CALIBRATING VEGETATION COVER AND POLLEN ASSEMBLAGES IN THE FLINT HILLS OF KANSAS, U.S.A.

by

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Abstract

The quantitative relationship between pollen assemblages in sediment and vegetation cover is largely unknown because many factors influence this relationship. This lack of quantitative relationship is particularly acute in grassland regions, where both past and future climate change have the potential to determine grassland composition and cover. The tool used to reconstruct past grassland cover is the relative abundance of distinct fossil pollen types preserved in sediment. However, the interpretation of grassland pollen assemblages as grassland vegetation types needs to be refined to improve these reconstructions. Using pollen found in the surface sediments from 24 artificially-constructed ponds in the Flint Hills ecoregion of Kansas, USA, I examined relationships between pollen and vegetation in the tallgrass prairie biome, which includes woody components. By comparing the pollen data to field-surveyed vegetation data and land cover classifications taken from Kansas Gap Analysis Program data, I correlated pollen and vegetation in this ecoregion. Pollen productivity estimates for *Artemisia, Ambrosia,* Asteraceae, Chenopodiaceae, *Cornus,* Fabaceae, *Juniperus, Maclura,* Poaceae, *Populus, Quercus,* and *Salix* were calculated via the Extended R-Value Model. Common pollen types identified in sediments are mostly herbaceous grassland plant species such as Poaceae, *Artemisia,* and *Ambrosia*, but woody plants such as *Populus, Quercus*, and *Juniperus* are also represented. PPEs have been calculated for four of these taxa in Europe, and values from the Flint Hills are higher. These are the first PPEs reported for eight of these taxa. This research will further advance quantitative vegetation reconstructions in the Great Plains of North America and refine interpretations of how climate change affects grasslands.

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CHAPTER 1 - Literature Review

The relationship between Quaternary climate change and pollen preserved in bog sediments was discovered in the early 20th century (Von Post, 1916). Subsequent decades saw improvements in the details of how vegetation cover is represented by pollen assemblages, particularly in Holocene sediments (Davis, 1965; Webb & Bryson, 1972; Prentice, 1985; Davis, 2000). However, the exact quantitative relationship still remains unknown for some types of landscapes, such as grasslands. While many studies have examined forested regions or forest/grassland mixed regions (Calcote, 1995; Sugita *et al.*, 2006; Soepboer *et al.*, 2007; Mazier *et al.*, 2008), very few studies have examined this relationship for grasslands, and none in North American grasslands. Grasslands are widespread on earth, and characteristically experience temporally and spatially variable precipitation (Gibson, 2009). Understanding grassland responses to climate change is important (Borchert, 1971) and examining the paleorecord is one way to do this. To understand how grassland vegetation responded to droughts and megadroughts in the past, we need to be able to interpret grassland pollen assemblages as quantitative vegetation cover.

In order to obtain accurate quantitative vegetation reconstructions for past landscapes through analysis of fossil pollen, we must have a quantitative understanding of pollen-vegetation relationships at the present day. For this reason, it is important to better quantify the relationship between pollen assemblages and vegetation cover in grassland regions. Since much less knowledge exists about the pollen-vegetation relationship for grassland regions compared to forested regions, this study advances quantitative vegetation reconstructions for grasslands.

Relevance to Geography

Understanding the Earth surface and the impacts that humans have on it is a major cornerstone of geography's purpose (Pattison, 1964; National Research Council, 1997). At the same time, a spatial understanding of vegetation on the landscape falls nicely into more than one "tradition" of geography. Pattison (1964) describes four main geographical traditions: 1) spatial tradition, 2) area studies tradition, 3) man-land tradition, and 4) Earth science tradition. My research not only emphasizes the spatial tradition by examining the spatial nature of pollen dispersal, but it also contributes to the man-land tradition by developing the potential to reconstruct past and present landscapes. Furthermore, it is entwined with the Earth science tradition, because it adds to current knowledge about pollination habits of grassland plants.

The amount of pollen that plants produce varies among taxa. For this reason, it is difficult to know exactly what fossilized pollen assemblages represent on the landscape, unless one accounts for the relative pollen productivity among plant taxa. Three different methods exist to interpret pollen assemblages in sediment samples. One way is to qualitatively estimate the plant species that were present on the landscape based on the appearance of their pollen in the sediment (Noe & Blom, 1982; Plunkett, 2009; Zerniskaya & Mikhailov, 2009). Another method is the Modern Analog Technique (e.g. Williams *et al.*, 2000), which essentially statistically matches pollen assemblages from a present-day landscape with pollen assemblages from an unknown past landscape to determine the vegetation composition of the unknown past landscape. While these two methods provide some way of understanding the landscape and are valuable in their own realms, they lack the quantitative capacity to reconstruct landscapes. A third method of interpretation makes use of the Extended R-Value method (ERV) (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1994; and Calcote, 1995) to quantitatively reconstruct past landscapes. This method produces taxon-specific estimates of pollen productivity that can be used for quantitative reconstructions of past vegetation composition.

With pollen productivity estimates, one can better interpret how a landscape looked in the past, and how it has changed over time. This has been particularly useful in reconstructing vegetation cover and human land use in Europe to supplement the archaeological record (Caseldine & Fyfe, 2006). Pollen productivity estimates have been used as an aid in interpreting sediment cores from Neolithic times (Tipping *et al.*, 2009). My study provides pollen productivity estimates for grassland species in North America, which could help other geographers, paleoecologists, and archaeologists interpret how the landscape has changed across the Great Plains.

Thus, this study contributes to the man-land tradition of Pattison's (1964) four traditions of geography, as well as the spatial tradition and the Earth science tradition. While using pollen productivity estimates to understand how humans have shaped the vegetation of the landscape is a useful endeavor in itself, knowing the differences in pollen productivity among species is intrinsically useful, and contributes to the Earth science tradition. Furthermore, this study examines the spatial relationship between pollen and vegetation in grassland regions of North America, which falls within the spatial tradition of geography.

The Pollen-Vegetation Relationship

Many studies across Europe and a few in North America have attempted to define the quantitative relationship between pollen assemblages and vegetation cover (Broström *et al.,* 2008; Broström *et al.,* 2004; Bunting *et al.,* 2005; Calcote, 1995; Mazier *et al.,* 2008; Nielsen & Sugita, 2005; Soepboer *et al.,* 2007; Von Stedingk *et al.,* 2008). While a reliable relationship applicable across multiple regions remains elusive, much understanding has been gained through past research. Three major advances have been: 1) investigating pollen source areas, 2) developing new models for calibrating pollen assemblages and vegetation cover, and 3) conducting studies in areas with different types of vegetation cover.

Relevant Source Area of Pollen

The first advance is the concept of the relevant source area of pollen (RSAP) (Sugita, 1994; Bunting *et al.,* 2004; Nielsen & Sugita, 2005; Broström *et al.,* 2005). The definition of RSAP is the distance at which the correlation between the pollen in the sediment and the vegetation on the landscape does not improve. It is sometimes called the “pollenshed” of a sedimentary basin. The general idea is that pollen found in a sediment sample represents mostly vegetation that is relatively close to a pond. Beyond a certain distance, plants will still contribute some pollen to the pond sediments, but this background pollen remains taxonomically and quantitatively similar among ponds in a region (Sugita, 1994). It requires pollen samples from many sites to calculate RSAP for a region. Thus, once the relative proportions of pollen contributed by both the RSAP and background areas is calculated, local vegetation can be reconstructed at a single site (Sugita, 1994).

The radius of the relevant source area is different among regions, because it depends on three factors. The spatial heterogeneity of the vegetation and the size of the basin are two primary factors (Bunting *et al.,* 2004). Small ponds have a smaller relevant source area of pollen than large lakes. The third factor that determines RSAP is pollen productivity, or the amount of pollen produced by a given plant taxon (discussed in the next section). Although we cannot know exactly how far pollen grains travel, the relevant source area of pollen can help determine the spatial relationship between the pollen sample and the landscape it represents.

A number of recent studies have estimated RSAP. Duffin and Bunting (2008) estimated RSAP and obtained pollen productivity estimates for plant taxa in a southern African savanna. Their study area contained a variety of botanically distinct landscapes including grassland and broadleaved deciduous woodlands. They estimated the relevant source area to be 600 – 900 m for 26 ponds ranging from 10 – 500 m in diameter. Mazier *et al.* (2008) studied a pasture-woodland landscape in the Swiss Jura Mountains using pollen from moss polsters. They determined an RSAP of about 300 m for moss polster samples taken from 20 different sites across the study area. While RSAP has been calculated in a variety of landscapes using both moss polsters and sediment samples, (Broström *et al.,* 2004; Bunting *et al.,* 2005; Nielsen & Sugita, 2005; Rasanen *et al.,* 2007; Von Stedingk *et al.,* 2008; Mazier *et al.,* 2008; Duffin & Bunting, 2008), grassland regions in North America have not previously been studied.

Pollen Productivity Models

The second major advance is the development of models for quantifying the pollen-vegetation relationship. First, models are necessary to calculate pollen productivity estimates, and then another set of models are necessary to use these PPEs for vegetation reconstruction. There are many advantages to using models for palynological research. In general, models are useful for data analysis and research design. They enable data analysis methods to be easily reproduced by allowing other researchers to use them. Additionally, models can display both the limits and potential of the data. Conversely, models are a simplification of reality, and cannot completely describe the quantitative relationships between vegetation and pollen. However, as long as the assumptions and limitations of the models are taken into account, they can be very powerful tools.

Many palynologists have contributed to the development of the Extended R-Value Model (ERV) (Davis, 1963; Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1994) to estimate pollen productivity relationships. It is important to quantify the amount of pollen that different plant taxa release, because plants produce varying amounts of pollen, and this must be taken into account when trying to examine pollen records to reconstruct landscapes. The original R-Value Model was first developed to obtain estimates of pollen productivity (Davis, 1963). The basis behind this model is that pollen loading, or the amount of pollen deposited per unit area on a surface, is a function of pollen productivity and vegetation abundance. If one knows the amount of pollen loading and the vegetation abundance for a taxon, then one can calculate the pollen productivity.

The theory behind the R-Value model has been utilized to produce Extended R-Value Models (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1994), which improve upon the R-Value Model in a number of ways. The Prentice model utilized the base model that Davis provided in her R-Value model, but also included fall speed of pollen, wind speed, and basin distance to estimate pollen dispersal-deposition (Prentice, 1985). Fall speed refers to how quickly a pollen grain will reach the ground after it is released from the plant. It is important to consider fall speed because heavy pollen will not disperse as far as light-weight pollen. Wind speed is also a factor, because it affects the distance pollen will travel across a landscape, and therefore could increase the relevant source area. Additionally, the distance between the basin and the plant is a factor, because plants nearest to the basin contribute the most to the pollen record (Prentice, 1985). This last factor is why distance-weighted vegetation estimates are used with the models.

The Prentice (1985) model assumes that pollen is deposited at a point in the center of a basin. This assumption is fine for pollen samples taken from bogs or moss polsters, but lakes and ponds do not operate in the same way. When pollen is deposited on the surface of a pond, it does not sink directly down into the sediment. The water causes the pollen to mix before it deposits on the bottom of the pond. Sugita (1994) further developed the Prentice model to account for mixing, which makes this model a better option for pollen samples taken from ponds or lakes. This model assumes total mixing, and accounts for pollen that lands anywhere on the surface of the lake, not just in the center.

Landscape Reconstruction Algorithm

Other pollen-vegetation models have been developed aside from those that estimate pollen productivity. One of these models is the Landscape Reconstruction Algorithm (LRA) (Sugita, 2007a; Sugita, 2007b). This algorithm includes two important submodels: REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) and LOVE (Local Vegetation Estimates). The idea behind the Landscape Reconstruction Algorithm is that large lakes can detect a pollen signal from a large area, while small lakes can detect a pollen signal from a small area. When samples from large lakes and small lakes are used in conjuction with one another, the LRA can predict the vegetation cover on a landscape. Pollen found in sediment samples from large lakes is representative of the regional vegetation, and samples taken from small lakes or ponds are better indicators of local vegetation. Large lakes are usually greater than 10 hectares in size, but preferably 100 to 500 hectares (Sugita, 2007a). Small lakes are less than 10 hectares in size (Sugita, 2007b). For both the regional and local estimates, one should take samples from more than one site within a study area. Regional estimates work best when samples are taken from 2 to 5 lakes. For the local estimates, several target sites should be chosen within the relevant source area of pollen of the large lakes, because the small target sites could provide an idea of the vegetation variation within a region.

Before using the Landscape Reconstruction Algorithm, it is important for one to obtain pollen productivity estimates for the plant taxa to be reconstructed on the landscape (Sugita, 2007a; Sugita, 2007b). If pollen productivity estimates have already been found for the taxa and the region one is studying, then those estimates could be used. If not, pollen productivity estimates will have to be obtained using the Extended R-Value Models (ERV) (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Sugita, 1994), which are based on the R-Value Model (Davis, 1963). In addition to pollen productivity estimates, pollen counts are necessary for each taxa being examined. The pollen counts can be from current or fossil pollen samples, depending on whether one is trying to reconstruct modern or historic vegetation. The LRA has been validated in an area in southern Sweden (Hellman *et al.*, 2008a; Hellman *et al.*, 2008b). It should be tested in other regions also, to account for any regional differences that might affect its validation.

Regional Studies

Studies examining pollen-vegetation relationships have been conducted in several different landscapes. Pollen assemblages from surface sediment samples have been calibrated with open spaces in forested landscapes in New England, USA (McLauchlan *et al.*, 2007). A synthesis of studies across Europe has shown that regional differences in pollen productivity estimates could be due to both methodological factors and environmental factors (Broström *et al.*, 2008).

While limited PPE work has been done in North America, many pollen-vegetation calibration studies have occurred in various areas of Europe (Broström *et al.*, 2004; Soepboer *et* *al.,* 2007; Mazier *et al.,* 2008). These studies have all aimed at developing pollen productivity estimates. Broström *et al.* (2004) conducted their study in southern Sweden. They calculated pollen productivity estimates for 11 herb taxa and 1 tree taxon. The landscape consisted of both open and semi-open areas. Mazier *et al.* (2008) examined a landscape in the Jura Mountains of Switzerland. They obtained pollen productivity estimates for 11 taxa. They acquired their pollen data from 20 different sites in this pasture-woodland area.

Soepboer *et al.* (2007) also sampled 20 different sites and estimated pollen productivity for 12 taxa. Their study area focused on the Swiss Plateau. The results for their pollen productivity estimates were generally lower than those in southern Sweden (Broström *et al.,* 2004) and also lower than another study in the United Kingdom (Bunting *et al.*, 2005). This could be due to either methodological differences or to regional differences in the pollen productivity of plants. Pollen productivity estimates for one region might not be directly applicable to another region.

In North America, there has only been one research project that estimated pollen productivity, and it was limited to a few forest types. This study compared PPEs for a pine-dominated area in northwest Wisconsin with a hemlock-hardwood-dominated area in Michigan's Upper Peninsula (Calcote, 1995). Monospecific taxa— such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and basswood (*Tilia americana*)— showed similar PPEs between the two regions. Some taxa, such as birch (*Betula* spp.) and pine (*Pinus* spp.), had slightly higher or lower PPEs for one region compared to the other region. This finding emphasizes the importance of having PPEs that are directly applicable to the region of interest when attempting to use PPEs for landscape reconstruction.

To date, no pollen productivity estimates for North American grasslands have been developed. My research fills this void, and the pollen productivity estimates can be directly applied to the Landscape Reconstruction Algorithm (Sugita 2007a; Sugita, 2007b). In addition, researchers striving to reconstruct past landscapes based on fossil pollen might also be able to use these estimates. Consequently, my research strives to fill in some of the gaps where knowledge is missing about pollen-vegetation relationships in grasslands areas. Climate change has the potential to greatly impact grassland areas, so knowing the quantitative connection between pollen and vegetation cover is important.

