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Distribution and Species Diversity of Gall-forming Insects on Young Oaks Within Two Restored Oak Forests of Southeastern Minnesota

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Distribution and Species Diversity of Gall-forming Insects on Young Oaks Within Two Restored Oak Forests of Southeastern Minnesota

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Abstract

The purpose of this investigation was to examine differences in gall distribution and infestation rates in two restored oak forests on the campuses of St. Olaf and Carleton Colleges in southeastern Minnesota. In fall of 2004, a survey examined three types of oaks--white oak (*Quercus alba*), red oak (*Quercus borealis*), and bur oak (*Quercus macrocarpa)*--and found fifteen gall maker species. The number of leaf and twig galls per oak tree, the percent of branches infested with galls, and the diameter at breast height (DBH) were measured. The study found a significant correlation between mean percent of oak branches infested with galls and DBH. There were significant differences in infestation rates between the three oak species with white oak have the highest rate of infestation. There were also different types and numbers of gall species at the two sites. Furthermore, the number of gall species on bur oak was positively correlated with DBH. Additional factors influencing gall distribution could be time since the forests were restored, presence of older host trees in the adjacent areas from which gall makers could disperse, as well as seasonal and annual fluctuations in gall maker populations.

Introduction

Oaks are one of the most important tree genera in North America and are considered to be keystone species (McWilliams, et al., 2002). They produce timber and are a valuable food resource for wildlife (ie: acorns). Oaks facilitate creation of communities rich in diversity and provide structure and habitat for a wide range of species. Oaks possess fire resistance, the ability to re-colonize following disturbance, and are long-lived (Frelich and Reich, 2002).

In North America, oaks range from Nova Scotia to California and from Southern Manitoba to Florida, although they do not occur in some places in the northern Rocky Mountains of Idaho, western Montana, or western Wyoming (McWilliams, et al., 2002). Oaks have been significant members of eastern deciduous forests for thousands of years, but their future abundance and distribution is in question as indicated by Frelich and Reich (2002). According to their analysis there are multiple forces at work, some of which are new or more extreme than they were in the past--mainly wind, deer, fire repression and exotic species—that when taken in combination could lead to failure of oaks to regenerate on their own.

In Minnesota, changes in land use over the past 150 years—particularly conversion from natural to agricultural and urban uses—has dramatically altered the distribution of oaks. For example, in 1850 forest, savannah, and shrub lands—which would have been rich in oak species—accounted for 80.0 % of the land area in Minnesota but by 1988 accounted for only 11.0 % (Milbert, 1994). During this same period, agricultural use of land increased from less than 1% to 62.0% and urban use increased from less than 1% to 13.9%.

Resistance to fire was one of the characteristics that allowed oaks to dominate in certain ecosystems such as oak savannah in the pre-European days of Minnesota history (Frelich and Reich, 2002). Fire repression resulting from land use changes favored sugar maple and basswood, which were less fire resistant than oaks but more tolerant of shade. A study of forest composition in Rice County Park near Northfield, Minnesota—a portion of the Big Woods—found no seedlings or saplings of northern red oak but large numbers of sugar maple (*Acer saccharum)* and basswood (*Tilia americana)* in these age classes (St. Olaf, 2004). Both Carleton and St. Olaf Colleges have made efforts at restoration of oak savannah or oak forest, and two of these sites were used in this study.

Another factor in oak distribution is the spread of diseases such as *Phytophthora ramorum* (sudden oak death) and parasites such as gall producers. Galls are deformities of plant tissues caused by the plant's reaction to attack by an insect or other gall producer, which usually results from the deposition of eggs within meristem tissue and subsequent larval growth. There are over 2,000 kinds of American plant galls. Of these, approximately 800 are formed by gall wasps and another 700 are induced by gall midges. A variety of other organisms also induce galls including assorted other types of flies, a few beetles, several moths, true bugs, plant mites, and fungal infections (Felt, 1940).

Oaks are attacked by a large number of gall makers and even one tree can support an array of galls on roots, leaves, twigs, bark, branches, catkins, and buds. Virtually every part of the oak tree is susceptible to some type of gall inducer (Felt, 1940). Two important producers of oak galls are midges—which are tiny flies (1/4" long or less)—and mites (microscopic insects).

However, Cynipid wasps are the main producers of galls on oaks. They are small in length (1/8" inch or less), sometimes flightless, and often parthenogenetic (Felt, 1940). Having a parthenogenetic life history means that there is alternation between sexually and asexually reproducing generations (Stone, et al, 2002). The sexual generation emerges from galls in the spring as adults. They mate, and then the females lay eggs (oviposit) on the terminal buds of trees (Eliason and Potter, 2001). Plant tissue grows around the larvae and enlarges to form galls, from which the next generation of adult asexual wasps emerges in late July or August. These wasps then oviposit on the trees again and the larvae overwinter in galls (Eliason and Potter, 2001).

