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THE INFLUENCE OF ACCELERATED ASPEN-DOMINATED FOREST SENESCENCE ON LOCAL INVERTEBRATE POPULATIONS

Abstract

An increase in plant diversity following aspen senescence should impact animal diversity, but the exact nature of such changes is not known. The present study, set in an aspen-dominated forest, focuses on the response of a food chain to induced acceleration of plant senescence. Invertebrate primary consumers, specifically insects, have repeatedly been demonstrated to respond rapidly to such changes. Thus, to answer the question of how a transitioning aspen-dominated forest ecosystem affects local insect assemblages, we sampled insects in an aspen- and birch-dominated forest at the University of Michigan Biological Station, on control sites and on similar sites where senescence has been induced by the girdling of aspens and birches in spring 2008. At this time, approximately one year after girdling, chi-square tests yield significant differences in guild densities between girdled and ungirdled areas. Regression tests, however, yield no statistically significant correlations between guild density and girdled / total tree density, indicating that more time may be necessary before the effects of aspen and birch senescence on higher trophic levels will be made manifest.

Introduction

By the early 20th century, logging and wildfire had eliminated the majority of forests in the upper Midwest, allowing aspen (*Populus*) and birch (*Betula*) to dominate the landscape (Karamanski, 1989; Friedman and Reich, 2005; both in Curtis et al., 2006). Approximately a century later, many aspen-dominated forests are approaching or have passed maturity. Their decline is expected to redirect resources toward an increasing minority of red oak (*Quercus rubra*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), and sugar maple (*Acer saccharum*). These species are expected to increase in numbers, resulting in increased diversity of the forests (Kneeshaw and Bergeron, 1998; Stearns and Likens, 2002; Wolter and White, 2002; all in Curtis et al., 1996).

An increase in plant diversity following aspen senescence should also impact animal diversity, but the exact nature of such changes is not known. Yet knowledge of these mechanisms is essential to understanding senescence-related changes in the diversity and distribution of organisms, which are expected to become more prevalent worldwide as a result of forests undergoing similar transitions due to climate change (Kneeshaw and Bergeron, 1998; Stearns and Likens, 2002; Wolter and White, 2002; all in Curtis et al., 1996).

The present study, set in an aspen-dominated forest, focuses on the response of a food chain to induced acceleration of plant senescence. The primary producers in this case are aspen, birch, and other trees; the primary consumers are predominantly invertebrates that, in comparison to other organisms, would be anticipated to respond most rapidly to changes in primary production associated with tree senescence. Primary consumer changes may be associated with changes in a variety of plants or plant products – decaying organic matter, starch-rich materials, and plant detritus – that occur as production shifts from aging trees to their successors. Changes in the primary producers may also affect physical habitat, such as temperature at various locations throughout the canopy and in soil. As ectotherms, invertebrate primary consumers should respond rapidly to such temperature changes.

There is a long tradition in using invertebrates, specifically insects, to monitor environmental change. In aquatic ecosystems, benthic macroinvertebrates have been employed since 1928 to measure water quality in the United States (Richardson, 1928). Similarly, EPT testing uses densities of Ephemeroptera (mayflies), Plecoptera (stoneflies), and

Trichoptera (caddisflies) to evaluate stream water quality (B. Scholtens, pers. comm.). In terrestrial ecosystems, beetles and other insects have been employed as bioindicators for forest ecosystems recovering from significant disturbance (Paquin, 2008; Butterfield, 1997; Heliola et al., 2001; all in Farner et al., 2009).

Thus the questions addressed are: How does a transitioning aspen-dominated forest ecosystem affect local insect assemblages? Will a gradual and long-term disturbance, such as accelerated aspen senescence, exercise a bottom-up effect on the food chain from trees to insects? If a bottom-up effect exists in senescing aspen-dominated forests, how are these manifested over time for insect communities?

To answer these questions, we sampled insects and other invertebrates in an aspen- and birch-dominated forest at the University of Michigan Biological Station, on sites where senescence has been induced by girdling of aspens and birches in spring 2008 and on similar control sites (Curtis et al., 2006). We hypothesized significant changes in insect population between the girdled and ungirdled plots, such as an increase in detritivores, fungivores, and xylophages in the girdled plots that would correspond with the increase in down wood, soil carbon content, and light gaps through the canopy.