Applications

Because pollen productivity estimates are used to reconstruct landscapes and past environments, one major application has been to reinterpret past cultural landscapes in Europe. Pollen records have long been used to interpret cultural landscapes in Europe (Iversen, 1973), but recent studies have improved the detection of anthropogenic impact on the landscape (Overland & Hjelle, 2009; Davies & Tipping, 2004). Pollen productivity estimates have particularly improved interpretation of pollen from crop plants like *Cerealia* that may cover large portions of the landscape without producing much pollen.

Traditional pollen interpretations in Europe have used the initial presence of *Cerealia* pollen in sediment records to determine the onset of agricultural practices in past cultures (Plunkett, 2009; Zernitskaya & Mikhailov, 2009). Similarly, the presence of *Plantago* pollen can serve as an indication of compacted soil (Noe & Blom, 1982), which would imply continuous compaction from some animal, potentially livestock or humans. Some pollen types that might explain interesting land use changes in the Flint Hills would include *Maclura* or

Juniperus. The former has been planted by ranchers and farmers as a hedge tree, while the latter tends to increase in abundance on the landscape if prairies are not burned regularly.

In landscape-level studies, qualitative interpretation or matching analogues are used to analyze the pollen record. For example, a comparison of the ratio of arboreal pollen to non-arboreal pollen was one method used in a study conducted in western Norway of farmed landscapes (Overland & Hjelle, 2009). The authors noticed a decline in arboreal pollen during the Neolithic as non-arboreal pollen types increased and overall pollen diversity increased. They attributed these changes to an increase in agriculture and grazing. Fyfe *et al.* (2003) also used traditional pollen methods in southwest England to infer the timing of dominant pastoral land use, and the switch from pastoral to mixed arable-pastoral farming. In addition, they were able to notice distinct woodland clearances during the Neolithic. They speculated that the woodlands were cleared to allow room for grazing, because charcoal was noted in the samples at the same time, which indicates that the woodlands were burned rather than cut.

While qualitative interpretation of pollen data is useful for making generalizations pertaining to the timing of events, there are limits to what it can tell us about the composition of a landscape. For example, the initial presence of *Cerealia* pollen can tell us when modern agricultural practices began, but it cannot tell us how much of the total landscape was agricultural land if we do not know the pollen productivity of *Cerealia*. Likewise, a noticeable increase in *Juniperus* pollen throughout time in a sediment core tells us that *Juniperus* trees likely increased on the landscape, but we will not know quantitatively what that increase looked like unless we know the productivity of *Juniperus* in reference to the other pollen types present in the sample. For these reasons, pollen productivity is an important factor in gaining better interpretations of all types of landscapes—both cultural and biological.

In addition to aiding in cultural landscape interpretation, PPEs can help inform knowledge about anthropogenic climate change. One example of this is a hypothesis (Ruddiman, 2003) which proposes that anthropogenic warming may have begun 5000-8000 years ago, rather than 150-200 years ago. This hypothesis is based on the timing of the onset of forest clearance for agricultural land use. While the timing of this onset can be estimated by examining paleorecords, the degree of forest clearance or agricultural expansion cannot be known without knowing the extent of their coverage on the landscape. PPEs provide a way to quantify vegetation cover so that the landscape composition can better inform hypotheses like Ruddiman’s.

CHAPTER 2 - Introduction

Despite years of study, reliable quantitative reconstructions of vegetation cover from pollen records remain a common goal of many paleoecologists and biogeographers (Seppa & Bennett, 2003; Davis, 2000). Because of differential pollen productivity among taxa, it is impossible to quantitatively reconstruct a landscape based on pollen percentages alone. Recent conceptual advances have allowed the calculation of pollen productivity estimates (PPEs) that account for differential pollen productivity among plant taxa (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Sugita, 1994). However, calibration efforts are labor-intensive and the application of PPEs to landscape reconstruction is far from routine. In North America, hardly any PPE work has been done, with the exception of a few studies limited to forest ecosystems (Calcote, 1995; Sugita *et al.*, 2006).

There are three ways to interpret pollen assemblages: 1) Qualitative analyses, 2) Modern Analog Techniques, and 3) Quantitative Modeling. While each of these methods is important for answering different questions, quantitative modeling is the necessary method for understanding land cover change. Qualitative analyses can help answer questions about landscape change based on raw pollen percentages, especially with indicator taxa (Noe & Blom, 1982; Plunkett, 2009; Zerniskaya & Mikhailov, 2009), however, pollen percentages do not account for differences in pollen productivity among taxa. Modern analog techniques can statistically match pollen records from an unknown past landscape with those of a known modern landscape, and large datasets are now available for performing these analyses (Whitmore *et al.,* 2005; Li *et al.*, 2007; Gajewski, 2008). This technique is not effective for reconstructing land cover if an analog is not present (Jackson & Williams, 2004) but see Gonzales *et al.*, 2009), or if detailed vegetation metadata are not available. The third approach, quantitative modeling is a relatively reliable method for understanding landscape changes over time (Prentice, 1985; Sugita, 1994). An understanding of land cover change is especially important in grassland regions because of extreme climate variability in the past (Michels *et al.*, 2007), and the potential for future climate change (IPCC, 2007). For example, past climate changes likely caused shifts in the borders of tallgrass, mixed grass, and short grass prairies, but these are currently unidentifiable in the North American pollen record.

Additionally, the spatial area represented by pollen in sediments is rarely investigated. Thus, pollen records can be presented without any information about the spatial scale they represent (Bellini *et al.*, 2009; Teed *et al.*, 2009; Lee *et al.*, 2010). Generally speaking, small basins reflect local vegetation and large basins reflect regional vegetation (Sugita, 2007a; Sugita 2007b). All sedimentary basins have a relevant source area of pollen (RSAP) which is sometimes referred to as the “pollenshed” of the basin. The basic idea is that only the vegetation in a certain area surrounding each basin corresponds to the types and quantities of pollen deposited there. Correlations between plant abundance and pollen loading will improve as distance increases. At a certain distance, however, the correlation does not continue to improve, even with continued vegetation sampling to greater distances. The area surrounding the basin beyond which the correlation between pollen and vegetation does not improve is defined as the relevant source area of pollen (RSAP) (Sugita, 1994). RSAP can be calculated using the Extended R-Value (ERV) models (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Sugita, 1994) which are also used to calculate pollen productivity.

The Extended R-Value (ERV) models were proposed to overcome the difficulties associated with the use of pollen percentages and made it possible to estimate pollen productivity. These pollen productivity estimates are, for a given plant taxon, the slope of the linear relationship between pollen loading in absolute units and the vegetation composition with distance weighting (Sugita, 1994). PPEs are calculated relative to a taxon that the user chooses, also known as a “reference taxon”. The ERV models have been extensively used to calculate pollen productivity estimates in the upper Great Lakes region (Calcote, 1995; Sugita *et al.*, 2006), southern Sweden (Broström *et al.,* 2004), central Sweden (Von Stedingk *et al.*, 2008), Denmark (Nielsen & Sugita, 2005), Switzerland (Soepboer *et al.,* 2007), Finland (Rasanen *et al.,* 2007), and the United Kingdom (Bunting *et al.*, 2005). Additionally, PPEs can be applied to landscape reconstruction models, such as the Landscape Reconstruction Algorithm (LRA) (Sugita, 2007a; Sugita, 2007b), which uses PPEs to reconstruct vegetation cover based on pollen data.

Objectives

In this study, I collected surface sediments from small ponds in a tallgrass prairie ecoregion to obtain PPEs for 12 selected plant taxa, and calculated the relevant source area of pollen for small ponds approximately 50 m in radius. I had three primary aims:

1) Provide pollen productivity estimates for 12 plant taxa found in the Flint Hills of Kansas, USA.

2) Aid in a better understanding of the spatial relationship between pollen assemblages in small ponds and vegetation cover on the landscape, through calculation of the RSAP.
3) Enable future use of the Landscape Reconstruction Algorithm (LRA) for grasslands in North America, by providing PPEs that are necessary for using the LRA.

Hypotheses

Based on these objectives, I have two hypotheses:

H1: Common grassland plant taxa will differ in pollen productivity (Table 2.1), with tree taxa being higher than Poaceae (the reference taxon), and most herbaceous taxa (except Chenopodiaceae and *Ambrosia*) being lower than Poaceae, because of their inherently different pollination habits. This hypothesis is based on the results of several PPE studies that have shown that tree taxa generally have higher PPEs than Poaceae, and most herbaceous taxa generally have lower PPEs than Poaceae (Broström *et al.,* 2008).

H2: Present-day pollen assemblages taken from sediment samples in ponds approximately 50 m in radius are correlated with vegetation cover at the family-level to a distance of about 1000 m. This hypothesis is based on the results of studies that have examined forest and grassland mixed landscapes, which have shown the connection between the pollen assemblages and chosen taxa (Broström *et al.,* 2008; Gaillard *et al.,* 2008).

Table 2.1: Plant taxa and hypothesized pollen productivity.

	Plant Taxa	Hypothesized Pollen Productivity
Herbaceous	*Ambrosia*	Very high
	Artemisia	Low
	Asteraceae	Very low
	Chenopodiaceae	Very high
	Fabaceae	Very low
	Poaceae	Average (reference taxon)
Non-herbaceous	*Cornus*	Low
	Juniperus	Very high
	Maclura	High
	Populus	High
	Quercus	High
	Salix	High

CHAPTER 3 - Study Area

The Flint Hills Tallgrass Ecoregion is located in eastern Kansas and stretches southward in a band from the Kansas-Nebraska border into northern Oklahoma (Fig. 3.1). Layers of Permian shale and limestone comprise the geology of the Flint Hills, with differential weathering generating the visible layers in the hills (Reichman & Mulligan, 1995). The erosion-resistant limestone, which contains silica, overlays the more easily-eroded mudstone.

Climate in the Flint Hills is variable and continental, being geographically close to the center of North America. Temperatures are variable throughout the year, with high temperatures of 25°C to 38 °C in the summer and low temperatures of -12°C to -6°C in the winter at the National Park Service's Tallgrass Preserve (U.S. National Park Service, 2010), which is close to the geographic center of the ecoregion. Average annual precipitation is generally greater than 75 cm (U.S. National Park Service, 2010). In the summer, severe thunderstorms with heavy downpours and hail are common. Winter snowfall events are not uncommon, especially in the northern part of the Flint Hills.

Tallgrass prairie dominates the vegetative cover of the Flint Hills (Fig. 3.1). Grasses such as Big Bluestem (*Andropogon gerardii)* and Indian Grass *(Sorghastrum nutans)* are very common. Mixed in with the grasses are a variety of forbs including various sunflower, goldenrod, sage, and ragweed species. Eastern Red Cedar *(Juniperus virginiana),* Bur Oak *(Quercus macrocarpa),* and Cottonwood (*Populus deltoides)* are some of the tree species present.

While a few thousand hectares of the grassland is managed for conservation purposes, for example at the Konza Prairie Biological Resesarch Station and the National Park Service's

Tallgrass Preserve, much of the land is privately owned and serves as important grazing land for cattle. Ranching is an important human activity in this area, since cultivation can be impossible on the slopes of the hills and the soils are shallow and rocky.

I chose to conduct this study in the Flint Hills for two reasons. First, it is the largest remaining expanse of tallgrass prairie in North America. While tallgrass prairie previously covered 140 million acres of land in North America, only 4% remains today (National Park Service, 2010). Second, the vegetation cover is predominantly grassland with some woody components, so it is a prime location for studying the pollen-vegetation relationships of grasses and other forbs, while also providing insight into the nature of arboreal versus non-arboreal pollen productivity.

The 24 pond sites were selected as randomly as possible while still covering the breadth of the study area (Fig. 3.1). Vegetation cover varied on a site-to-site basis for each of the ponds sampled (Fig. 3.2). The majority of the sites included woody components at the edge of the pond, with grasses and herbs beyond the woody areas. Some sites contained absolutely no woody species within 100 m, and some were dominated by woody species for the first 100 m.

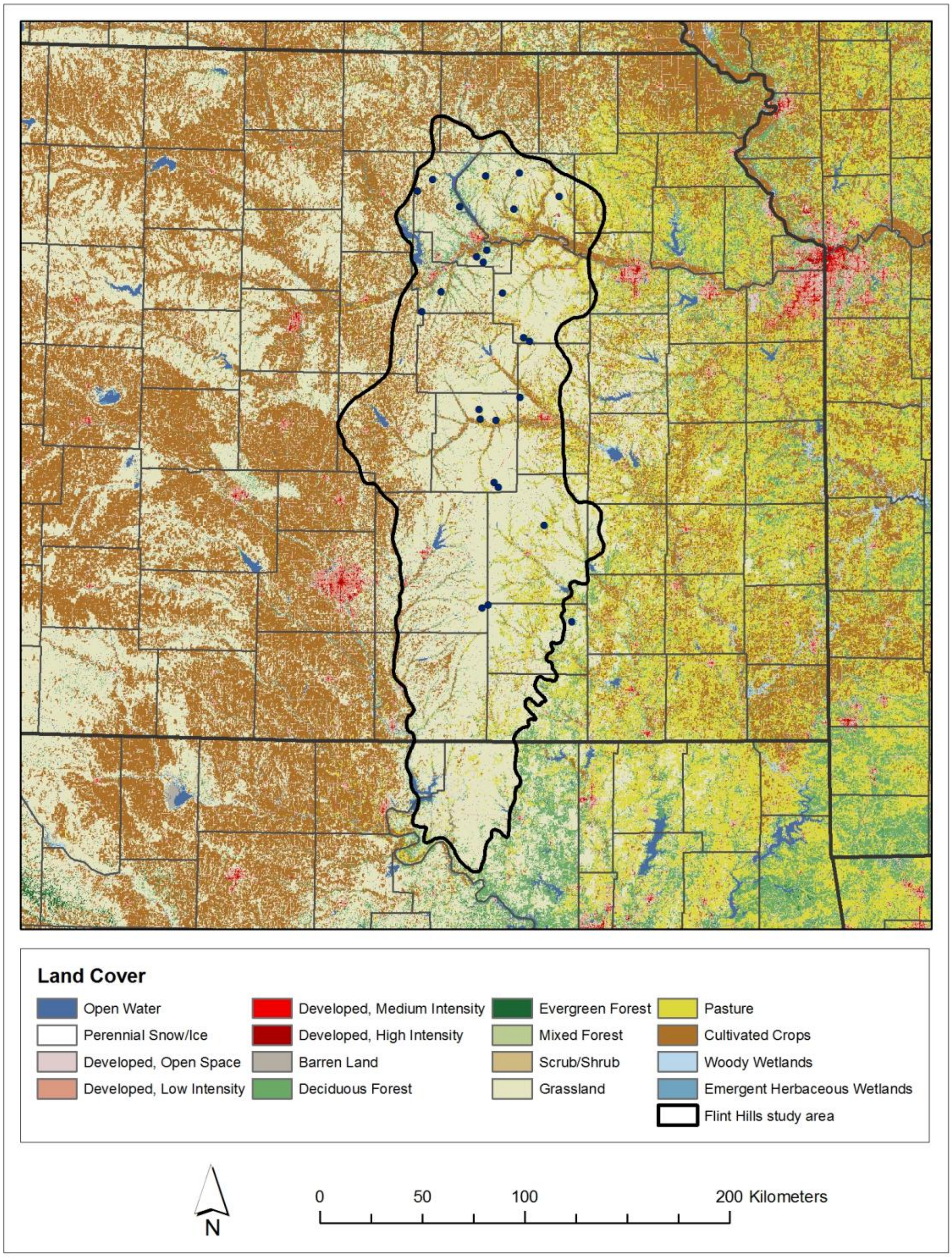

Figure 3.1: Location of 24 ponds for sediment acquisition in the Flint Hills study area with land cover types from U.S. National Land Cover Data set (2001). Flint Hills boundary follows U.S. Environmental Protection Agency.