Oak gall wasps are a diverse group of 1,000 species in 41 genera (Stone, et al., 2002) and have a long history of interaction with oaks. Many have evolved into highly specialized niches (Cornell, 1986). For example, *Disholcaspis mamma* seems to specialize on bur and white oaks and produces the rough bullet gall (Shour, 2004; University of MN, 2004). The diversity of gall shapes and sizes is seemingly endless. Oaks galls can be spherical, triangular, disk-shaped, or irregular masses, and can contain single or multiple larval cells. Likewise, a wide variety of outer coverings have evolved including smooth, rough, ridged, hairy, and spiney. Some gall larvae—including *D. mamma*—secret honeydew. Interestingly, ants are attracted to the honeydew, and they will defend the galls against parasitoid wasps that might try to attack the larvae inside (Seibert, 1993). Other causes of gall mortality include inquilines, fungi, birds, and small mammals (Wilson, 1995; Stone, et al., 2002).

Ovipositioning and a related issue--the chemical mechanisms involved in gall formation--are areas of great interest to researchers of gall-forming insects and their host plants. Knowledge of these important aspects in gall formation have implications in applied fields such agriculture, forestry, restoration, and conservation biology as well as theoretical fields including chemical ecology, evolutionary biology and population genetics (Price, 2002; Stone, et al., 2002; Soulé and Kohm, 1989). According to Stone, et al. (2002) in their review of the population biology of oak gall wasps, it is widely accepted among researchers that host tissue must include meristem or similarly omnipotent cells in order to induce gall formation. However, the exact mechanisms of gall induction are not known and the evolutionary significance of galls is up for debate as well (Stone, et al., 2002).

Available evidence suggests that galls do not usually kill oaks or even harm them appreciably except in a some cases where they are considered unsightly deformities by landowners or may attract annoying insect pests with their sticky nectar secretions (Seibert, 1993; Eckberg, 1994). For example, although in most cases rough bullet galls do not kill oak trees, they do appear to reduce growth (Shour, 2004). There is the possibility that in combination with other factors such as those discussed by Frelich and Reich (2002) wasp interactions with bur oaks could be more detrimental. It has been shown that other species of wasps such as *Callirhytis cornigera* do have very negative effects on pin oak (Eliason and Potter, 2001).

The objectives of the study were to compare oak gall distribution and species diversity on different tree types—white, red, and bur oak; to compare oak gall distribution in relation to tree size (DBH); and to investigate differences between the two study sites.

Methods

The study was conducted at two restored oak forests on St. Olaf and Carleton College campuses in Northfield, Minnesota. The St. Olaf site was located below Ytterboe Hall west of Tostrud Center. Planted with a mixture of oaks in 1993, this site was bounded by sustainable agriculture to the west, a parking lot to the north, and maple-basswood forest on the east and south sides. The second study site was in Carleton College's upper arboretum, within the area known as "Alumni Field." This area--planted approximately five years ago--was bounded by mainly deciduous forest on all four sides and was somewhat larger than the St. Olaf site. Several old bur oaks were located on its periphery.

A random transect method was used to identify trees included in the study (Brower, et al. 1998). After selecting a random starting point in the middle of each forest, I laid out a 50 x 4 m plot and sampled all of the oak trees within it. Seedlings were excluded from the final results, as were swamp and pin oaks, since these species amounted to a total of only four trees. The three species of trees included in the survey were white oaks (*Quercus alba* L.), red oaks (*Quercus borealis* and closely related sp.), and bur oaks (*Quercus macrocarpa* Michx.).

After the oak trees were identified and the diameter at breast height (DBH) measured, I conducted a one-minute survey of branches and counted how many were infested with galls on leaves or twigs. Twigs, leaf surfaces and undersides of leaves were examined from the ground up to a height of approximately seven feet. Galls were collected and returned to the lab for identification using Felt (1940) as a primary reference. When galls were not readily identified, but were clearly different morphologically, they were labeled as separate unidentified species.

The data were analyzed statistically using Stata 8.2. The number of individuals of each tree species was averaged for each site and expressed as a percentage. The mean percentage of branches infested with galls and the mean DBH was calculated per site, per oak species, and as a total for both sites together. Using regression analysis, I compared the number of gall species with DBH for each of the three oak species at both sites and for the St. Olaf College site alone. Sixteen of the trees at Carleton were very small—less than 1 cm in diameter—and were classified as a group at 0.5 cm if less than 1 cm DBH due to limits on measuring capacity of the equipment used. Therefore, this data was not analyzed separately in the regression analysis. Percent of branches infested for all trees was compared to DBH in another regression analysis.

ANOVA tests were used to examine relationship between percent of infestation and type of oak tree as well as number of gall species and type of oak tree. A contingency table was used to further analyze the correlation between DBH and presence or absence of galls.

