The Nebraska Sand Hills – Mid- to Late-Holocene Drought Variation and Landscape Stability Based on High-Resolution Lake Sediment Records

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A high-resolution multi-proxy analysis was used to reconstruct moisture balance fluctuations spanning the last 6500 years and to investigate the origins of interdunal lakes in the central Sand Hills of Nebraska. Detailed paleoecological data from Beaver Lake, plus analyses from two nearby lakes, were integrated to reconstruct regional climate history. Six episodes of multi-centennial droughts occurred, with a dramatic change in overall mean state between 4000 and 3800 yr BP. An extensive low lake stand between 6500-5750 yr BP was likely predominantly climatically driven rather than geomorphically induced.

Paleohydrological reconstructions of five lakes in the Nebraska Sand Hills were compared in order to 1) determine whether droughts of the past 4000 yrs were spatially and temporally coherent across the region, 2) distinguish local variation in climate from regional patterns, 3) compare the paleolimnological results with the existing dune records, and 4) assess the frequency of variation among the sites. Results indicate frequent alterations between high and low lake-levels during the past 4000 yr. Extended
droughts were more common prior to 2000 yr BP, while the last two millennia were hydrologically more complex, and climate shifts alternated on shorter timescales. This record refines the existing Holocene drought history of the Nebraska Sand Hills and aids in our understanding of how drought episodes can vary in terms of magnitude, spatial extent, and temporal scale.

Diatom diversity trends were analyzed for a suite of Nebraska lakes to evaluate the sensitivity of diatom communities to various environmental gradients. Diatom diversity of natural lakes showed the strongest correlation with total nitrogen, turbidity, and conductivity, whereas in reservoir lakes and sand pits, diversity was predominantly driven by phosphorus, nitrate-nitrogen species, turbidity, and pH. Differences in diversity trends are primarily a manifestation of nutrient and light availability, which in turn, is dependent on the physical and geographic properties that characterize each lake system.
Dedication

I dedicate this work to my family, particularly my dear wife Alison Wimmer, for her unlimited support and encouragement; to my lovely daughter Hannah-Louise, who put everything back into perspective when things weren’t going so well; and to my parents, who probably still have no clue what I have been doing for the last 4 and a half years, and why I came to Nebraska in the first place; and finally to everyone else who had to put up with me during my time here. Thanks!
Acknowledgements

My gratitude goes to the following people and institutions for their support and assistance during this research: University of Nebraska-Lincoln, Department of Geosciences, Nebraska Geological Society, and the Center of Great Plains Studies.

I am immensely grateful to my advisor Dr. Sherilyn Fritz for providing me the opportunity to do research in the Sand Hills, and whose guidance and patience broadened my world in a discipline that focuses on things microscopic. I would also like to acknowledge my committee members for their support and critique of this work; Dr. James Swinehart for his valued advice, support, and help in the field; Dr. David Loope for always being available for questions and time for a chat; Cathleen McFadden for the measurement of TC and TN; Daniel Snow at the Water Science Laboratory at UNL for TIC measurements; Jeffery Stone and Karlyn Westover for their unlimited help and support during my time here at UNL; Brandi Flyr for helping me out with all sorts of questions related to water chemistry and statistics; Will Hobbs for reading through my manuscript of Chapter 2 and general advice; Avery Shinneman for helping with the transfer functions; Diane Winter for introducing me to CANOCO; Aaron Young for assisting in the field; Ron Goble for processing OSL samples of Swan Lake; Kyle Herman for analyzing the Beaver and Rat Lake water chemistry.
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Chapter 1

INTRODUCTION
1.1 Background and scope

The Nebraska Sand Hills encompass an area of more than 50,000 km$^2$ of vegetated sand dunes stretching 425 km across Nebraska (Nicholson and Swinehart, 2005). It is considered the largest sand-dune area in the Western Hemisphere and the largest grass-stabilized dune region in the world, with dunes exceeding 100 m in height (Bleed & Flowerday, 1998). The Sand Hills sit atop the High Plains Aquifer, which stores about 50% of the total groundwater available in all of Nebraska (Bleed, 1998). The combination of a shallow groundwater table and abundance of water create ideal conditions for the development of wetlands and permanent shallow lakes in the low-lying interdunal valleys. About 10% of the landscape is occupied by such wetlands and lakes, making the Sand Hills one of the nation’s most extensive grass- and wetlands system and providing habitat for over 300 bird species, the second most productive waterfowl area in the United States (Labedz, 1998).