Figure 3.2: Vegetation at a non-woody site (left) and a woody site (right).

CHAPTER 4 - Methods

As outlined in Chapter 2, the primary goal of this research is to obtain pollen productivity estimates for 12 grassland plant taxa in the Flint Hills ecoregion. To obtain pollen productivity estimates using the Extended R-Value Models (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1994; Calcote, 1995), there are two data requirements: quantitative pollen data taken from a sample point, and distance-weighted vegetation data representing the area around the sample point. There are multiple ways to obtain these types of data. For example, pollen can be extracted from moss polsters or sediment samples. Vegetation data can be acquired through field surveys, aerial photos, and digital land cover maps.

Sediment Acquisition

From May through August 2009, I acquired sediment samples from 24 ponds across the Flint Hills of Kansas. A total of 24 ponds were chosen because the number of ponds should be double the number of taxa being examined. The ponds were selected to be placed as randomly as possible across the entire ecoregion. These ponds are artificially constructed by damming small streams. The ponds need to represent actual vegetation on the landscape, not selected vegetation types, so the sites varied in the amount of woody and herbaceous vegetation they contained. Since most of the land in the Flint Hills is privately owned, the locations of the selected ponds were determined by the availability of cooperating landowners located through county extension agents and local residents. Each pond was less than 10 hectares in size, and averaged approximately 50 m in radius (Table 4.1). Average water depth was 2.5 m. In the field, I marked the location of each pond using a global positioning system, and later imported these coordinates into GIS.

Table 4.1: Radius length and area of each pond in the Flint Hills study area.

Site	Shortest Radius (m)	Longest Radius (m)	Area (m^2)
1	12	16	578.8849
2	31	56	5950.693
3	14	78	5013.744
4	23	76	3943.919
5	19	62	3634.658
6	20	65	3462.785
7	35	110	10248.07
8	57	111	16940.91
9	28	80	5172.447
10	29	125	15103.13
11	18	39	1569.728
12	44	108	17562.07
13	23	76	5734.82
14	44	118	15588.55
15	20	64	3599.819
16	22	67	5424.173
17	24	84	6519.644
18	10	21	762.5506
19	22	65	4869.748
20	21	69	6034.045
21	30	150	13178.66
22	23	63	5015.103
23	38	92	10092.59
24	22	40	2775.99
Average	**26**	**76**	**7032.36**

I took three sediment samples from the center of each pond, which is the location most representative of the pollen landing on the surface of the water (Sugita, 1994). To obtain each sample, I used an Ekman dredge operated from an inflatable raft. This is a square-shaped dredge with opposable jaws that are left open as the dredge is lowered into the pond on a rope. After the trap reaches the pond sediment, the user sends a weighted messenger down the rope which closes the jaws and traps the sediment. I collected the top 2 centimeters of each sample, because it represents several years of modern vegetation, and this is the standard amount of sediment collected for surface samples for other studies of this nature (Hicks, 2001; Duffin & Bunting, 2008; Hellman *et al.*, 2008a).

In the lab, I created a composite sediment sample by mixing equal volumes of the three samples together for each site, and deposited 2 cubic centimeters of sediment into a plastic test tube. I sent all 24 samples to the Limnological Research Center at the University of Minnesota, where pollen was isolated from bulk sediment using a series of chemical digestions including acetolysis and other standard techniques (Faegri & Iversen, 1989). Pollen grains for each sample were identified visually in a light microscope at 400x resolution to a sum of at least 300 grains.

Field Surveys

Vegetation was surveyed at each site along four predetermined transects—one oriented along each cardinal direction—stretching from the edge of the pond to a distance of 100 meters (m) from the pond. For each transect, percent cover of the vegetation was estimated to the family or genus level at 5m, 10m, and 10 m increments, with one plot at each distance increment along each transect. I used a modified Daubenmire method for estimating vegetation cover where the quadrat size was 1 m^2, the taxonomic classes were as Table 4.2, and the cover classes were as Table 4.3 (Daubenmire, 1959). For example, a plot with approximately 60% cover of Poaceae, 20% Fabaceae, and 20% Bare Ground would have values of Poaceae-5, Fabaceae-3, and Bare-3 (Table 4.3). Three observers participated in these field surveys, and were trained in plant identification and field techniques prior to conducting the surveys so as to impose minimal bias.

Table 4.2: Taxonomic classes used in vegetation survey.

Herbaceous		**Non-Herbaceous**
Acanthaceae	Lamiaceae	Caprifoliaceae
Ambrosia	Linaceae	*Carya*
Anacardiaceae	Malvaceae	*Celtis*
Apiaceae	Onagraceae	*Cornus*
Apocynaceae	Orchidaceae	*Diospyros*
Artemisia	Oxalidaceae	*Fraxinus*
Asclepiadaceae	Plantaginaceae	*Juglans*
Asteraceae	Poaceae	*Juniperus*
Brassicaceae	Polemoniaceae	*Maclura*
Cannibaceae	Polygonaceae	*Morus*
Caryophyllaceae	Ranunculaceae	*Populus*
Chenopodiaceae	Rosaceae	*Quercus*
Convolvulaceae	*Rumex*	*Rhus*
Cyperaceae	Solanceae	*Salix*
Euphorbiaceae	Verbenaceae	*Ulmus*
Fabaceae	Violaceae	
Gerniaceae	*Vitis*	

Table 4.3: Cover classes used in vegetation survey.

Category	Percent Cover
1	1 plant
2	1 - 10%
3	10 - 25%
4	25 - 50%
5	50 - 75%
6	75 - 97%
7	97 - 100%

To prepare data for ERV analysis, I converted the vegetation classes into their midpoints (Table 4.4). Then, I averaged the four plots at each distance increment to get a single estimate of the percent cover of vegetation at each distance increment (5, 10, 20, 30, … , 100 meters). I adjusted these cover estimates so that the sum of cover classes equaled 100% by increasing or decreasing the percentage of each plant taxon proportionately. Originally, these sums ranged from 0.7 to 1.3 across all sites. I divided the sum of the total for each distance increment from 1, and then multiplied that value by the estimated cover of each family (plant taxon) present in the quadrat.

Table 4.4: Vegetation cover classes converted to midpoints.

Category	Proportion Covered
1	0.005
2	0.05
3	0.175
4	0.375
5	0.625
6	0.86
7	0.985

In addition to the quadrat data, I drew two field maps at each site to record the location of trees and patches of woody shrubs, since trees and shrubs are often missed in the vegetation surveys, yet still contribute to the pollen assemblage. From 0-10 meters in radius from the edge of each pond, I recorded the location of each individual tree and shrub, and identified it to the species level. From 10-100 meters in radius, I drew the location of all patches of trees and shrubs and identified the species present in the patch.

Land Cover Data

I acquired the digital land cover data for this study through the Kansas Data Access and Support Center (DASC). I used a state-wide vegetation map of Kansas from the Kansas Gap Analysis Project (GAP) (http://clone.kgs.ku.edu/land_surface_geology_soils/gap/raster/), produced by the Kansas Applied Remote Sensing Program. The GAP land cover map is based on multi-seasonal LANDSAT imagery that was acquired in 1993. It has a cell size of 30 meters by 30 meters. I selected this data set because of its high taxonomic resolution: 43 land cover classes, most of which pertain to natural land cover rather than human-induced land cover (Table 4.5). I also used imagery from the United States Farm Service Agency's National Agricultural Imagery Program (NAIP) as a base map for digitizing each pond (Fig. 4.1). The NAIP imagery was acquired in 2008, has a 1-meter spatial resolution, and a 4-band spectral resolution.

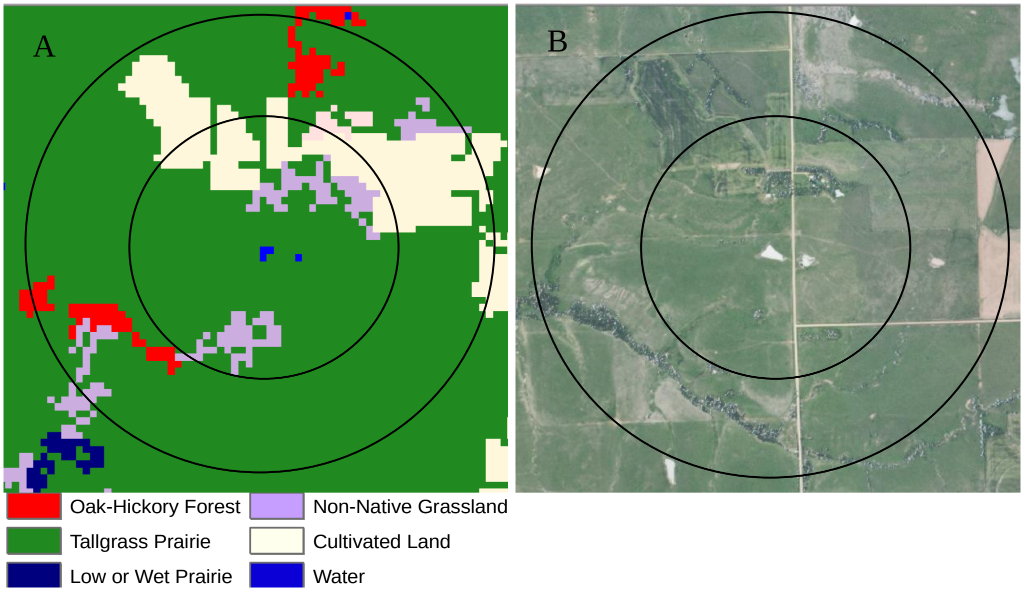

Figure 4.1: (A) GAP landcover map for site #15. (B) NAIP image for site #15. Pond location is in the center of the circle and buffers are shown at 500 m and 1000 m.

Table 4.5: GAP categories, cover types, and descriptions.

CATEGORY	COVER TYPE	NVCS_FORM	NVCS_NAME
1	Maple - Basswood Forest	Lowland and submontane cold-deciduous forest	Acer saccharum - Tilia americana - (Quercus rubra) Forest Alliance
2	Oak - Hickory Forest	Lowland and submontane cold-deciduous forest	Quercus alba - (Quercus rubra, Carya spp.) Forest Alliance
3	Post Oak - Blackjack Oak Forest	Lowland and submontane cold-deciduous forest	Quercus stellata - Quercus marilandica Forest Alliance
4	Pecan Floodplain Forest	Temporarily flooded cold-deciduous forest	Carya illinoinensis - (Celtis laevigata) Temporarily Flooded Forest Alliance
5	Ash - Elm - Hackberry Floodplain	Temporarily flooded cold-deciduous forest	Fraxinus pennsylvanica - Ulmus americana - Celtis (occidentalis, laevigata) Temporarily Flooded Forest Alliance
6	Cottonwood Floodplain Forest	Temporarily flooded cold-deciduous forest	Populus deltoides Temporarily Flooded Forest Alliance
7	Mixed Oak Floodplain Forest	Temporarily flooded cold-deciduous forest	Quercus macrocarpa - Quercus bicolor - (Carya laciniosa) Temporarily Flooded Forest Alliance
8	Bur Oak Floodplain Woodland	Cold-deciduous woodland	Quercus macrocarpa Woodland Alliance
9	Mixed Oak Ravine Woodland	Cold-deciduous woodland	Quercus muehlenbergii Woodland Alliance
10	Post Oak - Blackjack Oak Woodland	Cold-deciduous woodland	Quercus stellata - Quercus marilandica Woodland Alliance
11	Cottonwood Floodplain Woodland	Temporarily flooded cold-deciduous woodland	Populus deltoides Temporarily Flooded Woodland Alliance
12	Sandsage Shrubland	Microphyllous evergreen shrubland	Artemisia filifolia Shrubland Alliance
14	Willow Shrubland	Temporarily flooded cold-deciduous shrubland	Salix exigua Temporarily Flooded Shrubland Alliance
15	Buttonbush (Swamp) Shrubland	Semipermanently flooded cold-deciduous shrubland	Cephalanthus occidentalis Semipermanently Flooded Shrubland Alliance
17	Tallgrass Prairie	Tall sod temperate grassland	Andropogon gerardii - (Sorghastrum nutans) Herbaceous Alliance
18	Sand Prairie	Tall sod temperate grassland	Andropogon hallii Herbaceous Alliance
20	Western Wheatgrass Prairie	Medium-tall sod temperate or subpolar grassland	Pascopyrum (Agropyron) smithii Herbaceous Alliance
21	Sandstone Glade/Prairie	Tall sod temperate grassland	Schizachyrium scoparium - Sorghastrum nutans Herbaceous Alliance
22	Mixed Prairie	Medium-tall sod temperate or subpolar grassland	Schizachyrium scoparium - Bouteloua curtipendula Herbaceous Alliance
24	Alkali Sacaton Prairie	Medium-tall bunch temperate or subpolar grassland	Sporobolus airoides Herbaceous Alliance
25	Shortgrass Prairie	Short sod temperate or subpolar grassland	Bouteloua gracilis Herbaceous Alliance
26	Grass Playa Lake	Intermittently flooded temperate grassland	Pascopyrum smithii Intermittently Flooded Herbaceous Alliance
27	Salt Marsh/Prairie	Temporarily flooded temperate or subpolar grassland	Distichlis spicata - (Hordeum jubatum) Temporarily Flooded Herbaceous Alliance
28	Spikerush Playa Lake	Temporarily flooded temperate or subpolar grassland	Eleocharis macrostachya Temporarily Flooded Herbaceous Alliance
29	Playa Lake	Temporarily flooded temperate or subpolar grassland	Polygonum spp. - Echinochloa spp. Temporarily Flooded Herbaceous Alliance
30	Low or Wet Prairie	Temporarily flooded temperate or subpolar grassland	Spartina pectinata Temporarily Flooded Herbaceous Alliance
31	Freshwater Marsh	Seasonally flooded temperate or subpolar grassland	Typha spp. - (Scirpus spp., Juncus spp.) Seasonally Flooded Herbaceous Alliance
32	Bulrush Marsh	Semipermanently flooded temperate or subpolar grassland	Scirpus pungens Semipermanently Flooded Herbaceous Alliance
33	Cattail Marsh	Semipermanently flooded temperate or subpolar grassland	Typha (angustifolia, latifolia) - (Scirpus spp.) Semipermanently Flooded Herbaceous Alliance
38	Forb Playa Lake	Permanently flooded temperate or subpolar hydromorphic rooted vegeta	Heteranthera limosa Permanently Flooded Herbaceous Alliance
40	Non-Native Grassland	Temperate or subpolar grassland	Dominants: Bromus inermis, Festuca arundinacea, Andropogon bladhii
41	Conservation Reserve Program	Temperate or subpolar grassland	Dominants: Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, Panicum virgatum, etc.
42	Salt Cedar or Tamarisk Shrubland	Temperate broad-leaved evergreen shrubland	Dominants: Tamarix spp.
44	Cultivated Land		
50	Deciduous Forest - Mined Land	Cold-deciduous forest	Dominants: Populus deltoides, Salix nigra, Ulmus rubra
51	Maple Floodplain Forest	Temporarily flooded cold-deciduous forest	Dominants: Acer saccharinum, Betula nigra
52	Evergreen Forest - Disturbed Land	Temperate or subpolar needle-leaved evergreen forest	Dominant: Juniperus virginiana
55	Deciduous Woodland	Cold-deciduous woodland	Dominants: Maclura pomifera, Gleditsia triacanthos
60	Mixed Prairie - Disturbed	Temperate or subpolar grassland	Dominants: Sporobolus spp.
70	Weedy Marsh	Seasonally flooded temperate or subpolar grassland	Dominants: Typha spp., Scirpus spp., Ambrosia spp., Rumex spp.
71	Weedy Upland	Temperate or subpolar annual grassland or forb vegetation	Dominant: Ambrosia artemisiifolia
81	Urban Areas		
82	Water		

I imported the raster GAP file into GIS. To make the file more manageable, I constructed a buffer of 3000 meter radius from the shore of each digitized pond. Using this buffer, I extracted the cells within 3000 meters and converted this new raster to a vector file. In a separate file, I digitized the field maps of the single trees within 10 meters in radius from the shore, and the patches of trees within 100 meters from the shore. Each tree was classified into a GAP category. For trees in the genera *Cornus, Rhus,* or *Morus*, which were not included in the original GAP categories, a new cover type was created for each. This separate file was then used to update the vector GAP file. The resulting map contained the original GAP files as a base, with the digitized field maps on top.