Results

A total of 68 trees were included in the survey--approximately half from each site. Composition of oak species varied considerably between the two sites. In the restored oak forest at St. Olaf College, white oak (45.5%) and bur oak (42.4%) predominated, and red oak (12.1%) was less prevalent (See Table 1). At Carleton College, red oak accounted for 71.4% of the trees in the survey, bur oak for 22.9%, and white oak for only 5.7%. Another difference between the two sites was that the trees at St. Olaf were larger--the average DBH was 6.77 cm compared to 1.20 cm at Carleton. The percent of trees infested with galls was also higher at St. Olaf (74.1%) on average in comparison with the mean percentage of trees infested at Carleton (38.1%).

Regression analysis showed that there was a highly significant positive correlation between DBH and the percentage of branches infested with galls (P=0.0001, See Fig. 1). This analysis included all trees at both sites. The average infestation rate on the 68 trees surveyed was 55.6% and mean DBH was 3.98 cm (See Table 1).

The study found highly significant differences between oak tree species in terms of percent of branches parasitized by gallers (P=0.0005). White oaks had the highest infestation rates of leaf and twig galls at St. Olaf (84.1%) and at Carleton (50.0%). Next highest infestation rates were found on bur oak branches (64.8%) at St. Olaf and at Carleton (38.9%). The rate of parasitism by gallers on red oaks was lower at Carleton (36.7%) compared to St. Olaf (46.7%).

Fifteen types of galls were found between the two sites. Fourteen of these galls were found at St. Olaf and seven at Carleton. At St. Olaf most species were found on leaves (10), while four gall types were found on twigs (See Table 2). The same pattern was true at Carleton, where six out of the seven species of galls were found on leaves (See Table 3).

There were differences in the types of galls found on white, red, and bur oak and on the types found at the two sites (See Table 2 and 3). White oaks at St. Olaf were most often parasitized by *Disholcaspis globulus* (bullet gall found on twigs) and by *Acraspis villosa* (found on the midrib of leaves). Another common galler found on twigs of white oak at St. Olaf was unidentified but accounted for approximately one fifth of the galls found. White oaks at Carleton were attacked by two types of gallers—both of which could not be identified—that differed from those at St. Olaf. One type attacked leaf surfaces and undersides while the other attacked only the surface of leaves.

Red oaks at St. Olaf were attacked primarily by *Cynips dimorphus*, a galler of leaf midribs. At Carleton, mainly the same two types of gallers that attacked white oaks at Carleton attacked the red oaks. *D. mamma* (rough bullet gall) was the most prevalent gall found on bur oaks at both Carleton and St. Olaf. Another significant galler of bur oaks was *Acraspis pezomachoides* (oak pea gall), which was only found at St. Olaf.

The three types of oaks had similar levels of species diversity at St. Olaf College as measured by the Shannon and Simpson Diversity Indices (See Table 2). There was more variation in species diversity between the types of oaks at Carleton (See Table 3). Red oak showed the highest species diversity according to the Shannon D.I. (1.16) compared to white oak (0.69) and bur oak (0.45).

The study found significant differences in the number of gall species found on the three types of oaks (P=0.024). The number of gall species was highest on white oaks at 2.5 species on average per tree in both sites combined (See Fig. 3). This number was slightly higher at St. Olaf (2.7). Bur oak had the next highest average number of species at St. Olaf (2.4) and second highest overall (1.7). However, the pattern was different at Carleton, where red oak had the highest average number of gall species (1.2) followed by white oak (1.0) and bur oak (0.6).

The number of gall species was positively correlated with DBH in bur oak (P=0.0029, See Fig. 4) at both sites combined. However, no significant relationships were found between DBH and number of gall species in white or red oaks.

Discussion

Comparison of Two Sites

The two oak forests in this study were shown to differ in several respects: 1) St. Olaf had more white and bur oak while Carleton had more red oak; 2) the average DBH was 5-6 times greater at St. Olaf –as would be expected since these trees were about ten years older; and 3) there was a much higher average rate of infestation by gall makers on oaks at St. Olaf (See Table 1). The reason for the greater percent of infestation at St. Olaf as well as greater diversity of gallers is most likely a result of tree size and time since disturbance (tree planting). The older trees have more surface area of leaves, twigs, and branches, making it easier for gall makers to locate suitable ovipositing sites. In addition, there has been more time for communities of gall makers to become established on the oaks at St. Olaf College.

Gall Diversity and Tree Size

As expected, increased species richness was positively correlated with host size (See Fig. 1 and Table 2). Mean percent infestation of branches increased as DBH increased when data for all trees at both sites were combined. Additionally, the number of gall species found on bur oaks was significantly higher in larger trees (See Fig. 4). These results are congruent with the island biogeography model (MacArthur and Wilson, 1967) generally and the findings of Cornell (1986) in relation to cynipid wasps specifically. Cornell (1986) suggests that as trees age they become larger and more structurally complex, and it is these traits that increase regional and local species richness. Therefore, this study supports evidence that DBH is one factor in determining species diversity of gall makers on oaks, although it was not the only factor involved and not significant for every species.