Materials and Methods

Girdled and control sites

The insect populations were sampled within the 60-meter-radius control site that surrounds the AmeriFlux control tower (at 45.5598, -84.7137) and the 60-meter-radius girdled site that surrounds the FASET control tower (at 45.5621, -84.7036), both approximately two miles west of the University of Michigan Biological Station. Each site contained five pseudo-replicated plots, all located on different transects at varying distances from the tower (Table 1).

Insect sampling

Insect traps were placed in the plots at three heights: flight-interception traps at the canopy (top) level, flight-interception traps one meter above the ground, and pit traps at ground level. The three trap levels ensured that the vertical range of diversity in a plot was sampled as accurately as possible.

Each flight-interception trap in the canopy and at the 1-meter level comprised two clear Plexiglas sheets measuring 29.85 cm by 16.51 cm and a large coffee can containing antifreeze (propylene glycol). The Plexiglas sheets formed an X-shape wired above the can. Insects fly into the Plexiglas walls and fall into the can, where the antifreeze traps them. Each 1-meter trap was hung with a wire loop from an L-shaped PVC pipe structure; each canopy trap was hung from a high branch with fishing line. The ten plots each contained one canopy trap and one 1-meter trap.

Each pit trap consisted of a plastic tub, containing antifreeze, set in a hole with the top flush with the ground. Four plastic “fences” surrounded the tub at right angles to increase each pit trap's area. Invertebrates contacting a fence tend to move along the fence and fall into the cup. Ground invertebrates tend to have a more restricted range than flying or climbing insects; therefore, each 60-meter-radius site contained five pit traps spaced evenly along a twenty-meter transect.

Trap contents were collected weekly over three weeks. However, identifying insects and sorting them into guilds requires a considerable period of time, which the brief UMBS summer session did not afford. Consequently, only the first week of samples was sorted and analyzed. Insects and some other invertebrates were sorted into guilds: detritivores, xylophages, fungivores, and other (Arnett, 1960; Johnson and Triplehorn, 2004). Numbers of individuals in each category were recorded and analyzed for significance by chi-square and regression testing.

Results

Chi-square tests, using the calculator at <http://people.ku.edu/~preacher/chisq/chisq.htm>, revealed significant differences in all three guilds between girdled and ungirdled areas: detritivores (chi-square = 18.255, df = 2, p-value = 0.00011), fungivores (chi-square = 13.795, df = 2, p-value = 0.0010), and xylophages (chi-square = 10.099, df = 2, p-value = 0.0064). On average, xylophages numbered 40% less in the girdled than in the ungirdled area; but fungivores and detritivores, both numbering 21% more in girdled than in ungirdled areas, demonstrated the opposite trend (Figure 1).

To identify a possible correlation between guild densities and girdling densities in each plot examined, the plot area around each set of traps was standardized. Because the plots lie on concentric circles that surround the AmeriFlux and FASET towers, measuring areas that were exactly equal was not feasible. Instead, concentric circles were traced around the AmeriFlux and FASET towers, producing concentric slices ten meters deep. Each slice was further divided into transects that surrounded each trap by ten meters on each side. Each resulting area – approximately twenty meters (along a transect) by twenty meters (along an arc) – was cross-checked against the girdling project's database of girdled / ungirdled trees, and the absolute number of girdled *Populus* and *Betula* within each area was recorded. Regression tests for guild densities versus girdling densities were then run for the girdled plots. The ungirdled plots were excluded from this step, as they would have a girdled tree count of zero. The samples used for these regression tests included only the 1-m and canopy samples, because only these samples were specifically assigned to a plot within each girdled / ungirdled area; pit traps were assigned to an entire girdled / ungirdled area, with one pit-trap transect to one 60m-radius area. All tests showed no statistically significant correlation between guild densities and girdling densities for the 1-m and canopy samples in each plot (detritivores, R^2 = 0.13, total df = 4, p-value = 0.56; fungivores, R^2 = 0.087, total df = 4, p-value = 0.63;

xylophages, $R^2 = 0.0019$, total df = 4, p-value = 0.94). Test results are plotted in Figures 2, 3, and 4.