In GIS, I constructed buffers every 10 meters from the edge of the ponds out to 2000 meters. To create rings 10 meters in width to use as clips for the vegetation map, I used the erase tool to erase the inner part of each buffer using the next smallest buffer. For example, the 1000 meter buffer was cut with the 990 meter buffer, creating a 10-meter-wide ring between 990 and 1000 meters from the pond. Using a batch clip tool, I clipped the vegetation map with each 10-meter ring.

I used an area tool to calculate the area in square meters of each polygon of land cover in each 10-meter ring. Using the summary statistics tool, I calculated the sum of area of each cover type in every 10-meter ring. These sums for each cover type from every ring at each distance increment (10, 20, 30, … , 1000 meters) were compiled into Excel spreadsheets for every site. An example of this is shown for the first 200 meters of one site (Table 4.6).

Table 4.6: Area (in m^2) of GAP Categories for the first 200 m for site #11.

		GAP Category							
dist from	dist to	5	7	9	17	22	41	55	83
0	10	38.58	0.00	0.00	1813.04	0.00	0.00	9.27	38.99
10	20	0.00	0.00	0.00	2266.88	0.00	0.00	10.87	249.88
20	30	0.00	0.00	0.00	3012.06	0.00	0.00	0.00	143.34
30	40	0.00	0.00	0.00	3713.54	0.00	0.00	0.00	69.61
40	50	0.00	0.00	0.00	4352.19	0.00	0.00	0.00	58.73
50	60	0.00	0.00	0.00	5023.16	0.00	0.00	0.00	15.52
60	70	0.00	0.00	0.00	5666.44	0.00	0.00	0.00	0.00
70	80	0.00	0.00	0.00	6294.21	0.00	0.00	0.00	0.00
80	90	0.00	0.00	0.00	6921.99	0.00	0.00	0.00	0.00
90	100	0.00	0.00	0.00	7549.79	0.00	0.00	0.00	0.00
100	110	0.00	0.00	0.00	8177.56	0.00	0.00	0.00	0.00
110	120	0.00	0.00	0.00	8805.43	0.00	0.00	0.00	0.00
120	130	0.00	0.00	0.00	9204.18	229.04	0.00	0.00	0.00
130	140	0.00	0.00	0.00	9463.10	597.90	0.00	0.00	0.00
140	150	0.00	0.00	0.00	10054.17	634.62	0.00	0.00	0.00
150	160	0.00	0.00	0.00	10746.04	570.55	0.00	0.00	0.00
160	170	0.00	0.00	0.00	11601.85	342.56	0.00	0.00	0.00
170	180	0.00	0.00	0.00	12259.62	312.60	0.00	0.00	0.00
180	190	0.00	0.00	0.00	12724.60	475.45	0.00	0.00	0.00
190	200	0.00	0.00	0.00	12846.46	981.42	0.00	0.00	0.00

As indicated in the GAP metadata, each cover type contains one or more associated species. For example, Evergreen Forest – Disturbed Land (Category 55), is described in the GAP metadata as consisting of *Juniperus virginiana*. Therefore, all of the calculated area of this category was considered *Juniperus virginiana* in my data sheets. Ash-Elm-Hackberry Floodplain Forest (Category 5) is described as containing *Fraxinus*, *Ulmus*, and *Celtis*, so I divided all areas in this category evenly among these three genera.

For all categories that are grassland or some variation of grassland, I applied the field data for percent cover of each family. This is a crucial step, because the grassland taxa are not represented in the GAP maps in the same detail as the tree taxa. At each site, I multiplied the total area of grassland by the percent cover of each family at that distance. For example, I multiplied the total area of grassland within the 0-10 meter ring by the percentages from the 10-meter field quadrats at each site. This procedure was followed to 100 meters. Because my field vegetation surveys extended only to 100 m, I selected four quadrats from that overall site and multiplied those percentages by the grassland category for distances greater than 100 m. Within a site, the composition of the grassland vegetation from the field survey had minimal variation. This procedure was followed to a 2000 m radius, which is the largest distance likely to be contributing local pollen to the pond, based on other studies in Europe that have estimated this distance for similar size basins (Broström *et al.*, 2008).

Fall Speed of Pollen

To acquire pollen productivity estimates for the 12 target taxa, an estimate of fall speed was required for each pollen type. Pollen dispersal for a pollen taxon is partially dependent on its fall speed in the air. The speed at which pollen falls is dependent on the size and shape of the pollen, and is thus unique to a pollen type (Gregory, 1973). The fall speeds for *Juniperus,* Poaceae, *Quercus,* and *Salix,* were calculated in previous studies (Eisenhut, 1961; Sugita *et al.*, 1999). Those values were used for this study as well. For *Ambrosia, Artemisia,* Asteraceae, Chenopodiaceae, *Cornus,* Fabaceae, *Maclura,* and *Populus,* fall speeds had not been previously calculated. I calculated these fall speeds according to Stoke's Law (Gregory, 1973), which is the same method used by Sugita *et al.* (1999). These values are necessary for using the ERV Model, and the values I used were as Table 4.7.

Table 4.7: Fall speed of pollen grains for selected taxa.

	Plant Taxa	Fall Speed (m/s)	Reference cited for fall speed of pollen
Herbaceous	*Ambrosia*	0.019	this paper
	Artemisia	0.013	this paper
	Asteraceae	0.014	this paper
	Chenopodiaceae	0.011	this paper
	Fabaceae	0.021	this paper
	Poaceae	0.035	Sugita *et al.* (1999)
Non-herbaceous	*Cornus*	0.044	this paper
	Juniperus	0.016	Eisenhut (1961)
	Maclura	0.016	this paper
	Populus	0.027	this paper
	Quercus	0.035	Eisenhut (1961)

	Salix	0.022	Gregory (1973)

ERV Modeling

I calculated pollen productivity estimates and relevant pollen source areas with a modified Extended R-Value (ERV) model (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Prentice, 1985; Sugita, 1994; and Calcote, 1995). This pollen-vegetation model was written by Shinya Sugita (University of Tallinn, Estonia), has been extensively tested in Europe (Gaillard *et al.*, 2008), and operates in a Windows environment. With several input files and parameter specifications, the ERV Model calculates PPEs for all selected taxa (Fig. 4.2), and estimates the RSAP (Fig. 4.3). The ERV Model describes the pollen-vegetation relationship as a linear function.

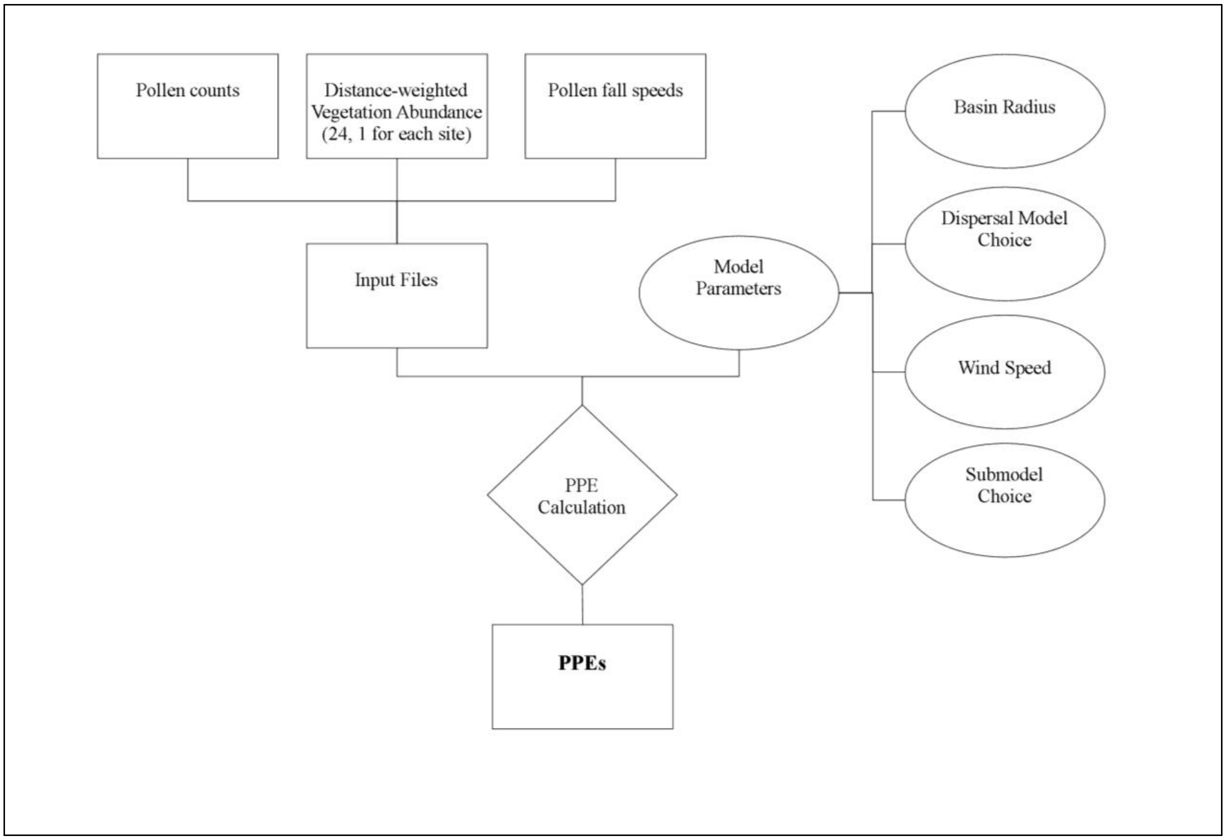

Figure 4.2: Flowchart of ERV Model process for estimating pollen productivity.

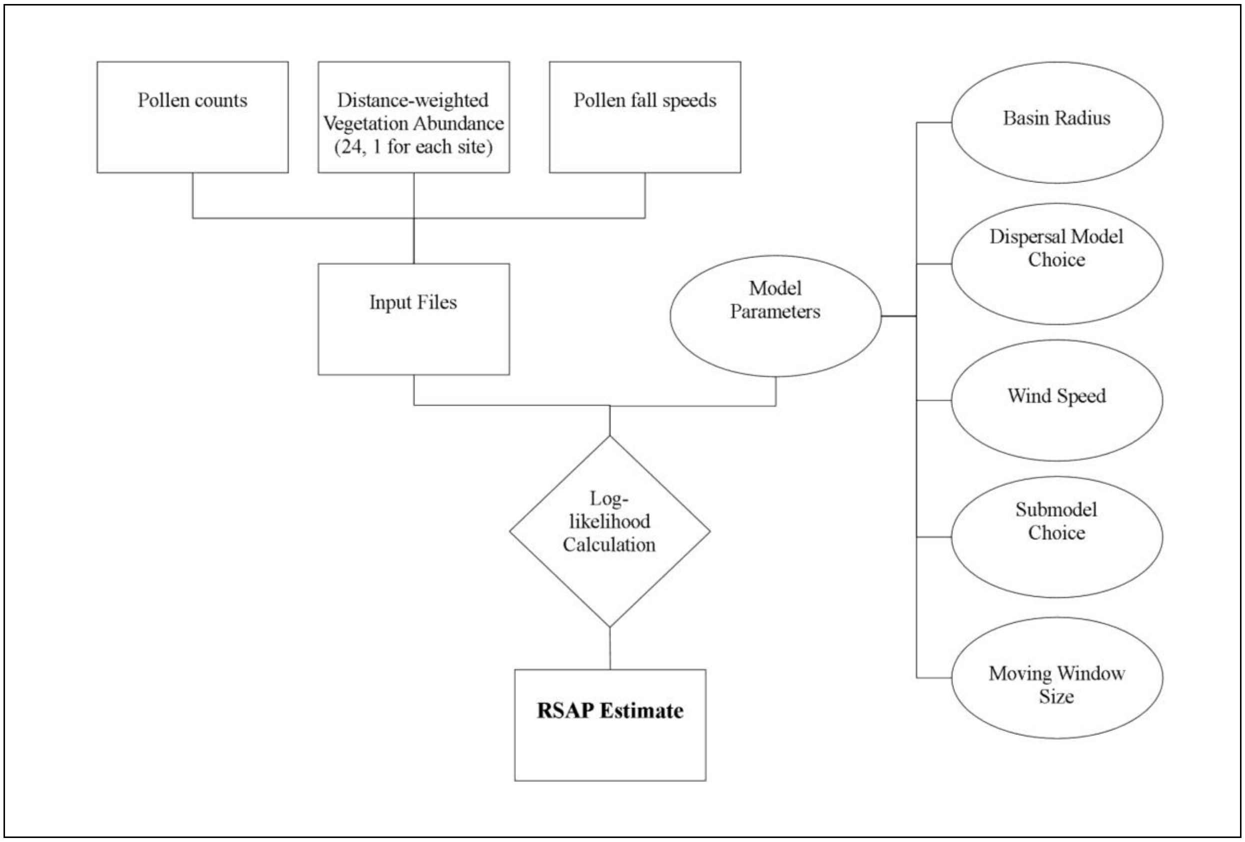

Figure 4.3: Flowchart of ERV Model process for estimating relevant source area of pollen (RSAP).

Equation 4.1: ERV function

$$y_{ik} = \alpha_i x_{ik} + \omega_i$$

where,

y_{ik} = pollen loading of species *i* at site *k*

x_{ik} = vegetation abundance of species *i* at site *k*

α_i = pollen productivity of species *i*

ω_i = background pollen loading for species *i*

A total of 51 pollen taxa were present in the surface sediments from the 24 ponds. I chose 12 pollen taxa for this analysis (Table 4.7), since pollen productivity estimates can reliably be obtained for the number of taxa approximately one half of the number of sites sampled (Broström *et al.,* 2004). Three sets of files are required for ERV modeling: distance weighted vegetation abundance for each site, pollen counts for each site, and fall speed of each taxon. The vegetation abundance set of files contains one spreadsheet for each of the 24 sites, with distance increments set at 10 meters. The pollen counts file contains one sheet with the total number of pollen grains of each taxon at each site. The fall speed file contains one sheet listing each plant taxon and its associated fall speed (Table 4.7).

In addition to these files, ERV requires the user to specify the wind speed, the basin radius, and the pollen dispersal model (Table 4.8). I used a wind speed of 5 m/s, and a basin radius of 50 m, which is the average radius of all 24 ponds. For the pollen dispersal model, I used the Ring Source – Lake/Pond Model. Furthermore, an estimate of the relevant source area of pollen (RSAP) can be acquired if a moving-window size is specified. This spatial moving-window value affects the shape of the curve of the likelihood function score used to estimate RSAP. With this method, the RSAP is estimated to be the distance at which the likelihood function score approaches an asymptote, or when the difference between values becomes 0.1 or lower for a distance of 50 m. I entered a moving window of 300 m. Typical values fall between 200 m and 400 m (Gaillard *et al.,* 2008).

Table 4.8: ERV parameters and input values used for analysis.