Factors Influencing Rates of Gall Infestation

When data from both sites were combined, white oaks showed the highest infestation rates, followed by bur oaks and then red oaks (See Fig. 2). At St. Olaf, this result could be related to the fact that approximately 80% of the trees were either white or bur oak and so with more trees available, the gallers were more likely to locate suitable sites. But this argument is limited because red oak accounted for only 12.1% of the trees at St. Olaf yet experienced an infestation rate of 46.7%. Only three white oaks were found at Carleton, so this data is inconclusive.

The Carleton site was largely comprised of red oaks, and their rate of infestation was similar to bur oaks at the same site, even though the number of bur oaks was less. A number of old bur oaks on the periphery of this area could have "seeded" the gall community on bur oaks. A cursory inspection of these older trees revealed the presence of the three types of galls found on bur oaks nearby. Therefore, proximity to other trees with the potential to host gall maker communities could be an important factor influencing gall maker distribution and infestation rates as well as rate of colonization following oak plantings.

Gallmaker community composition

The study revealed differences in the composition of gall maker communities at the two sites (See Table 2 and Table 3). For example, out of a total of fifteen galler species the sites had only six in common. Eight species were found only at St. Olaf and 1 was found only at Carleton. More species were found on every type of oak at St. Olaf. Without further study, it is difficult to know the causes behind these differences other than size of trees and age of the plantings. Again there is the possibility of infestation spreading from nearby trees of the same species since some gallers tend to specialize on certain oaks. For example, *D. mamma* specializes on white and bur oaks (Felt, 1940). Therefore, the presence of other tree species in the surrounding forests could play a part in gall colonization of restored oak forests.

However, it is possible that there are other reasons for the differences, especially between tree species and within species. There could be advantages to placement of galls on various trees that have not yet been discovered yet, such as varying tannin levels (Taper and Case, 1987) or genetic differences in the gall makers or trees. The ability of trees to withstand attack was not reflected in this study because only the results of successful gall formation were visible. In order to identify resistant trees, one would need to observe ovipositing and measure rates of successful gall induction. Seasonal and annual fluctuations could also have influenced these findings, and such differences were not detectable due to the limited time frame of the survey.

Collection of data was limited to searches of lower branches, which could influence the results of the study if significant differences occur between lower and upper branches. However, Cornell (1986) used similar methods to assess species richness of Cynipid wasps in relation to tree characteristics in Californian oaks. Researchers checked the accuracy of this method by climbing a limited number of trees to examine upper canopy and found that visual identification by from the ground had a high accuracy rate.

Conclusions

The study found that distribution of gall makers is related to tree size and differs on white, red, and bur oaks. Mean percent of gall infestation was positively correlated with increasing DBH, was greatest at St. Olaf College and on white oaks at both sites. The next highest rate of infestation was on bur oaks, followed by red oaks. Fifteen species of oak galls were found, and six species were common to both sites. Oaks at St. Olaf had fourteen species and oaks at Carleton had seven. Colonization by oak gallers may be related to time since planting and presence of older host trees in the adjacent forest. Future studies are needed to determine whether or not there are mature host trees prevalent in the surrounding forests that could act as sources of gall producer communities and facilitate colonization of younger oaks in the restored areas.

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Table 1. A survey of leaf and twig galls on 68 young oaks in southeastern Minnesota found that white oaks had the highest percentage (80.3%) of branches infested with galls. Bur oaks were the next most infested with on average 55.4% of branches bearing a gall of some type. Red oaks were the least infested with only 37.9% of their branches affected. The survey was conducted in two restored oak forests on the campuses of St. Olaf and Carleton Colleges in Northfield. The largest trees were found at St. Olaf, which could account for the higher rates of gall infestation at that site.

Site	Oak Species	Number of Individuals	Percent (%) of each tree species	Mean DBH (cm)	Percent (%) infested with galls
St. Olaf College	White	15	45.5	7.91	84.1
	Red	4	12.1	6.09	46.7
	Bur	14	42.4	4.68	64.8
Total St. Olaf		**33**	**100.0**	**6.77**	**74.1**
Carleton College	White	2	5.7	1.05	50.0
	Red	25	71.4	1.37	36.7
	Bur	8	22.9	0.76	38.9
Total Carleton		**35**	**100.0**	**1.20**	**38.1**
Both Colleges	White	17	25.0	7.10	80.3
	Red	29	42.6	1.88	37.9
	Bur	22	32.4	4.06	55.4
Total Both Colleges		**68**	**100.0**	**3.98**	**55.6**