Today, Sand Hills dunes are almost completely stabilized and held in place by native grassland or shrub steppe vegetation. Winds in this region exceed the threshold velocity for sand entrainment about 50% of the time and are capable of mobilizing sparsely vegetated dune sand. Therefore, vegetation cover is the key limitation on dune activation, whereas vegetation density is strongly affected by effective moisture (Muhs and Maat, 1993). Because of this delicate balance between moisture availability and vegetation density, the Sand Hills is a highly drought-sensitive landscape that has experienced a series of severe drought events over the course of the Holocene. These droughts led to the loss of stabilizing grass cover and remobilization of the sand dunes (e.g. Loope and Swinehart, 2000; Miao et al., 2007). The regional extent of these drought
events is still under debate, although the latest large-scale drought episode, between 900 and 700 years ago, was widespread across the Sand Hills (Miao et al., 2007; Mason et al., 2004). Future droughts of similar magnitude could have devastating effects on North American society, resulting in massive reductions of water availability and quality due to the depletion of the High Plains Reservoir, crop failure, loss of rangeland, increase of wildfires, etc. (Klineberg 2002). Understanding the mechanisms, as well as the timing and frequency of past severe droughts is crucial and can serve as a basis for understanding the sensitivity of this landscape to future drought events.

Most paleoclimatological reconstructions in the Sand Hills are based on eolian dune sand and loess records (Forman et al. 2001, Mason et al. 2004, Miao et al. 2007), as well as interspersed paleosols (Jacobs and Mason 2004, Goble et al. 2004). Only a handful of studies on lake and wetland deposits exist (Loope 1995, Nicholson and Swinehart 2005). However, the abundance of shallow lakes and wetlands in this region (La Baugh 1986) provides an opportunity for high-resolution Holocene climate studies based on the information stored in the sediments. A synthesis of multiple sites across this region offers an approach for robust climate interpretations.

The research reported in this dissertation focuses on some of the unresolved and ongoing issues that pertain to climate research in this area. Because diatoms are used as a primary proxy for assessing environmental changes, I dedicated one part of this dissertation to providing insights into the intricate relationship between diatom diversity and environmental gradients across different lake types throughout Nebraska.

Among the main questions addressed in this dissertation are:
1) What is the history of lake-level change at the series of lakes investigated?

2) Are there common intervals of change among the five study sites? If so, do they show coherent changes or site-specific responses?

3) What is the relationship between the lake and dune records?

4) What do the lake records suggest about the triggers of dune mobilization?

5) Are there common frequencies of variation among the sites?

6) How do these lake sites compare with other regional records of climate change, particularly to eolian records?

7) How do these records relate to other records from the Great Plains and western U.S., and what does this suggest about environment and climate?

8) Is nutrient availability the main driver with respect to diatom diversity in Nebraska lakes?

9) Are diversity trends different in natural lakes than in man-made lakes?

1.2 Thesis overview

The thesis consists of three primary papers, each of which will be submitted to a peer-reviewed journal. In each paper, I carried out the analyses, unless otherwise specified; analyzed and interpreted the data; and took primary responsibility for writing the manuscript.
Chapter 2: A high-resolution diatom record, in conjunction with pollen, grain-size analyses, and bulk sediment chemistry, was studied to reconstruct moisture balance fluctuations of the last 6500 years and to find evidence for the origins of interdunal lakes in the central Sand Hills. Results reveal at least six episodes of multi-centennial droughts over the last 6500 cal yr BP and distinct wet periods between 5750-5300 cal yr BP and 3800-1950 cal yr BP. By far the most dramatic climate change accompanied by regional cooling and lake-level rise, occurred between 4000 and 3800 cal yr BP. No convincing evidence was found for dune blockage events in the central Sand Hills region similar to those events observed in the western portion. This study shows ample evidence of extensive drought and eolian activity between 6500-5750 cal yr BP, and suggests that most of the lake-level fluctuations were climatically driven and not a product of geomorphic alteration of drainage patterns.