Parameter	Input
Wind speed	5 m/s
Pollen Dispersal Model	Ring Source (Lake and Bog)
Basin Radius	50 m
Moving Window	300 m

There are three submodels to ERV, which vary according to how they define background pollen. Background pollen is the pollen coming from beyond the RSAP. Submodel 1 (Parsons & Prentice, 1981) describes background pollen relative to the total pollen loading for each taxon. Submodel 2 (Parsons & Prentice, 1981) describes background pollen as being the ratio of the pollen coming from beyond the distance of the vegetation data used in the analysis, to the total vegetation abundance within the area of the vegetation used in the analysis. In submodel 3 (Sugita, 1994), the background pollen simply represents the pollen coming from outside the area of the vegetation data used for the analysis. All three submodels were tested in order to obtain the best and most reliable estimate of pollen productivity for each taxon.

CHAPTER 5 - Results

Relevant Source Area of Pollen

The RSAP estimate for the 24 ponds in this study varies between 1050 m and 1060 m, depending on which submodel is used. Submodel 1 produced an RSAP of 1050 m, and Submodel 3 produced an RSAP of 1060 m. Submodel 2 was unable to produce an RSAP. The RSAP values of 1050 m and 1060 m suggest that the differences in the pollen assemblages among the 24 samples become negligible beyond a distance of 1050 m or 1060 m. Pollen originating beyond this distance (background pollen) is considered to be taxonomically and quantitatively similar among the sites.

The jagged shape of the curve of the log-likelihood values for Submodel 1 suggests that it may not be suitable for this environment (Fig. 5.1). However, it is still useful to compare the results from both submodels in order to fully understand the estimates that they provide regarding the pollen-vegetation relationship. Since Submodel 1 assumes that background pollen loading in the pollen proportions is a species-specific constant among sites, settings with large site-to-site variation in background pollen would not be a proper fit for Submodel 1. Log-likelihood values for Submodel 3 display a smooth curve, and thus Submodel 3 is a better fit for the Flint Hills study area.

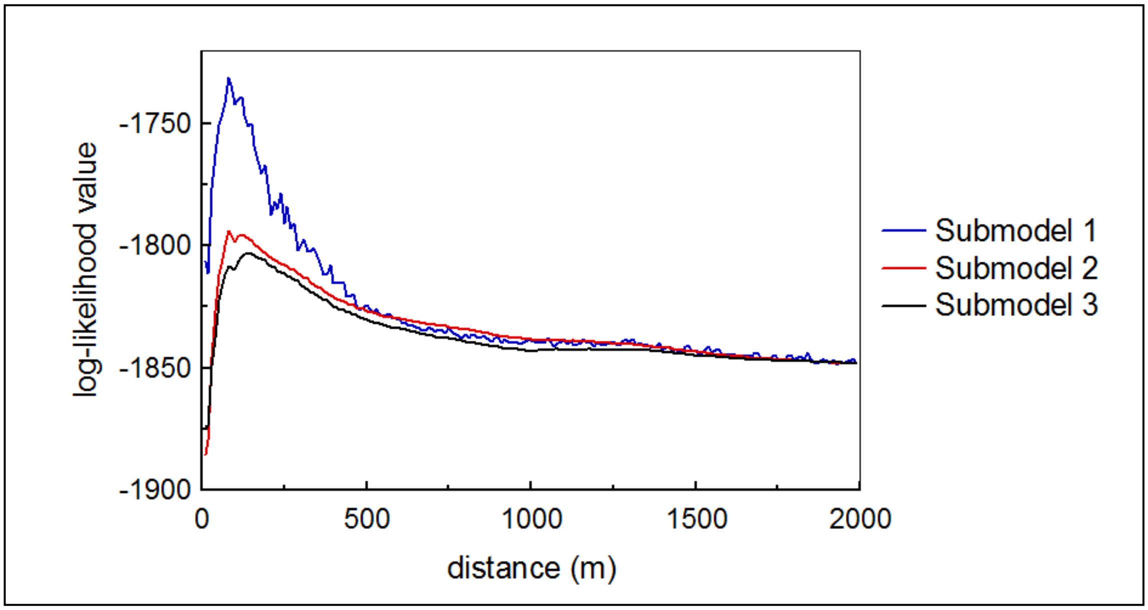

Figure 5.1: Log-likelihood plots for ERV Submodel 1, 2, and 3.

Pollen-Vegetation Relationship

The submodels of ERV attempt to find the best linear relationship between the pollen and the vegetation. Scatterplots of the pollen-vegetation relationship with submodels 1 and 3 show that there is a relationship between the pollen and vegetation data. It is important to visualize the data first with the original vegetation proportions and pollen proportions (Fig. 5.2). Submodel 1 uses original pollen proportions and adjusted vegetation proportions (Fig. 5.3). Submodel 3 uses relative pollen loading and absolute vegetation proportions (Fig. 5.4). While these plots are helpful for visualizing the pollen-vegetation relationships, PPEs are calculated separately by the model, so an r-value of correlation is not necessary.

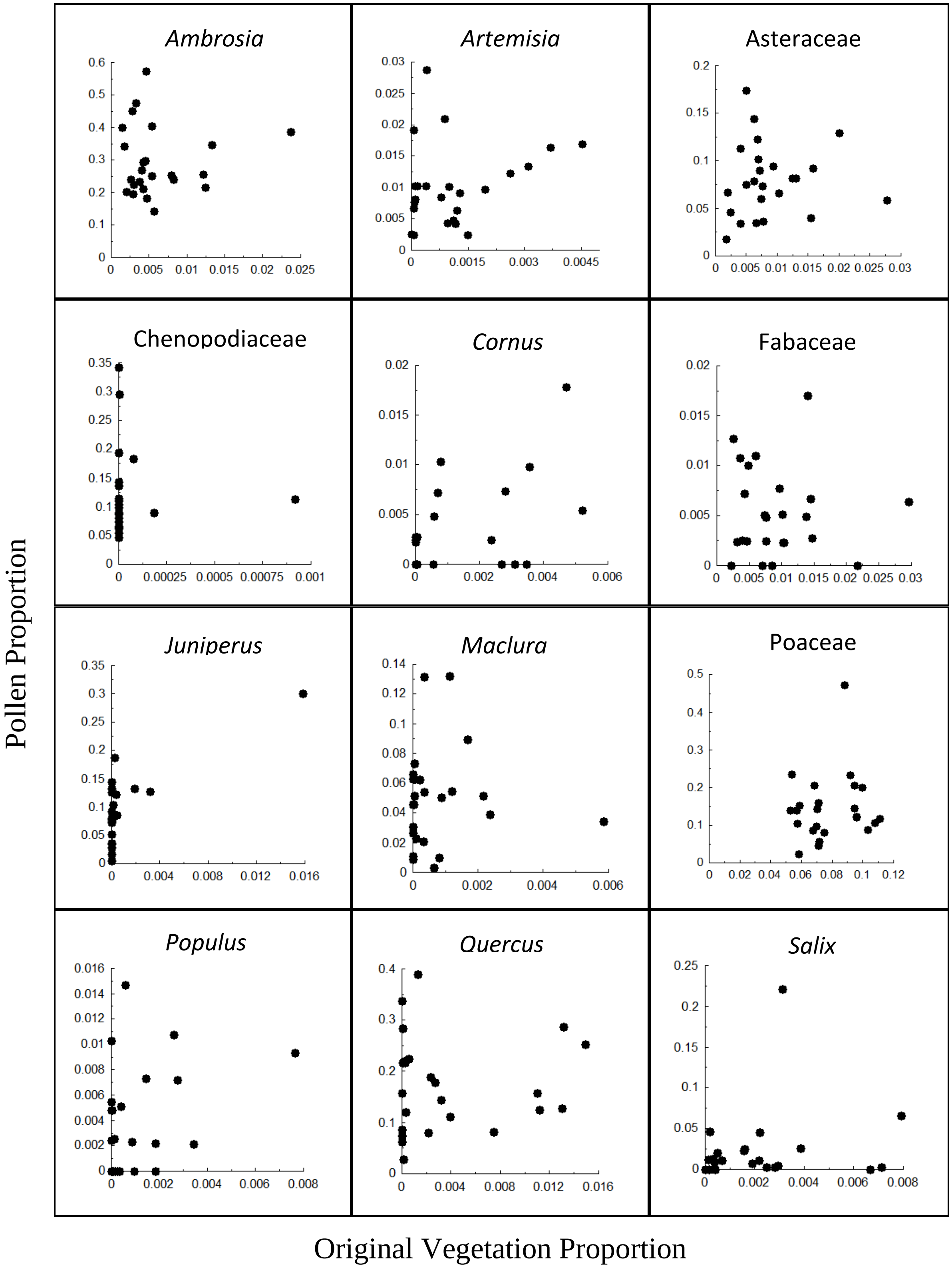

Figure 5.2: Original pollen proportion versus original vegetation proportion. Each dot represents one site.

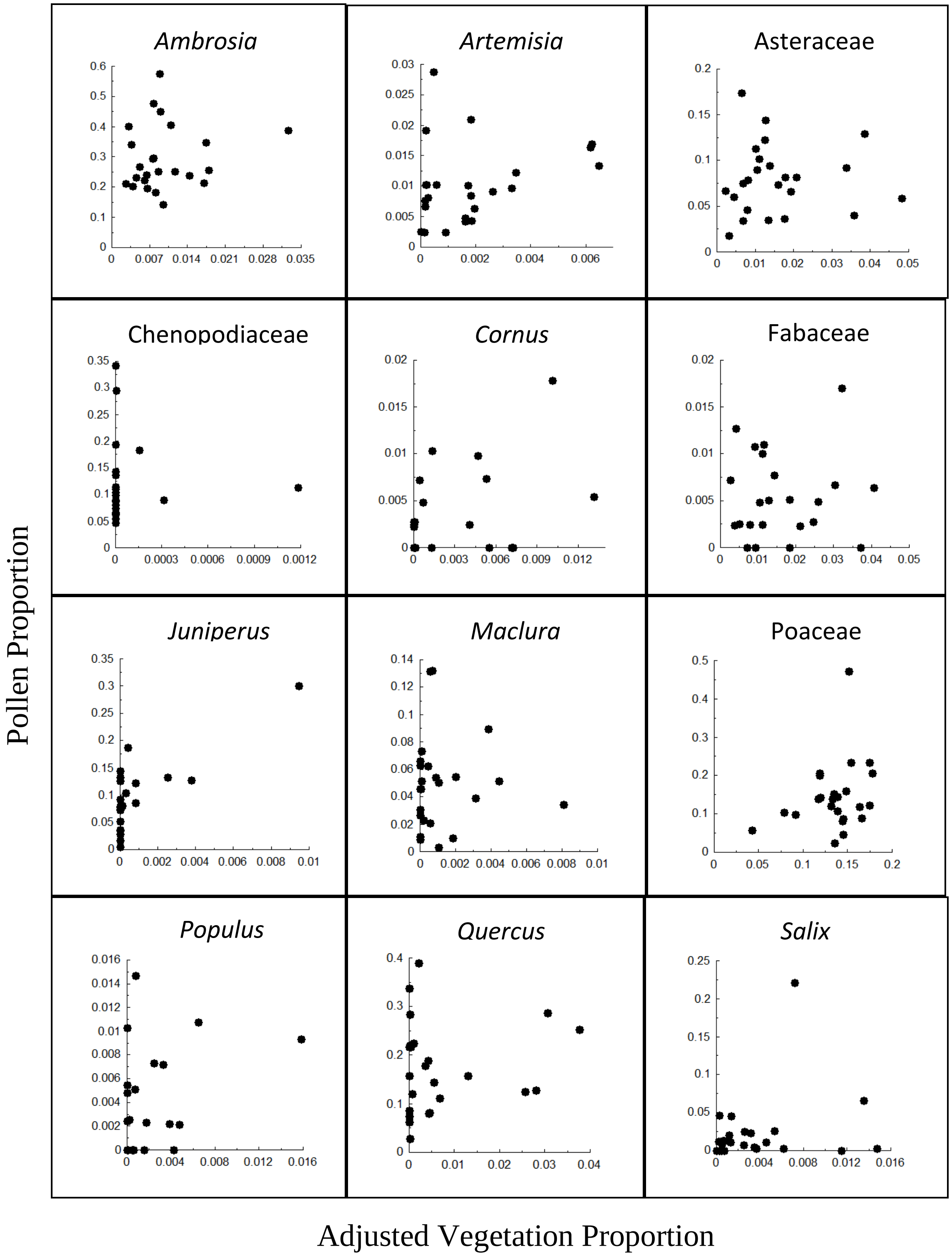

Figure 5.3: Submodel 1. Pollen proportion versus adjusted vegetation proportion. Each dot represents one site.

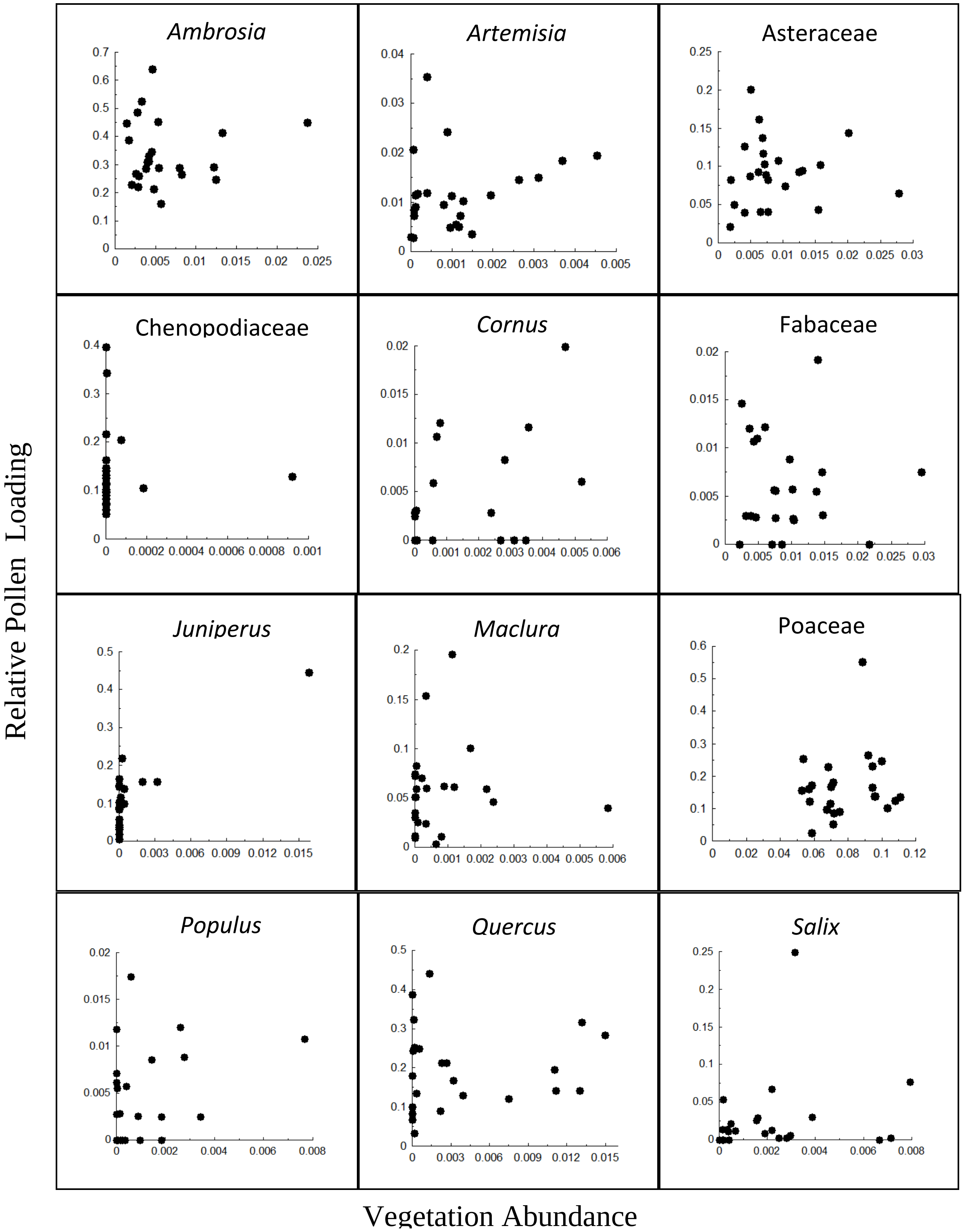

Figure 5.4: Submodel 3. Relative pollen loading versus absolute vegetation. Each dot represents one site.