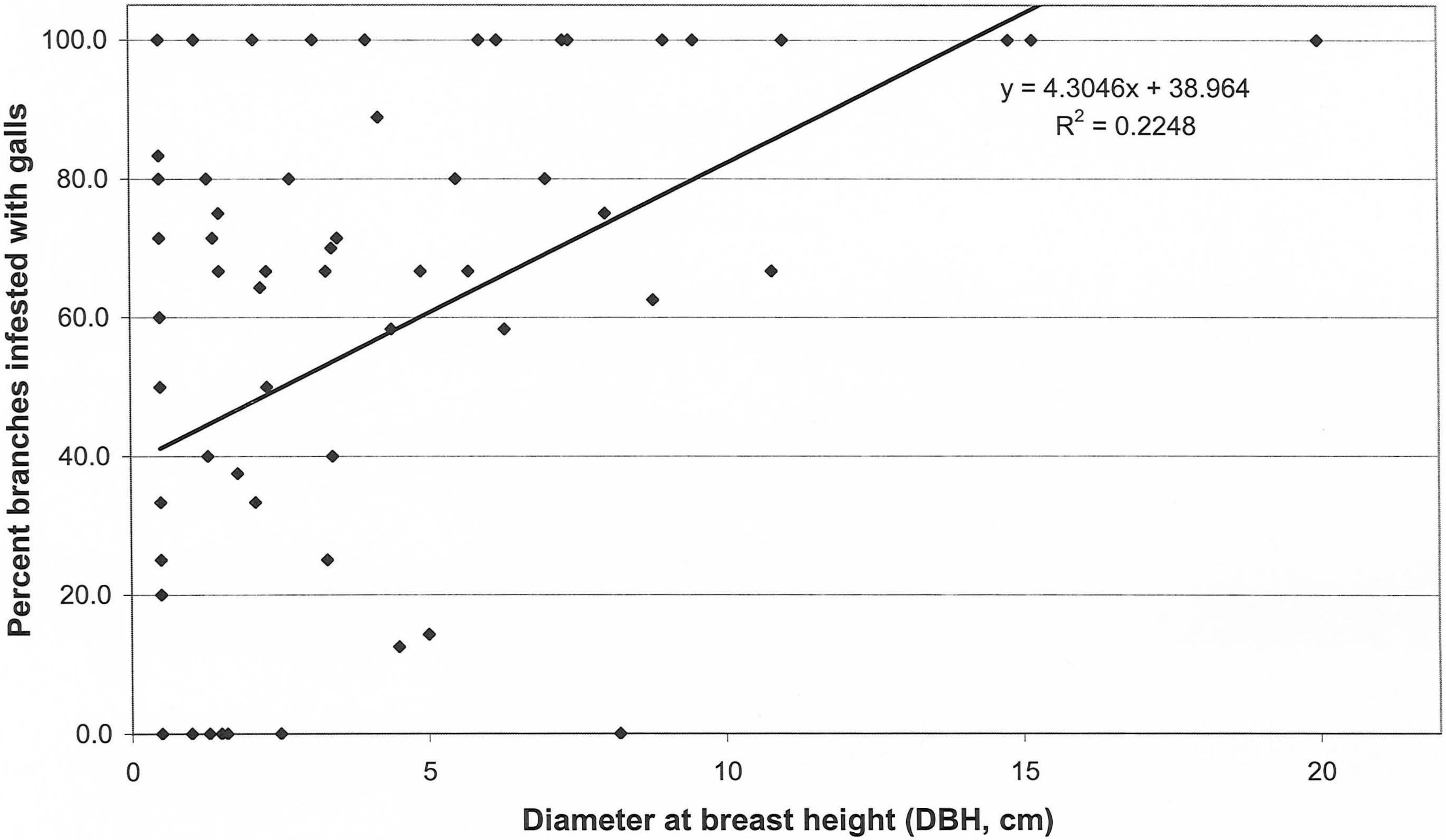

Fig. 1 Percentage of oak branches whose leaves or twigs were infested with galls ~~was positively correlated with~~ varied as a function of increasing DBH of young oaks in two restored oak savannahs in southeastern Minnesota.

Table 2. At St. Olaf College in southeastern Minnesota fourteen different types of galls were found on oaks in a restored oak forest. Most species (10) were found on leaves, while four gall types were found on twigs. The most prevalent gall species on white oak were *Disholcaspis globulus* (bullet oak gall). Of the galls found on red oak, one third were *Cynips dimorphus*. On bur oak, *Acraspis pezomachoides* (oak pea gall) were the most common. The three types of oaks had similar levels of species diversity as measured by the Shannon and Simpson Diversity Indices.