To explore the possibility that the total number of trees in a standardized area may be a factor affecting the insect guild density, regression tests were run that included both girdled and ungirdled areas, with guild density plotted against the number of all trees in the area. These tests showed no statistically significant correlation between guild densities and total tree density in each plot. Test results are plotted in Figures 5 to 10.

Detritivore invertebrates sampled included Staphylinidae (rove beetles), Phoridae (scuttle flies), Latridiidae (minute brown scavenger beetles), Diplopoda (millipedes), and Collembola (springtails). (Collembola feed on fungus; however, they feed on mycelia on detritus and not on sporocarps as true fungivores do.) Fungivores included Mycetophagidae (hairy fungus beetles) and Drosophilidae (fruit or vinegar flies). Xylophages included Cerambycidae (long-horned beetles) and Eucnemidae (false click beetles).

Discussion

The statistically insignificant correlations between insect guild density and girdled tree density indicate that the differences in all three guilds between the girdled and ungirdled sites, though statistically significant, are unlikely at this point in time to have stemmed from the girdling of aspen and birch. A previous girdling study reported that 74% of all aspen in a mixed broadleaf-conifer forest died after one year (Simard et al., 2005; in Curtis et al., 2006), and aspen is generally expected to die one to three years after girdling (Schier and Smith, 1979; Simard et al., 2005; both in Curtis et al., 2006). However, the aspen and birch canopy in the girdled FASET site, observed qualitatively, still appears to be of a thickness uniform with the surrounding ungirdled canopy. Approximately one year after girdling, the roots appear to be the element undergoing most change. Root respiration is lower in the girdled than in the ungirdled area, presumably because roots run out of carbohydrates; in contrast, above the girdle, aspens are still continuing to grow (C. Vogel, pers. comm.). Neither are the correlations between insect guild density and total tree density statistically significant, indicating that total tree density was unlikely to have caused the girdled / ungirdled differences in insect guild density obtained in this study. Thus, other factors may have exerted a stronger influence on guild densities and distributions. The girdling project established AmeriFlux and FASET as replicates, with similar leaf covers and primary production (Curtis et al., 2006). Yet enough distance separates the two sites that spatial bias may be a problem, and invertebrate composition may already have differed significantly between the two sites even before girdling took place.

The experimental design can be improved. The current set-up rules out the inclusion of the pit traps in several statistical tests, which may have played a role in the statistically insignificant results. This might be remedied for future studies by supplying each standardized area with a complete set of traps (pit, 1-m, and canopy) instead of planting only a pit and a canopy trap in each standardized area and setting a single pit-trap transect to sample an entire 60m-radius plot. In the short term, complete analysis of our three weeks of data is desired: one week of analysis provides little statistical strength. With such a small sample, the lack of correlation may turn out to be an artifact that can be minimized with more samples. In addition, considering the “other” wastebasket guild in the calculations and converting the detritivore / fungivore / xylophage numbers into a ratio of ([# of guild members] / [total sample, including other]) may also provide a more complete picture of events resulting from accelerated senescence.

The statistical results demonstrate that the changes taking place in the declining aspen and birch, one year after girdling, are unlikely to have already crossed upwards to the next trophic level. Thus a continuous study of this forest throughout the year, for several successive years, would be useful in pointing out the possible relationships between guild density and girdling / total tree density. With extended study, changes in season will bypass any summer-specific environmental changes that may have skewed guild densities.

At this time, most of our questions remain unanswered. Yet, in the long term, a statistically significant correlation between insect guild density and girdling density may still be derived once aspen and birch senescence have achieved a magnitude strong enough to affect the trophic levels above them.

Tables and Figures

Table 1. Locations of the 1 meter and canopy traps for Ameriflux and FASET.