Pollen Productivity Estimates

Pollen productivity estimates for each of the 12 taxa were produced using ERV Submodel 1 and Submodel 3 (Table 5.1). Because the best estimate of PPE is obtained at the distance of the RSAP and beyond, the average and standard deviation of all PPE for each taxa from a distance of the RSAP to 2000 m was calculated. This is used to smooth out any slight variation in PPE beyond the RSAP (following Brostom *et al.*, 2004). PPEs were calculated relative to Poaceae because of its intermediate relative pollen productivity, and thus Poaceae has a PPE of 1.0 for both submodels. *Juniperus* had the highest PPE using Submodel 3, and Chenopodiaceae had the highest PPE using Submodel 1 (Fig. 5.5). Fabaceae had the lowest PPE with both submodels (Fig. 5.6).

Table 5.1: PPEs average and standard deviation for all selected taxa from distance of RSAP to maximum survey distance.

	Average PPE		Standard Error	
Taxon	Submodel 1	Submodel 3	Submodel 1	Submodel 3
Poaceae	1	1	0	0
Ambrosia	3.52	1.36	0.81	0.36
Artemisia	1.25	1.35	0.43	0.24
Asteraceae	0.87	0.37	0.20	0.16
Chenopodiaceae	35.04	0.52	11.86	1.17
Cornus	0.89	1.72	0.18	0.14
Fabaceae	0.02	0.02	0.02	0.02
Juniperus	17.01	20.67	1.72	1.54
Maclura	0.17	1.1	0.34	0.55
Populus	0.87	1.23	0.23	0.17
Quercus	0.91	2.08	0.23	0.43
Salix	2.52	6.02	0.51	0.75

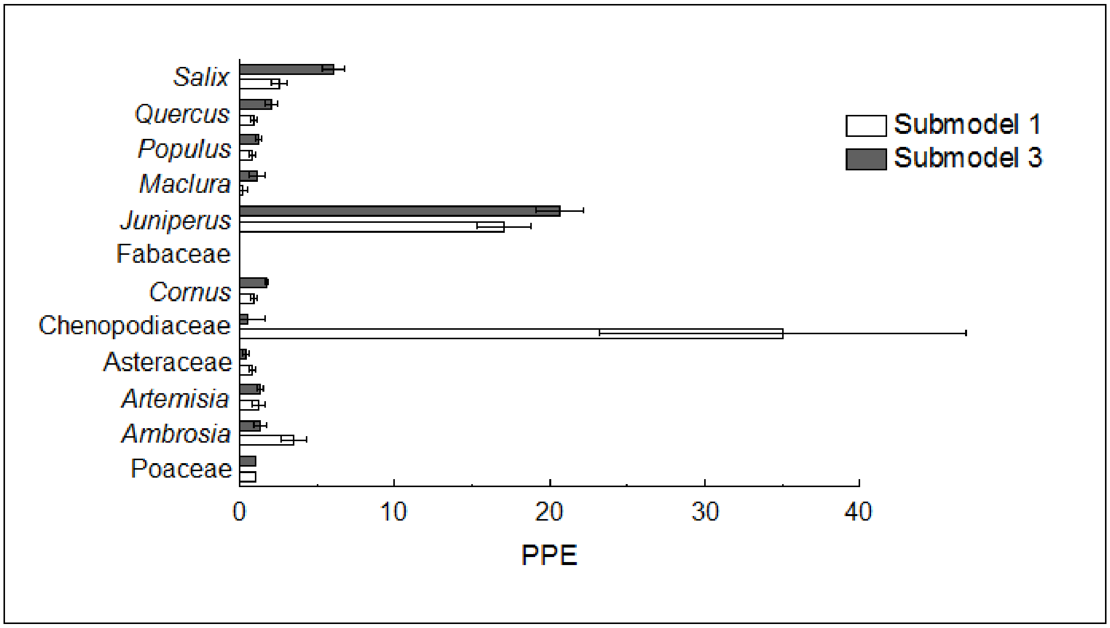

Figure 5.5: PPEs with standard errors for all taxa.

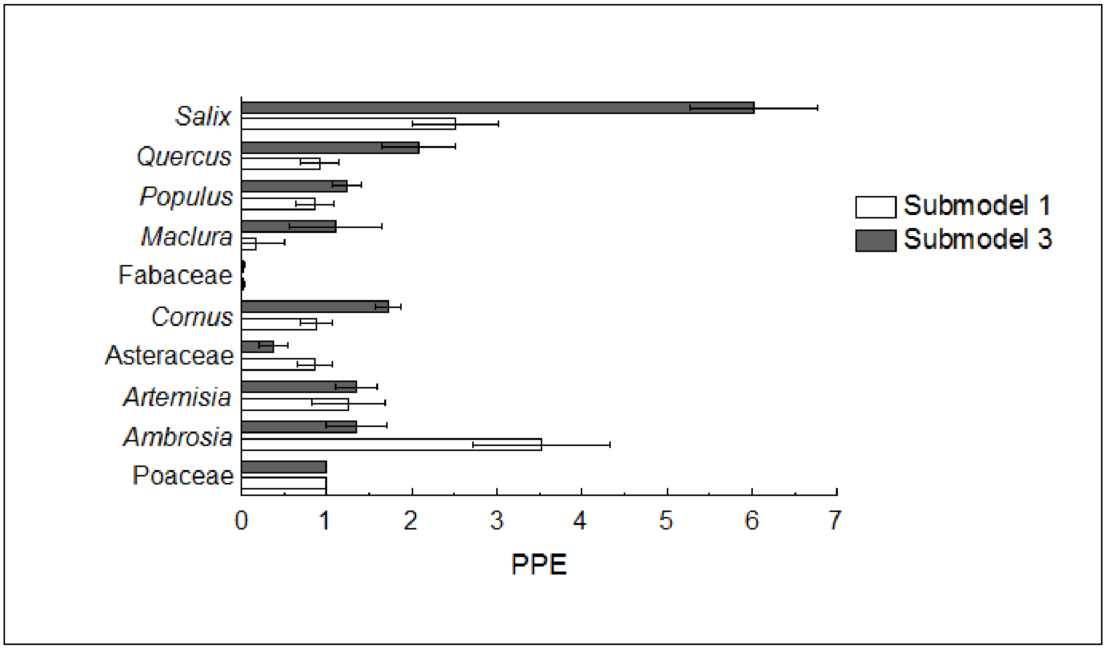

Figure 5.6: PPEs with standard errors for all taxa, excluding Chenopodiaceae and *Juniperus*.

Submodel 1

When submodel 1 was used, two woody plant taxa (*Juniperus,* and *Salix*) had PPEs higher than Poaceae, the reference taxon. Three herbaceous taxa (*Ambrosia*, *Artemisia,* and Chenopodiaceae) also had PPEs higher than Poaceae. Four woody taxa (*Cornus, Maclura, Populus,* and *Quercus*), and two herbaceous taxa (Asteraceae and Fabaceae) had PPEs lower than Poaceae. Chenopodiceae had a very high standard error (i.e. 11.86), indicating high variation in PPEs from the distance of the RSAP (1050 m) to the maximum survey distance (2000 m). All other taxa had relatively low standard error, indicating that the PPE generally show low deviation beyond the RSAP.

Submodel 3

Because of the smooth log-likelihood curve (Fig. 5.1), and the lower standard errors for each taxon compared to Submodel 1 (Table 5.1), Submodel 3 is the better model for my data. When submodel 3 was used, all woody taxa had PPEs higher than Poaceae. Two herbaceous taxa (*Ambrosia* and *Artemisia*) also had PPEs higher than Poaceae. Asteraceae, Chenopodiaceae, and Fabaceae were the only three taxa that had PPEs lower than Poaceae. Standard errors for these taxa were similar between the two submodels, except for Chenopodiaceae, which had a much lower standard error (i.e. 1.17) with Submodel 3.

CHAPTER 6 - Discussion

Relevant Source Area of Pollen

Previous studies have estimated RSAP to be between 300 and 1700 m for small lakes approximately 100 m in radius (Sugita, 1994; Sugita *et al.,* 1999; Nielsen & Sugita, 2005; Soepboer *et al.,* 2007), and 50 and 400 m for moss polsters (Sugita, 1994; Calcote, 1995; Broström *et al.,* 2005; Bunting *et al.,* 2005). The RSAP of 1060 m for small lakes in the Flint Hills falls near the middle of the appropriate range, and also supports Hypothesis 2, in which I predicted RSAP to be approximately 1000 m. While basin size clearly has an effect on RSAP, because small basins serve as catchments for pollen originating from relatively local areas surrounding the ponds, landscape openness and vegetation patch sizes also have been shown to have an effect (Sugita *et al.,* 1999). In northern Wisconsin, landscapes with larger patches of vegetation were shown to have a larger RSAP (Calcote, 1995). In addition, Sugita *et al.* (1999) examined RSAP for simulated open and semi-open landscapes in southern Sweden, and noted that ponds in open and semi-open landscapes had a RSAP of 800 to 1000 m. In closed forests of northern Michigan, Sugita (1994) simulated the RSAP for small ponds to be 300 m. The drastic difference in RSAP between the open and semi-open landscape versus the closed landscape was predicted to be due to the distribution of the vegetation on the landscape. In the closed landscape, vegetation patches were much more frequent, and therefore the distance required to achieve constant background pollen among sites was much smaller.

The Flint Hills more closely resemble the southern Sweden landscape, in that there is a matrix of herbaceous taxa with occasional tree taxa punctuating this matrix. Since the RSAP for this study was 1060 m, it is similar to the RSAP for semi-open landscapes in Sweden. There are several possible reasons for this similarity. First, tree taxa at my sites were usually present within the first 10 m from the edge of the pond, with scattered clumps beyond 10 m. This vegetation distribution would probably lead to an RSAP that most closely aligns with the semi-open landscape. Although the grasslands of the Flint Hills appear to be very open, the presence of trees directly adjacent to the sampled ponds could cause the landscape to behave more like a semi-open landscape than an open landscape. Second, the presence of rare taxa in a landscape lead to an increase in RSAP (Bunting *et al.,* 2004). In the Flint Hills, the tree taxa would be considered rare taxa, since herbaceous taxa typically comprise the majority of the vegetation cover on the landscape. These taxa make the landscape less homogenous, causing the RSAP to be reached at a greater distance than if there were no rare taxa present.

PPE Interpretation

The PPE values for each of the 12 taxa represent the productivity of each taxa in reference to Poaceae (1.0). With the results from submodel 3, most tree taxa seem to have higher PPE values than Poaceae, which has also been a trend in previous studies (Broström *et al.,* 2008). The herbaceous taxa—*Ambrosia, Artemisia,* Asteraceae, Chenopodiaceae, Fabaceae, and Poaceae—have lower PPEs than most of the woody taxa (except *Maclura* and *Populus*). Even though some of the herbaceous taxa are wind-pollinated, they are much smaller organisms than trees and thus produce smaller amounts of pollen on average. Additionally, herbaceous taxa that are insect-pollinated such as Fabaceae have very low PPEs, consistent with their pollination biology (Real, 1983). This finding is consistent with Hypothesis 1, which predicted that herbaceous taxa would have generally lower PPEs than most of the woody taxa.

In Europe, PPEs have been previously obtained for some of the same taxa that I am examining: *Juniperus,* Poaceae, *Quercus,* and *Salix*. In the Flint Hills, *Juniperus* has an especially high PPE (20.67), which is higher than the PPEs previously obtained for *Juniperus*:

0.11 measured in west-central Sweden (Von Stedingk *et al.,* 2008) and 2.10 measured in southern Sweden (Brostom *et al.,* 2004). *Salix* has a PPE of 6.02, which is slightly higher than the PPE for *Salix* found in European studies (Bunting *et al.,* 2005; Broström *et al.,* 2004). These differences could be due to climatic or environmental factors, and this emphasizes the importance of obtaining PPEs for multiple regions.

Quercus has a PPE of 2.08, which is comparable to the PPE of 2.56 from the Swiss Plateau (Soepboer *et al.,* 2007). Their study also obtained their pollen assemblages through lake sediments, in a manner similar to mine. Two other studies (Bunting *et al.,* 2005; Broström *et al.,* 2004) obtained PPEs for *Quercus* using moss polsters, and obtained values of 7.60. Moss polsters have been suspected to be more sensitive to annual variation in pollen productivity, since the exact number of years represented is not generally known. While the difference between my PPE for *Quercus* and the moss polster PPEs cannot be completely attributed to sampling differences, sampling could be another factor to consider, in addition to the usual climatic or environmental differences. This difference in PPE between moss polsters and lake sediments has been seen in previous studies in Europe (Broström *et al.,* 2008).

The PPEs for the woody taxa are consistently higher when submodel 3 was used rather than submodel 1, while the PPEs for the herbaceous taxa are lower (except *Artemisia*). The presence of higher PPEs from submodel 3 for the woody taxa is consistent with a study in Southern Sweden (Broström *et al.,* 2004), however, in their study, the herbaceous taxa also had higher PPEs with submodel 3. In my case, all herbaceous taxa except *Artemisia* have lower PPEs with submodel 3. This means that while PPEs tend to be higher for woody taxa when submodel 3 is used rather than submodel 1 or 2, the same cannot be said for the herbaceous taxa in all environments. One reason for this might be the vegetation composition of the study area.

While my study area was predominantly grassland with a few woody components, other studies had greater amounts of forest cover (Broström *et al.,* 2004; Bunting *et al.,* 2005; Soepboer *et al.,* 2007; Von Stedingk *et al.,* 2008). My study area contains the most grassland of other studies of its kind.

Chenopodiaceae seems to be an outlier among the other taxa, because it has a very high PPE (35.04) with submodel 1, and a very low PPE (0.52) with submodel 3. Neither of these values seems to be a good indicator of the actual PPE for Chenopodiaceae, for several reasons. First, Chenopodiaceae should have a high PPE in theory, because it had a very high presence in the pollen assemblage, but very low presence in the vegetation surveys. Since the standard error was also high (11.86) with submodel 1, neither submodel seems to accurately predict. Second, in order to obtain accurate PPEs, it is recommended that the selected taxa be present in both the pollen and vegetation record of at least half of the sites (Brostom *et al.,* 2008). In my case, Chenopodiaceae was present in the pollen of at least half of the sites, but was not present in the vegetation survey of at least half. It is possible that Chenopodiaceae was present in the vegetation at half of the sites, but was simply missed in the vegetation survey due to quadrat placement or surveyor error.

The problem that arises with Chenopodiaceae may not be unique to this taxon, but is likely due to its rare presence on the landscape, coupled with its strong presence in the pollen data. If a taxon is very rare on the landscape but shows a strong presence in the pollen data, it would theoretically have a high PPE, but there would be insufficient site-to-site data to mathematically calculate this PPE with the ERV Model. This situation occurred with Chenopodiaceae. Other taxa, such as *Juniperus* also had a strong presence in the pollen data, but had an average presence in the vegetation surveys at the sites, and was present at almost all of the sites. This presence in the vegetation data allowed for a more accurate calculation of PPE with a lower standard error for *Juniperus*.