		Percent of gall species found on each type of oak tree		
Gall-forming species	**Gall location**	**White Oak**	**Red Oak**	**Bur Oak**
Disholcaspis mamma	Twig	4.9	0	32.2
Disholcaspis globulus	Twig	29.3	11.1	0
Callirhytis clavula	Twig	4.9	0	0
Unidentified—1	Twig	19.5	0	0
Andricus petiolicola	Petiole	2.4	0	0
Acraspis villosa	Leaf midrib	26.8	0	12.9
Cynips dimorphus	Leaf midrib	0	33.3	9.7
Acraspis pezomachoides	Leaf vein	0	11.1	29.0
Andricus singularis	Leaf vein	0	11.1	0
Philinox nigra	Leaf vein	4.9	0	0
Neuterus saltarius	Leaf tissue	0	0	6.5
Unidentified—2	Leaf tissue	0	0	9.7
Unidentified—3	Leaf tissue	7.3	11.1	0
Unidentified—4	Leaf surface	0	22.2	0
		100%	**100%**	**100%**
Total # Species Found	**14**	**8**	**6**	**6**
Shannon D.I.		**1.76**	**1.68**	**1.61**
Simpson D.I.		**0.81**	**0.89**	**0.80**

Table 3. At Carleton College in southeastern Minnesota seven different types of galls were found on oaks in a restored oak forest. Most species (6) were found on leaves, while one gall type was found on twigs. There were two types of galls found on white oak leaves, but neither was positively identified. These two gall species were also most prevalent on red oak. On bur oak, *Disholcaspis mamma* (rough bullet gall) was the most common. Of the three types of oaks, the highest level of species diversity was found on red oaks as measured by the Shannon and Simpson Diversity Indices.

		Percent of gall species found on each type of oak tree		
Gall-forming species	**Gall location**	**White Oak**	**Red Oak**	**Bur Oak**
Disholcaspis mamma	Twig	0	0	83.3
Acraspis villosa	Leaf midrib	0	0	16.7
Cynips dimorphus	Leaf midrib	0	3.7	0
Unidentified—2	Leaf tissue	50.0	48.2	0
Unidentified—3	Leaf tissue	0	3.7	0
Unidentified—4	Leaf surface	50.0	37.0	0
Unidentified—5	Leaf underside	0	7.4	0
		100%	**100%**	**100%**
Total # Species Found	**7**	**2**	**5**	**2**
Shannon D.I.		**0.69**	**1.16**	**0.45**
Simpson D.I.		*	**0.65**	**0.33**