Site	**Degrees from North**	**Distrance from central tower (m)**
Ameriflux	115	40
	105	60
	95	40
	135	60
	155	40
FASET	280	20
	260	40
	300	60
	200	60
	240	60

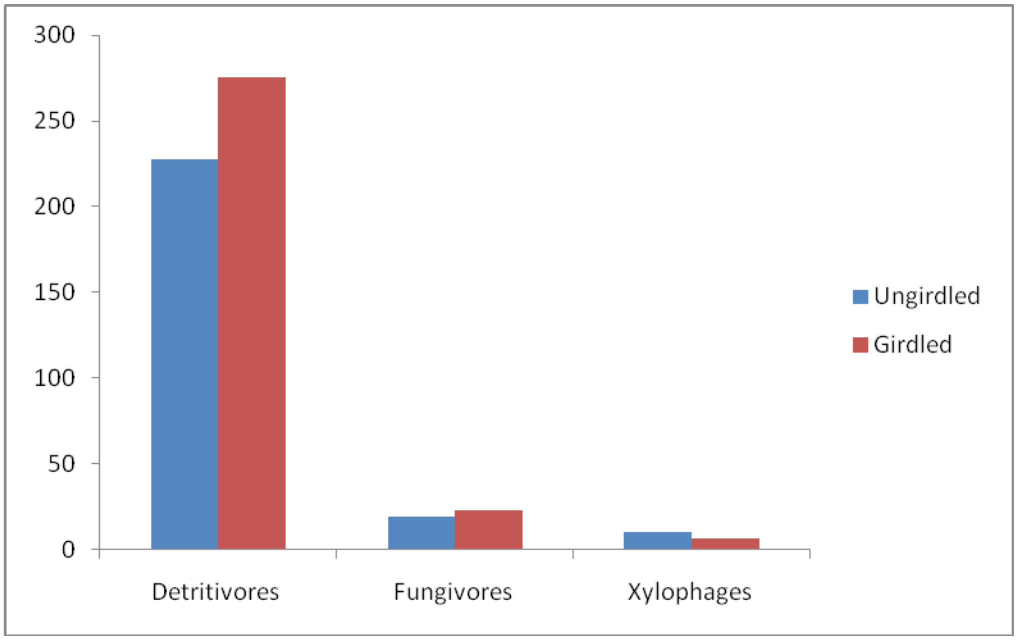

Figure 1. Mean values of insect guild densities plotted between ungirdled and girdled areas. Values are from samples at all three heights. On average, xylophages numbered 40% less in the girdled than in the ungirdled area; but fungivores and detritivores, both numbering 21% more in girdled than in ungirdled areas, demonstrated the opposite trend.

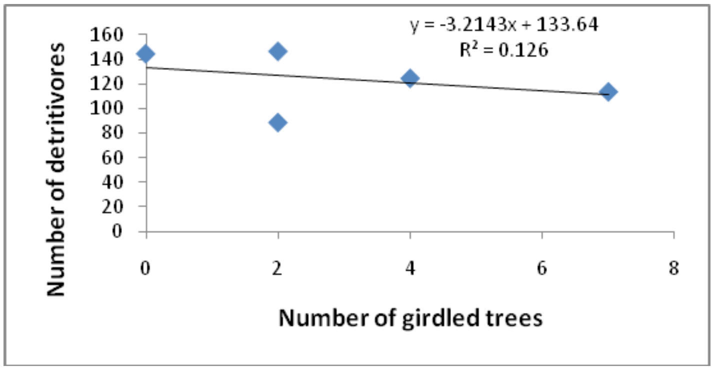

Figure 2. Correlation between the number of girdled trees and the number of detritivore insects per standardized area in the FASET girdled site. Trees comprise all aspen and birch 8cm and greater in trunk diameter. Detritivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.56; correlation not statistically significant.

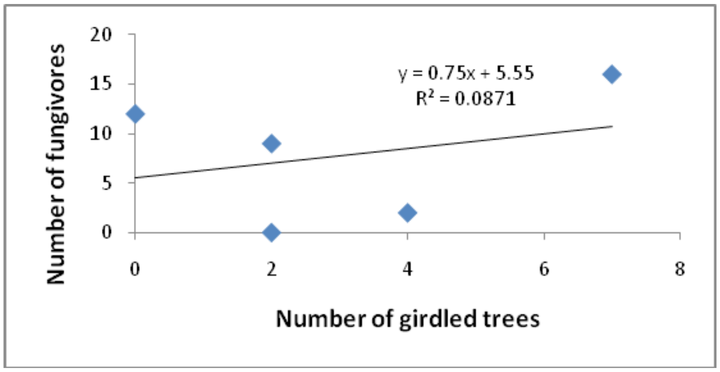

Figure 3. Correlation between the number of girdled trees and the number of fungivore insects per standardized area in the FASET girdled site. Trees comprise all aspen and birch 8cm and greater in trunk diameter. Fungivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.63; correlation not statistically significant.