Variations between my PPEs and the PPEs from other studies (Broström *et al.,* 2008), might be affected by the species present in each taxa. For example, most of the *Quercus* present in my study area was *Quercus macrocarpa,* a species that is common in riparian areas in the Flint Hills. The *Quercus* taxon in European studies was composed of *Quercus robur* (Soepboer *et al.,* 2007; Bunting *et al.,* 2005; Broström *et al.,* 2004). In west central Sweden, it has been observed that PPEs may vary among species, and therefore taxa composed of different species might not be directly comparable (Von Stedingk *et al.,* 2008). This distinction supports the necessity of obtaining PPEs for a particular study area before attempting to use the PPEs for vegetation reconstruction, since PPEs might not be directly transferrable from one region to another.

Submodel Selection

The suitability of submodel 3 shown by the log-likelihood curve (Fig. 5.1) and the low standard errors (Table 5.1) suggests that its method of defining the pollen-vegetation relationship is a suitable fit for the Flint Hills ecoregion. All taxa except for *Maclura, Quercus,* and *Salix* had lower standard errors using submodel 3 compared to submodel 1. The better suitability that submodel 3 provides for my data is reasonable, as my data included absolute vegetation abundance at distance-weighted increments, and submodel 3 is often chosen for other PPE studies when absolute vegetation abundance data is available (Broström *et al.,* 2008).

Differences between the results from submodel 3 and submodel 1 can be explained by their differences in defining the pollen-vegetation relationship, and in how the submodels define background pollen. Submodel 3 defines the pollen proportion for a taxa as being relative to the total pollen loading, and uses distance-weighted plant abundance for defining the vegetation component, whereas submodel 1 uses pollen and vegetation proportions. In addition, submodel 1 assumes a species-specific constant background in the pollen proportions, whereas submodel 3 assumes constant background loading among all the sites. Because most woody vegetation at my sites was located directly adjacent to the ponds, and there is limited variation in vegetation among the sites beyond the distance of the RSAP, submodel 3 is a logical choice. The individual woody components located at a close distance to each pond should not be considered when deriving the background pollen loading, but would be greater factors in the background pollen with submodel 1.

Modeling Limitations

While the PPEs obtained for the 12 selected taxa provide useful insight regarding the nature of the relationship between vegetation cover and pollen assemblages in the Flint Hills, there are a few limitations that should be addressed. The ERV Model is currently one of the most comprehensible models to quantitatively estimate pollen productivity. However, all models are simplifications of reality, and the ERV Model operates on several underlying assumptions: 1) Circular basins, 2) Even pollen dispersal from all directions, 3) Constant wind speed throughout the study area, 4) Total pollen mixing within a basin, and 5) Constant interannual pollen productivity.

First, ERV assumes that all ponds or basins are perfectly circular, when in reality, they take various shapes. In the Flint Hills, the ponds are formed by dams, and thus there is a relatively straight side on most of the ponds. Second, ERV assumes that pollen is evenly deposited in the basin from all directions. In most study areas, including the Flint Hills, there is a prevailing wind direction, and thus the vegetation on one side of a pond might theoretically have a larger weight in the pollen assemblage than vegetation at the same distance on the other side of a pond. However, this is only an issue if the vegetation is drastically different on one side of the pond, and my sites had fairly homogenous vegetation distribution within the grassland category in all directions. In the vegetation surveys, transects were oriented in all four cardinal directions from each pond, so as to account for any variations in grassland vegetation composition due to topography or other factors. Thus, any minor heterogeneity present due to direction would have been accounted for in the surveys. Furthermore, any heterogeneity present in the vegetation is what the pond sees also. Third, ERV assumes that all sites within the study area have the same wind speed, which may not be true when dealing with geographically large study areas. Fourth, it is assumed that pollen productivity for a given taxon is the same from year to year, when in reality, pollen productivity can vary with climate. Certain plants may produce more pollen in a hot, wet summer when they are able to grow larger, or less pollen if they are limited by a lack of moisture or heat. Fifth, ERV assumes that pollen is completely mixed within a pond, and that pollen assemblages taken from the middle of the pond are representative of the entire sedimentary basin. In reality, the amount of mixing is probably somewhere between total mixing and zero mixing, but no study has exactly quantified this relationship.

In addition, there are a couple of other limitations that are not necessarily assumptions, but are still limits of the model. First, bare ground was present in the vegetation surveys at many of the sites, but the ERV Model can only obtain PPEs for plant taxa that actually produce pollen. Thus, with the current ERV model, an accurate quantitative account for bare ground cannot be provided. Second, taxa need to be present in both the pollen and vegetation data from at least half of the sites. This makes it difficult to accurately estimate pollen productivity for species that have a strong presence in the pollen data but a rare presence in the vegetation data (ie: Chenopodiaceae). While these limitations should be considered when interpreting the results, other studies that have used ERV Models to estimate pollen productivity have faced many of these same limitations.

CHAPTER 7 - Conclusion

The pollen productivity estimates obtained in this study are the first PPEs to be obtained for grassland regions in North America. While some of the PPEs obtained for taxa in this study have been obtained in other regions, regional differences promote the necessity of obtaining PPEs that are directly applicable to the region that one is studying. The PPEs here can be used for landscape reconstruction, and add to a growing understanding of the quantitative relationship between vegetation cover and pollen assemblages. This research contributes to geographic and paleoecological knowledge in a few important ways: First, the PPEs provided for these 12 selected taxa will contribute directly to future research using the Landscape Reconstruction Algorithm (Sugita, 2007a; Sugita, 2007b). Second, this has been the first time that the ERV Model has been used in a grassland region in North America. By using the ERV Model for this research, I have demonstrated it can be used for obtaining PPEs in grasslands in North America. Third, this research encourages a better understanding of how the spatial distribution of vegetation on a landscape can be recognized in pollen data, and can help answer questions about past landscapes in North America.

While the RSAP is very similar between submodel 1 and submodel 3, the obtained PPEs show some slight differences between the submodels. In comparison to submodel 1, submodel 3 produces slightly higher PPEs for tree taxa, and slightly lower PPEs for herbaceous taxa. Submodel 3 is a better fit for the data because of the lower standard errors for each taxa, and because of the smoother relationship shown on the log-likelihood curve. Only three taxa produced PPEs that were lower than the reference taxon: Asteraceae, Fabaceae, and Chenopodiaceae. All of the tree taxa—*Cornus, Maclura, Juniperus, Populus, Quercus,* and *Salix*—plus herbaceous taxa *Artemisia* and *Ambrosia* have PPEs that are higher than Poaceae.

The PPE for Chenopodiaceae had a very high standard error, and thus should be used with caution.

With the PPEs provided by this research, landscape reconstruction for grassland areas in North America is within reach. Sediment cores dating back hundreds or thousands of years can provide pollen data that indicate the extent to which certain vegetation types were present on the landscape. Previously, it would have been impossible to quantitatively reconstruct the vegetation associated with the pollen data in those cores. However, with pollen productivity estimates for the pollen taxa present in those cores, those pollen assemblages can be translated into quantitative landscape reconstructions. In addition to quantifying the amount of vegetation cover at a taxon-specific level, one can also estimate the distance corresponding with that vegetation because the RSAP for bodies of water 50 m in radius is known (1060 m).

By enabling vegetation reconstruction of historic environments, we can also begin to answer bigger questions about how landscapes have changed over time, and how these changes have occurred in accordance with climate. For example, the prairie-forest ecotone of the upper Midwest has undergone large biogeographic shifts due to climate, fire, and human activities. A comparison of pollen and charcoal records from Moon Lake, North Dakota, (a modern tall-grass prairie lake) and Deming Lake, Minnesota (a modern pine-deciduous forest) has shown that this boundary has expanded and contracted several times during the Holocene (Clark *et al.*, 2001). This expansion and contraction can be noted by pollen percentages of C_4 grasses in Deming Lake records that were as high as C_4 grass percentages in Moon Lake records. While this information is intrinsically valuable, the pollen productivity estimates I have obtained through this research would allow quantitative vegetation reconstructions of this region. These estimates could inform not only the timing of the prairie-forest boundary shift, but the quantitative extent of this shift. More specifically, the PPEs I have provided indicate that *Quercus* (oak) has a value that is about double the value for Poaceae (grass). Equal amounts of *Quercus* and Poaceae in the pollen record would correspond with twice as much *Quercus* than Poaceae on the landscape. Comparisons and reconstructions can also be made with the other taxa I have provided, especially those that can be indicators of human activity, such as *Ambrosia, Maclura,* and *Cornus.*

Although this research provides information that can be used in a variety of contexts by scientists, there are a few improvements that could be made for the next time that someone completes a piece of research similar to this. First, a more objective method for estimating vegetation cover would allow the vegetation data to be more accurate and would help eliminate bias. The digital land cover imagery that is currently available provides a good indication of the location of clusters of vegetation, but provides a greater taxonomic resolution for tree taxa versus herbaceous taxa. The GAP land cover data set contains fewer grassland categories than tree categories, and there is typically no distinction in the types of species present in one grassland category compared to another grassland category. Since herbaceous taxa tend to be physically smaller than tree taxa and are more dispersed rather than clustered, the resolution of the grassland category is limited by current remote sensing technology. The best sensor would be one that had a very high spatial resolution, such as 0.5 m or finer, and a high temporal resolution that accommodated the variation in flowering dates of the selected plant taxa. However, even if this sensor was affordable and available, some taxa would still be eliminated from this data set. One taxa in particular is Chenopodiaceae, which usually achieves a height that is shorter than the height of the grassland canopy. In addition to plants that are shorter than the grassland canopy, plant taxa that do not have noticeable flowers or characteristics to set them apart from other taxa would also be hard to record. Thus, even with a very high resolution sensor or aerial photos, grassland vegetation cover on a taxon-specific basis would still be difficult to estimate.

A second improvement that would benefit this research would be more comprehensive vegetation surveys, including both closer timing of the field vegetation surveys from site-to-site and multiple survey dates throughout the season to match phenology of grassland species. In this study, I was only able to survey the vegetation at each site one time. Additionally, the date of the vegetation survey for each site depended on landowner availability. Timing was also limited by the number of people involved in the vegetation surveys. Two undergraduate researchers and I completed all of the vegetation surveys between the end of May and the beginning of August, and thus the field surveys may have been affected by the varied growing season among the plant taxa. For example, some taxa, including certain types of Asteraceae, bloom mid-season and are difficult to identify without their flowers. Some of these plants could have been misidentified early in the season because they lacked a flower. In an ideal setting, vegetation surveys would be completed among sites within a one-week time period and vegetation would be surveyed several times, however, with a small group of people, this is not feasible. Furthermore, all vegetation surveys have temporal problems to some degree (Bunting *et al.* 2004, Broström *et al.* 2008), and thus the temporal problems I faced were not any greater than the temporal problems faced by other studies that also require extensive vegetation surveys.

The 12 PPEs provided in this paper are the first ones to be provided for a grassland region in North America, and thus provide valuable insight into the nature of pollen dispersal and vegetation composition in grassland areas. However, their utility is much greater when examined in a larger context. These PPEs will become most valuable when they are used by future researchers to reconstruct landscapes, and in turn, they can begin to answer some of the bigger questions about how vegetation composition in the Great Plains has shifted over time. Furthermore, vegetation shifts can be examined in accordance with past climate, and thus we can better understand how vegetation has changed with climate in the past and begin to anticipate how climate-vegetation relationships can change in the future.

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Appendix A - Data Tables

Site Locations

Table A.1: Site numbers and latitude and longitude coordinates for 24 ponds in the Flint Hills study area. Most of the land is privately owned.

Site Number	Latitude	Longitude
1	39.10792 N	96.58682 W
2	39.32581 N	96.68479 W
3	39.39222 N	96.92773 W
4	39.44299 N	96.84036 W
5	39.13735 N	96.52992 W
6	38.94875 N	96.78072 W
7	38.43413 N	96.56287 W
8	38.40768 N	96.55949 W
9	38.86420 N	96.90096 W
10	38.39846 N	96.46892 W
11	39.09327 N	96.55032 W
12	37.57927 N	96.54244 W
13	37.59356 N	96.50719 W
14	38.75622 N	96.31238 W
15	38.74162 N	96.28054 W
16	37.51917 N	96.04391 W
17	37.93732 N	96.20042 W
18	38.94819 N	96.44138 W
19	39.31019 N	96.36695 W
20	39.47264 N	96.34693 W
21	39.46012 N	96.53732 W
22	38.10643 N	96.45797 W
23	38.12769 N	96.48081 W
24	39.3727 N	96.11724 W

Pollen Counts

Table A.2: Number of grains of pollen counted for each site. A minimum of 300 terrestrial pollen grains were counted for each site.

Taxa	Site Number																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	24	25
Abies	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Acer negundo	1	0	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	2	0	1
Acer saccharinum-type	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acer saccharum	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Alnus incana	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	3	0
Alnus viridis-type	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Betula	3	0	0	2	1	1	0	0	2	1	1	0	0	2	0	1	1	0	2	1	1	0	0	1
Carya	2	8	1	1	6	5	7	2	3	6	10	6	15	18	3	6	12	11	5	3	6	12	9	6
Celtis	7	0	2	2	0	0	0	0	2	2	1	0	0	3	0	0	0	2	0	0	0	2	1	3
Cornus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera-type	2	2	1	0	4	1	0	0	0	0	3	1	0	1	0	0	1	7	0	3	0	0	0	4
Corylus	0	1	0	0	0	0	1	0	0	0	2	0	1	0	1	0	1	0	0	0	0	1	0	0
Juniperus	30	53	13	37	54	77	29	35	55	52	21	13	23	6	52	24	32	41	37	125	17	36	56	2
Juniperus-stomata	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
Ephedra trifurca-type	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephedra viridis-type	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Fraxinus	6	3	7	5	7	4	10	4	14	8	5	3	6	1	12	2	9	12	8	10	2	10	15	0
Juglans nigra	8	7	5	5	5	8	9	5	6	10	12	4	5	33	14	4	12	13	15	21	2	12	8	7
Maclura pomifera-type	20	21	4	22	16	54	12	10	28	26	30	4	1	20	18	3	11	18	42	55	16	26	20	8
Morus	5	6	1	17	8	4	0	4	3	5	0	0	3	1	1	0	4	0	5	6	0	0	2	0
Myrica	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0
Ostrya-type	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Picea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinus subg. Pinus	18	13	12	4	15	13	24	6	11	27	43	10	27	29	16	7	20	15	4	8	7	39	37	25
Pinus subg. Strobus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pinus undiff.	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Platanus	6	4	0	2	3	2	1	1	2	1	0	1	11	2	3	0	4	0	2	1	0	4	4	1
Populus tremuloides-type	4	3	0	4	6	3	0	1	1	0	1	0	0	2	1	0	2	0	0	2	1	2	4	0
Prunus-type	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Quercus	94	66	23	37	73	59	85	35	54	91	77	34	106	143	88	86	117	50	59	34	13	85	61	43
Rhus	1	2	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0

