern Appalachian sites and may have been different in years of heavier weevil abundance. Also, although much of the observed defoliation was characteristic of *C. castaneus* feeding (e.g., narrow, blocky, meandering lines chewed through the entire leaf blade), to more clearly understand the impact *C. castaneus* have on chestnut, we suggest that future studies be designed to distinguish specific herbivory patterns among the native and exotic insect species that feed on *Castanea* spp. (cf. Packard 1890, Pinchot et al. 2011).

Peak emergence of adult *C. castaneus* occurred in late June and early July at our TEN site, slightly earlier than the peak emergence of mid-late July reported previously in Delaware (Triplehorn 1955) and central Missouri (Roling 1979). Notably, *C. castaneus* adults
were observed in our first trap collection on May 29, suggesting adult emergence may begin earlier in the southern Appalachians than reported at more northerly locations (Triplehorn 1955, Roling 1979). Similar to our observations, Triplehorn (1955) and Roling (1979) also observed a tapering off of *C. castaneus* emergence in October corresponding to the onset of *Castanea* spp. dormancy. Triplehorn (1955) noted *C. castaneus* was also abundant in New Jersey, Maryland, Delaware, and adjacent states. To our knowledge, this study is the first to assess abundance and defoliation associated with this insect in the southern Appalachians and suggests patterns of adult emergence similar to, but possibly earlier than, more northerly parts of the United States.

More *C. castaneus* adults were captured in emergence traps located beneath a *Quercus* canopy than non-*Quercus* canopy, consistent with Johnson’s (1956) observation that *C. castaneus* occurred in higher numbers near oaks. We also saw a secondary and more prominent peak of emergence in early July on traps located under *Quercus* canopy. This suggests that silvicultural treatment and site preparation applied can have an effect on *C. castaneus* populations. Managers should be aware that more weevils may occur in oak dominated forests compared to nonoak dominated forests. Peak emergence may differ between forest types which may be of interest for targeted pest management.

The degree to which *C. castaneus* defoliation affects growth, however, is uncertain and was not addressed in this study. Studies have demonstrated leaf damage may have a substantial impact on plant growth, seed viability (Marquis 1984), and tree mortality (Eichhorn et al. 2010). Herbivory has also been shown to reduce trees photosynthetic rates (Zangerl et al. 2002) and the predominant
mechanism of pathogen establishment (García-Guzmán and Dirzo 2001). Additional research is suggested to replicate evaluations under different silvicultural treatments to identify the ideal treatment that promotes successful establishment and minimizes specialized phytophagous insects. Our findings may also be relevant to population dynamics with regard to invasive species. C. castaneus may act as an agent of indirect competition between Ca. dentata and Ca. mollissima (White et al. 2006). Ca. mollissima may help to sustain C. castaneus populations, but weevil numbers may have a stronger adverse effect on Ca. dentata. A better understanding of how Castanea spp. growth and survival is impacted by insect herbivory will be important as development of blight-resistant chestnuts continues to proceed toward eventual restoration.

Levels of insect defoliation on chestnuts at two southern Appalachian sites were less than 25% in 2012. C. castaneus densities and collection frequency were higher on Ca. dentata and its most closely related breeding generation (BC$_3$F$_3$) than on Ca. mollissima. C. castaneus emergence in TEN began in May was highest under oak overstory and peaked in late June and early July. Establishing Ca. dentata beneath a retained oak overstory may increase C. castaneus abundance and herbivory relative to other overstory conditions. Future studies are suggested to understand the effect that silvicultural treatments have on C. castaneus and other phytophagous insects in addition to how defoliation and weevil abundance affects survival, growth, and health of newly introduced chestnuts. As blight resistant chestnuts are reintroduced, it will be important to understand and anticipate potential threats to successful establishment, including phytophagous insects.

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