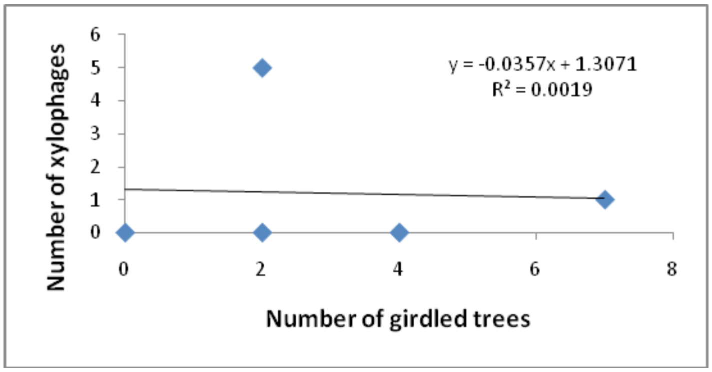

Figure 4. Correlation between the number of girdled trees and the number of xylophage insects per standardized area in the FASET girdled site. Trees comprise all aspen and birch 8cm and greater in trunk diameter. Xylophage counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.94; correlation not statistically significant.

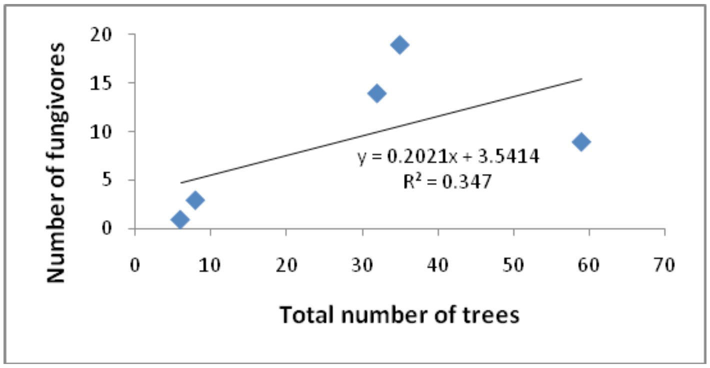

Figure 5. Correlation between the total number of trees and the number of fungivore insects per standardized area in the AmeriFlux ungirdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Fungivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.30; correlation not statistically significant.

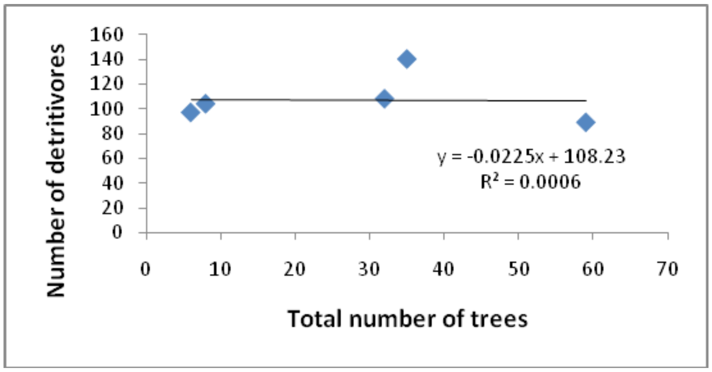

Figure 6. Correlation between the total number of trees and the number of detritivore insects per standardized area in the AmeriFlux ungirdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Detritivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.97; correlation not statistically significant.