Salix	1	2	0	1	3	27	1	10	5	4	0	5	8	0	5	6	5	5	104	19	12	0	18	0
Sambucus	0	0	0	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Sarcobatus vermiculatus	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0
Shepherdia argentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ulmus	16	17	8	20	27	17	19	23	19	20	17	12	12	51	27	12	14	28	22	10	5	22	9	12
Viburnum trilobum-type	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Vitis	2	0	2	1	0	1	2	0	0	0	2	0	2	0	0	1	0	1	0	0	2	0	1	0
Poaceae	52	84	86	60	40	59	42	20	72	50	84	37	28	86	81	7	60	34	72	24	49	48	46	183
Cerealia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ambrosia-type	89	97	165	96	142	75	105	177	154	89	83	262	79	52	94	143	106	157	92	88	181	115	98	115
Artemisia	3	12	7	9	5	4	4	4	6	7	1	2	2	6	4	2	2	3	4	1	2	4	4	1
Asteraceae subf. Asteroideae undiff.	42	28	17	15	32	14	68	63	33	34	27	59	32	30	23	12	39	36	17	25	35	48	35	7
Achilea-type	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1
Bidens-type	3	2	0	3	0	0	1	2	2	1	2	0	1	2	1	0	0	0	0	0	0	1	2	9
Iva xanthifolia-type	2	0	2	1	0	3	1	0	2	0	0	0	0	0	0	0	1	0	1	0	1	1	3	0
Iva annua-type	11	5	5	3	4	3	7	4	7	10	2	24	2	6	10	0	34	5	5	1	2	6	8	49
Asteraceae subf. Cichorioideae	0	0	12	0	0	1	3	0	0	0	0	3	0	1	0	0	1	0	0	1	0	7	1	1
Apiaceae	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Campanula aparinoides-type	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Caryophyllaceae	0	0	1	2	1	1	2	0	0	1	0	0	0	2	0	0	0	0	0	0	1	1	2	1
Chenopodiaceae undiff.	30	48	50	147	33	37	44	80	39	59	79	34	31	20	25	14	37	41	35	37	138	26	43	24
Convolvulus	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Calistegia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cystaceae	2	0	0	0	0	0	1	0	0	0	1	0	0	8	0	0	1	1	5	0	0	0	0	0
Epilobium	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Oenothera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gallium-type	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Fabaceae undiff.	4	1	0	1	0	1	1	1	3	2	2	5	4	1	2	3	1	0	8	3	3	2	3	0
Dalea purpurea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dalea candida-type	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trifolium pratense	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hedysarum	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopus-type	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Malvaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalis	2	1	0	0	0	0	1	0	1	0	1	2	0	0	2	1	0	0	0	0	0	1	0	0
Phlox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Potentilla palustris-type	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus undiff.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
Thalictrum	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1

Rosaceae undiff.	1	1	2	1	0	2	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0
Spirea-type	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum aviculare-type	0	0	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Polygonum bistorta-type	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex	0	1	1	0	4	2	3	7	0	1	0	1	1	0	4	2	2	1	5	2	4	2	4	3
Rumex mexicanus-type	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Salsola	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Sanguisorba	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solanaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Urtica-type	1	0	0	1	1	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Verbenaceae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
Violaceae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Xanthium	1	2	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0
Zygadenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0
Equisetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Monolete spore undiff.	1	0	0	1	0	0	3	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	3
Pteridium aquilinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Selaginella densa-type	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trilete spore undiff.	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gelasinospora	0	0	0	0	0	2	3	0	2	1	36	0	1	0	0	0	0	3	1	0	0	1	0	0
Glomus	16	3	3	2	7	0	4	0	1	5	22	2	6	5	0	1	7	6	0	15	0	3	5	2
Meliola	2	3	1	0	0	4	1	1	0	1	0	0	3	0	1	0	0	0	0	0	1	1	0	0
Podospora	0	5	1	0	0	0	1	0	0	0	2	1	3	1	0	0	3	0	0	0	1	2	1	1
Sporomiella	12	11	8	7	6	11	0	3	2	7	11	9	11	0	4	1	2	3	0	0	16	3	7	3
Botriococcus	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	1	3	0	1
Cyperaceae	4	30	21	6	19	6	24	17	6	21	44	13	23	16	37	2	19	8	11	13	10	9	22	23
Lemna	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polygonum lapathifolium-type	0	0	37	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1
Potamogeton/Triglochin	0	4	0	0	22	8	0	7	0	0	5	0	1	0	12	0	0	17	0	1	1	1	0	0
Typha latifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sparganium-type	1	2	0	1	23	4	2	0	28	0	2	0	2	0	10	48	3	4	30	3	5	7	0	2
Unknown	7	5	4	5	11	8	5	5	3	2	7	2	9	4	2	6	4	5	4	1	3	1	3	2
Microspheres	373	595	421	352	295	350	466	611	357	906	429	899	719	24	720	847	814	1224	317	1408	423	534	589	21
Diporotheca	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0
Arboreal Pollen (AP)	232	210	81	164	237	278	201	137	207	255	226	95	227	314	245	153	246	206	309	300	85	254	251	114
Non-arboreal Pollen (NAP)	246	284	361	341	266	204	286	361	319	258	287	431	181	216	255	187	289	279	251	185	416	276	253	396
Ferns	3	0	0	1	2	0	4	1	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	3
Fungi	30	22	13	9	13	17	10	4	5	14	71	12	25	6	5	2	12	12	1	17	18	10	13	6
Aquatics	5	37	58	10	64	18	27	24	37	21	51	13	26	16	59	53	23	29	43	17	17	20	22	27
Unknown	7	5	5	5	11	9	5	5	3	2	7	2	9	4	2	6	4	5	4	9	3	1	3	2
AP+NAP	478	494	442	505	503	482	487	498	526	513	513	526	408	530	500	340	535	485	560	485	501	530	504	510
AP+NAP+Loc.el.	523	558	518	530	593	526	533	532	571	550	643	553	468	556	567	401	575	531	608	529	540	561	542	548

Vegetation Data

Table A.3: Plant taxa present in field surveys at each of the 24 sites in the Flint Hills study area.

		Site																							
	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Herbaceous	Acanthaceae			x												x	x	x	x	x		x	x	x	x
	Ambrosia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Anacardiaceae	x				x				x		x		x			x		x	x					
	Apiaceae	x	x			x			x					x	x	x						x			
	Apocynaceae																		x						
	Artemisia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
	Asclepiadaceae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Asteraceae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Boraginaceae																							x	
	Brassicaceae		x			x	x	x	x		x		x						x				x		
	Canabaceae																								x
	Caprifoliaceae	x	x		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x					
	Caryophyllaceae												x												
	Chenopodiaceae					x	x	x	x													x			
	Convolvulaceae	x		x		x	x	x	x	x	x		x	x		x	x	x			x				x
	Cyperaceae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Euphorbiaceae	x									x									x		x	x	x	
	Fabaceae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Gerniaceae	x							x	x	x														
	Lamiaceae	x		x								x		x										x	
	Linaceae			x																x	x	x	x	x	
	Malvaceae							x	x	x	x	x	x	x		x	x	x					x		x
	Onagraceae	x					x	x	x	x	x		x	x				x		x	x	x			
	Orchidaceae																							x	
	Oxalidaceae	x	x	x		x		x	x		x		x	x	x	x	x		x	x		x	x	x	x
	Plantaginaceae		x		x	x	x	x	x		x	x	x	x		x				x	x	x	x		x
	Poaceae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Polemoniaceae										x				x										
	Polygonaceae																					x			x
	Ranunculaceae					x		x		x					x		x								
	Rosaceae	x	x		x	x				x		x		x	x	x	x	x	x	x	x	x			x
	Rubus		x											x				x							
	Rumex										x												x		

	Scrophulariaceae																x								
	Solanaceae		x	x					x		x		x	x	x	x		x	x	x	x	x		x	x
	Verbenaceae			x								x										x	x	x	
	Violaceae	x				x			x										x			x			
Non-herbaceous	*Celtis*	x															x								
	Cornus	x	x		x		x			x		x			x		x		x	x	x				x
	Fraxinus									x											x				
	Juglans																					x			
	Juniperus	x	x		x	x	x			x									x		x				
	Maclura		x		x		x							x	x	x	x			x	x	x		x	x
	Morus		x		x				x											x					x
	Platanus													x											
	Populus	x					x			x									x	x					x
	Quercus	x																	x						
	Rhus	x			x	x	x			x		x		x	x		x		x	x					
	Salix		x			x	x	x	x	x	x		x		x	x	x	x	x	x	x	x		x	x
	Ulmus	x	x		x		x	x		x		x			x		x		x					x	

Table A.4: Average percent cover of taxa for all quadrats at each of the 24 study sites in the Flint Hills study area.

		Site																							
	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Herbaceous	Acanthaceae	0	0	1E-04	0	0	0	0	0	0	0	0	0	0	0	0.006	0.012	0.003	0.005	0.004	0	0.007	0.008	0.005	1E-04
	Ambrosia	0.027	0.027	0.028	0.047	0.086	0.044	0.041	0.035	0.025	0.065	0.02	0.044	0.055	0.04	0.058	0.047	0.086	0.027	0.015	0.065	0.155	0.036	0.058	0.032
	Anacardiaceae	0.001	0	0	0	0.004	0	0	0	0.001	0	0.007	0	0	0	0	0	0	0.004	0.004	0	0	0	0	0
	Apiaceae	0.008	0	0	0	0.017	0	0	0.001	0	0	0	0	1E-04	0.003	1E-03	0	0	0	0	0	1E-04	0	0	0
	Apocynaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0
	Artemisia	0.003	0.01	0.001	0.013	0.031	0.026	0.005	0.014	0.019	0.028	0.001	0.008	0.022	0.036	0.01	0.002	0.007	0.002	0.012	0.017	0.016	0.001	0.007	0
	Asclepiadaceae	0.003	0.007	0.004	0.017	0.001	0.024	0.008	0.003	0.002	0.001	0.004	0.007	0.004		0.012	3E-04	0.02	0.01	0.001	0.001	0.009	0.003	0.004	0.001
	Asteraceae	0.054	0.021	0.045	0.078	0.081	0.053	0.06	0.098	0.072	0.098	0.112	0.155	0.068	0.154	0.194	0.135	0.091	0.092	0.108	0.086	0.084	0.077	0.06	0.028
	Boraginaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E-03	0
	Brassicaceae	0	0.002	0	0	0.005	0.006	0.004	0.004	0	0.002	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0
	Canabaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E-04
	Caprifoliaceae	0.002	0	0	0.001	0.005	0.002	0.004	0.005	0.015	1E-04	0.003	0.004	0.05	0.02	0.002	0	0.001	0.008	0.006	0	0	0	0	0
	Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0	0.004	0	0	0	0	0	0	0	0	0	0	0	0
	Chenopodiaceae	0	0	0	0	0	0.003	0.005	0.001	0	0	0	0	0	0	0	0	0	0	0	0	1E-04	0	0	0
	Convolvulaceae	1E-03	0	1E-04	0	0.002		0.021	0.007	0.004	1E-04	0	0.003	0.004	0	0.009	0.001	1E-04	0	0	0.003	0	0	0	0.033
	Cyperaceae	0.033	0.003	0.199	0.048	0.025	0.024	0.006	0.116	0.009	0.002	0.034	0.078	0	0.026	0.103	0.085	0.047	0.028	0.017	0.093	0.023	0.1	0.025	0.082
	Euphorbiaceae	0.001	0	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0	0	0	0.004	0	2E-04	0.001	0.003	0
	Fabaceae	0.032	0.018	0.03	0.041	0.031	0.03	0.056	0.077	0.073	0.084	0.101	0.095	0.019	0.087	0.095	0.035	0.047	0.085	0.149	0.039	0.185	0.068	0.091	0.122
	Gerniaceae	0	0	0	0	0	0	0	0.003	0.004	1E-04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lamiaceae	0.001	0	0.009	0	0	0	0	0	0	0.001	0.001	0	0.001	0	0	0	0	0	0	0	0	0	0	0
	Linaceae	0	0	2E-04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.017	0.002	0.002	1E-04	1E-04	0
	Malvaceae	0	0	0	0	0	0	0.012	0.014	0.002	0	0.001	0.002	0.006	0	0.001	0.076	0.005	0	0	0	0	1E-04	0	1E-04
	Onagraceae	1E-03	0	0	0	0	4E-04	1E-04	0.003	0.001	1E-04	0	0.006	0.001	0	0	0	0.002	0.013	0.008	0.004	1E-04	0	0	0
	Orchidaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E-04	0
	Oxalidaceae	0.007	0	3E-04	0	0.003	0	0.003	0.012	0	0.006	0	1E-04	0.001	0.003	0.004	0.003	0	0.001	0.004	0	0.013	4E-04	0.001	0.001
	Plantaginaceae	0	2E-04	0	0.002	0.005	0.005	0.004	0.004	0	0.006	0.002	0.009	0.002	0	9E-04	0	0	0	0.001	0.003	0.002	0.001	0	0.001
	Poaceae	0.444	0.697	0.671	0.69	0.508	0.637	0.682	0.501	0.646	0.661	0.607	0.497	0.62	0.576	0.455	0.513	0.623	0.58	0.581	0.586	0.426	0.651	0.71	0.672
	Polemoniaceae	0	0	0	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Polygonaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0	0	0.009
	Ranunculaceae	0	0	0	0	0.003	0	0.001	0	1E-04	0	0	0	0	1E-04	0	0.001	0	0	0	0	0	0	0	0
	Rosaceae	0.012	0.002	0	3E-04	0.006	0	0	0	0.01	0	0.014	0	0.011	0.001	9E-04	0.032	0.003	0.025	0.018	0.007	0.003	0	0	1E-04
	Rubus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Rumex	0	0	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0
	Scrophulariaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0	0	0.018
	Solanaceae	0	0	0.001	0	0	0	0	0.001	0	0.001	0	0.001	0.001	2E-04	0.003	0	0.002	0.001	0.001	0.03	0.004	0	1E-03	0
	Verbenaceae	0	0	0.004	0	0	0	0	0	0	0	0.003	0	0	0	0	0	0	0	0	0.001	0.008	0.001	0.013	0
	Violaceae	0.003	0	0	0	0.001	0	0	0.001	0	0	0	0	0	0	0	0	0	0.001	0	0	0.001	0	0	0

Non-herbaceous	*Celtis*	3E-04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cornus	0.013	0.003	0	0.005	0.015	0.013	0	0	0.022	0	0.017	0	0	0	0	0.004	0	0.027	0.01	0.001	0	0	0	0
	Fraxinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Juglans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Juniperus	0	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0	0	0	0	0	0.023	0	0	0	0
	Maclura	0	0	0	0	0	0	0	0	0	0	0	0	0	0.023	0	0	0	0	0	0	0	0	0	0
	Morus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Platanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Populus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Quercus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	0	0	0	0	0	0
	Rhus	0.001	0	0	0.009	0.004	0.031	0	0	0.001	0	0.008	0	0.027	0.009	0	0.006	0	0.002	0.039	0	0	0	0	0
	Salix	0	0	0	0	0.024	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.022	0	0	0
	Ulmus	0	0	0	0	2E-04	0	0	0	1E-04	0	0	0	0	0	0	1E-04	0	0.009	0	0	0	0	0	0
	Bare	0.352	0.21	0.008	0.049	0.143	0.098	0.089	0.1	0.093	0.041	0.064	0.087	0.106	0.021	0.044	0.046	0.063	0.037	0	0.039	0.019	0.051	0.022	0

Pollen Fall Speed Data

Equation A.1: Stoke's Law Equation used for calculating pollen fall speed

$v_s = [2r^2 \cdot g\ (\rho_0 - \rho)]/9\mu$

where,

v_s = spherical settling velocity (cm s^{-1})

r = pollen grain radius (cm)

g = acceleration due to gravity (cm s^{-2}) taken as 981 cm s^{-2}

ρ_0 = particle (grain) density (cm^{-3}) taken as 1 cm^{-3}

ρ = fluid (air) density (cm^{-3}) taken as 1.27×10^{-3} cm^{-3}

μ = dynamic viscosity ($cm^{-1}s^{-1}$) 1.8×10^{-4}

Table A.5: Grain radius (*r*) in centimeters for each pollen taxon. Grain radius values for *Juniperus,* Poaceae*,* *Quercus,* and *Salix* were not needed, as fall speed values had been previously calculated in other studies.

Taxon	Grain radius (cm)
Ambrosia	0.00125
Artemisia	0.00105
Asteraceae	0.001075
Chenopodiaceae	0.00095
Cornus	0.0019
Fabaceae	0.00133
Maclura	0.00115
Populus	0.0015