* Insufficient data

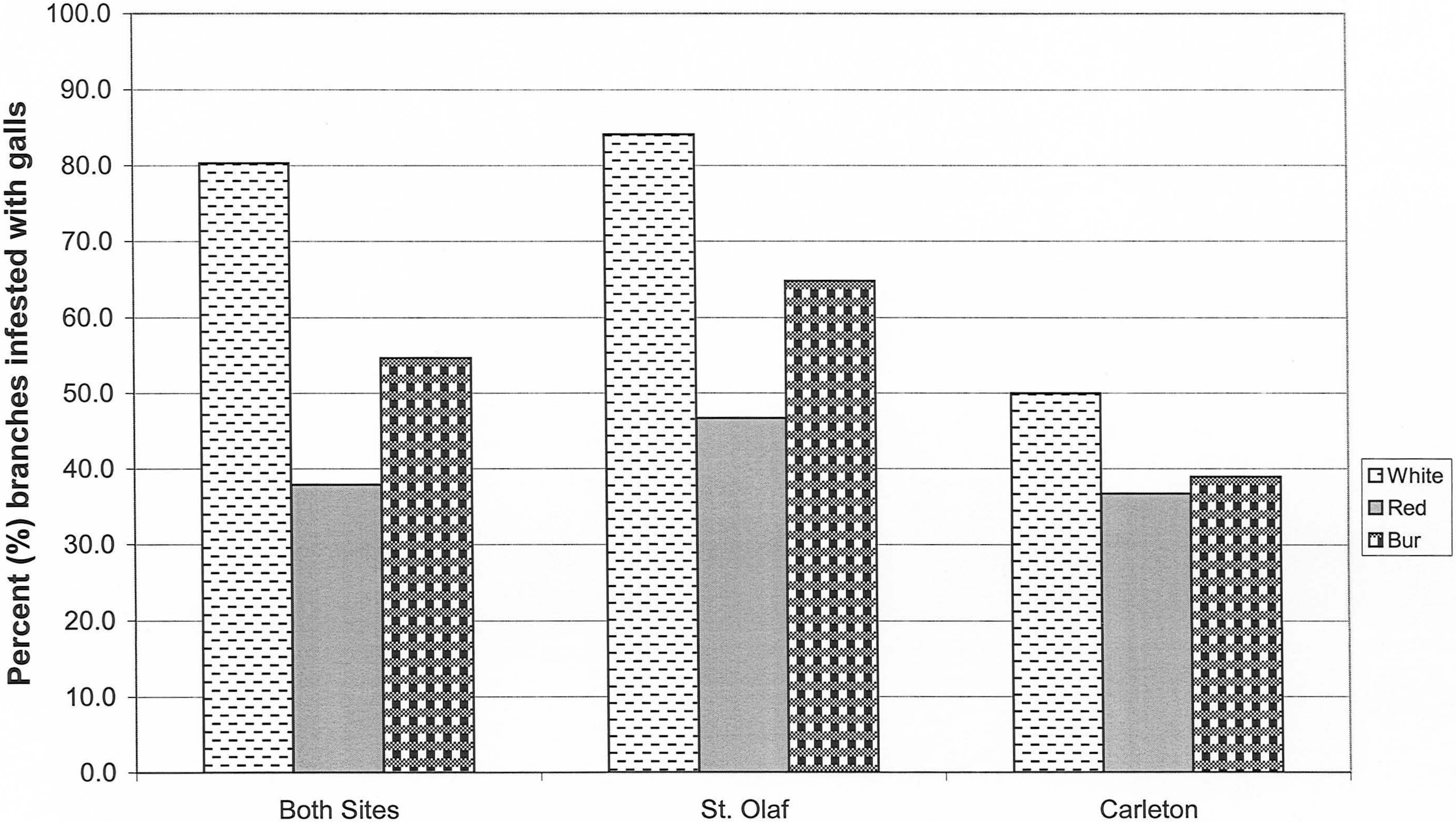

Fig. 2 White oaks in the restored oak forests at St. Olaf and Carleton Colleges had the highest infestation rates of leaf and twig galls. At both sites, the next highest were bur oaks and the least infested were red oaks.