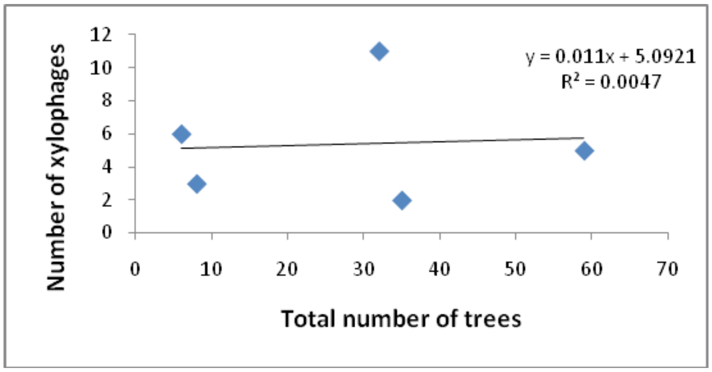

Figure 7. Correlation between the total number of trees and the number of xylophage insects per standardized area in the AmeriFlux ungirdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Xylophage counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.91; correlation not statistically significant.

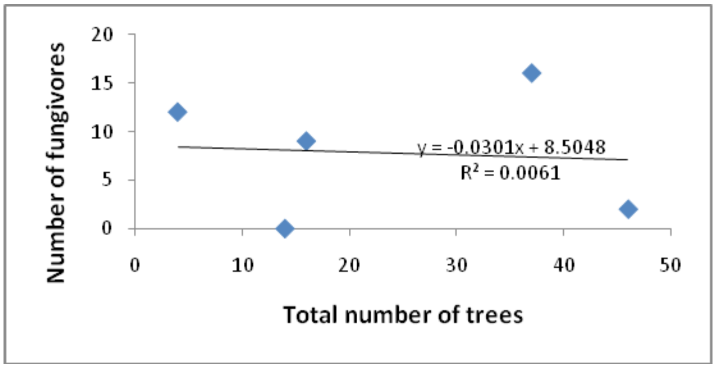

Figure 8. Correlation between the total number of trees and the number of fungivore insects per standardized area in the FASET girdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Fungivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.90; correlation not statistically significant.

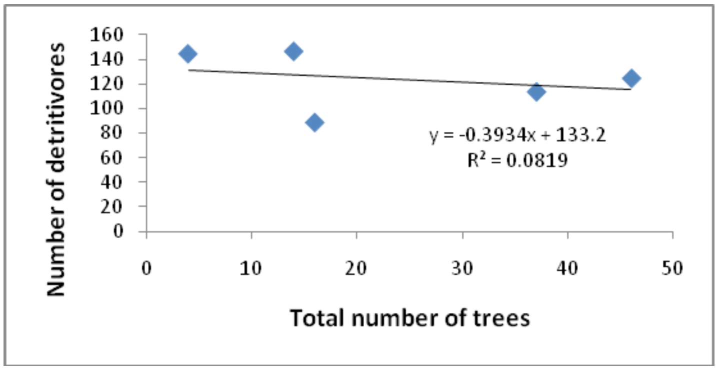

Figure 9. Correlation between the total number of trees and the number of detritivore insects per standardized area in the FASET girdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Detritivore counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.64; correlation not statistically significant.

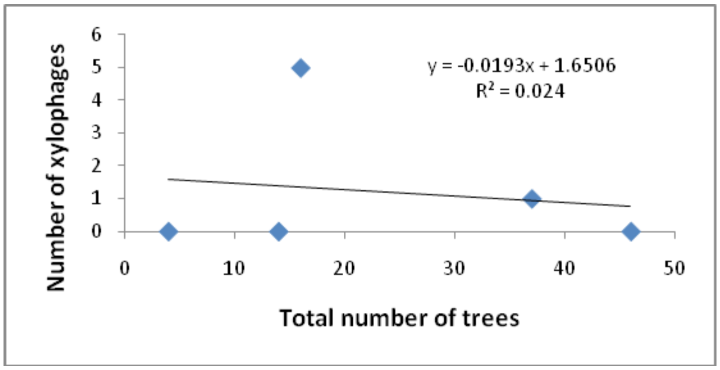

Figure 10. Correlation between the total number of trees and the number of xylophage insects per standardized area in the FASET girdled site. Trees comprise all individuals 8cm and greater in trunk diameter. Xylophage counts are sums only from 1-m and canopy samples, excluding pit samples. Total degrees of freedom = 4; p-value = 0.80; correlation not statistically significant.

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