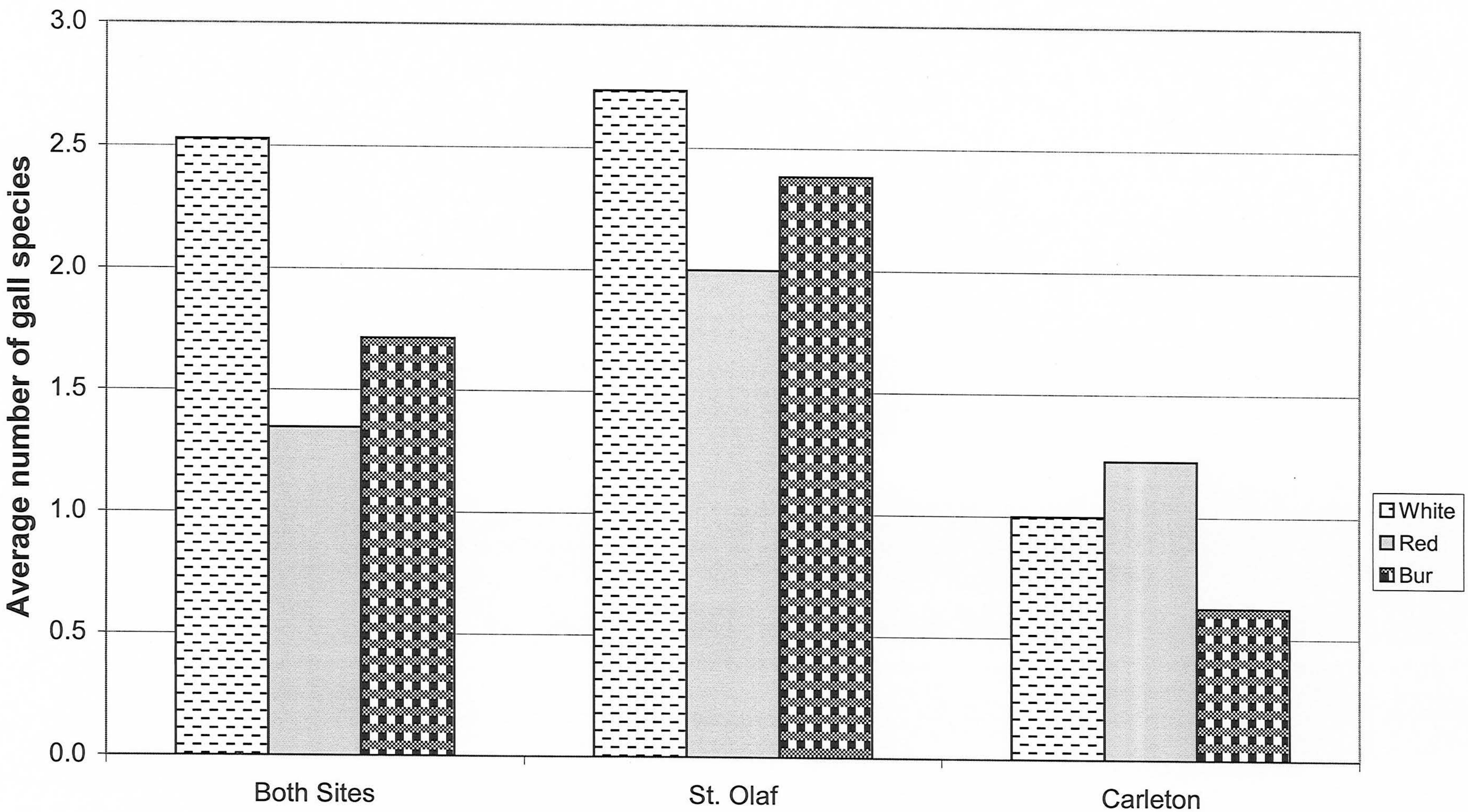

Fig. 3 The highest number of gall species were found on white oaks in two restored oak forests. The oaks at St. Olaf College had a higher number of gall species compared to the oaks at Carleton College.

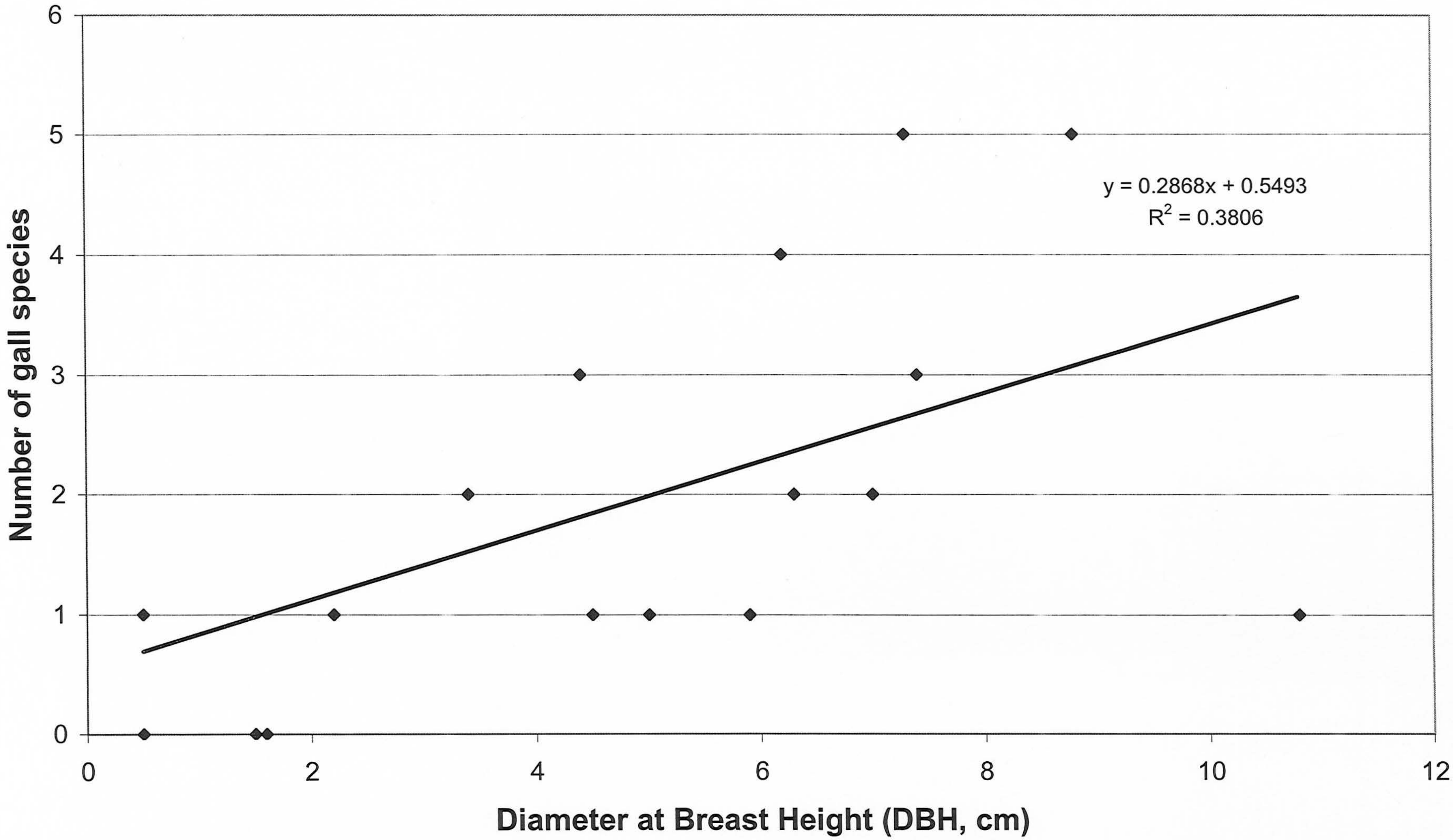

Fig. 4 On Bur Oak in two restored oak forests, the number of gall species was positively correlated with DBH (P=0.0029).