This part of my dissertation was a collaborative effort. Dr. Eric Grimm performed the field work and analyzed the pollen data for the primary site, Beaver Lake. Kim Jacobs counted the majority of the diatom samples at Beaver Lake, and Stefan Kollet ran the grain size analysis. Dr. Sherilyn Fritz and Dr. James Swinehart provided valuable feedback on the manuscript, as did Dr. Will Hobbs. Dr. Avery Cook Shinneman provided help with the ordination of modern diatom surface sample data and the construction of depth-transfer functions.

Chapter 3: High-resolution paleohydrological reconstructions of five shallow lakes in the Nebraska Sand Hills were made to determine the spatial and temporal coherency of
climate variability across the region during the last ~4000 years and to distinguish between local and regional climate variation. Paleolimnological results were compared with the existing dune records, and the frequency of variation among the sites was assessed. Reconstructed lake-level curves, sand input, and bulk sediment chemistry suggest that the Sand Hills region was characterized by frequent shifts between dry and wet periods during the past 4000 yr. Extended multi-decadal to centennial-scale droughts were more common prior to 2000 yr BP, while the last two millennia were hydrologically more complex, and climate shifts alternated on shorter timescales. Time-series analysis showed significant centennial and multi-decadal variation in all lakes, but only a few common peaks are regionally representative and allow for comparisons with large-scale climate drivers. Despite some discrepancies among the five records, this study improves the existing Holocene drought history of the Nebraska Sand Hills, and at the same time it raises awareness of the inherent complexities of climate reconstructions from shallow lakes in fragile landscapes, such as the Sand Hills.

This research project was a collaborative effort. Dr. Sherilyn Fritz provided the research idea and funding and helped with valuable feedback on the manuscript. Dr. James Swinehart was the driving force in the field and offered many constructive ideas that improved this research project. Dr. Alexander Wolfe, Dr. Giff Miller, and Noah Daniels provided the diatom counts, bulk density and LOI data from Round Lake. Kim Jacobs counted the majority of the diatom samples from Beaver Lake, and Stefan Kollet ran the grain size analysis. Dr. Avery Cook Shinneman helped with the ordination of modern diatom surface sample data and the generation of depth- transfer functions.
Chapter 4: Lakes are intricately tied to the climate system, because their hydrologic budget is controlled by the balance between inputs (precipitation, surface water inflow, runoff, and groundwater inflow) and outputs (evaporation, surface water outflow, groundwater recharge) (Mason et al., 1994). Variations in effective moisture are interrelated to changes in lake-level and water chemistry, which, in turn, alter physiological responses and species composition of biota, including those of diatoms. The distributional pattern of diatoms reflects ionic and nutrient composition, light availability, etc. (Fritz et al., 1999). In order to test to what extent nutrients (P, N), light, pH, and conductivity influence diatom composition and diversity in natural and man-made lakes across Nebraska, we statistically analyzed diversity trends along nutrient and geochemical gradients. Results reveal that diatom diversity of natural lakes is predominantly driven by nitrogen, turbidity, and conductivity, in contrast to reservoir and sand pits, where diversity shows strongest correlation with phosphorus and nitrogen, and is secondarily correlated with turbidity and pH. In general, diversity is higher in low to intermediate ionic and nutrient concentrations for all lake types.

The final portion of my dissertation is a revision of a part of my comprehensive exams. Dr. Sherilyn Fritz and Dr. Johannes Knops both provided the research idea and helped with feedback on the manuscript. Dr. Fritz also provided her extensive Nebraska lake database, which contained all diatom counts and environmental data. Dr. Danuta Bennett organized the database and aided in the field collection of samples. Dr. Steve Juggins provided assistance in the statistical analysis.
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Chapter 2

MID-TO LATE- HOLOCENE MULTI- PROXY CLIMATIC AND HYDROLOGIC VARIABILITY IN THE NORTH- CENTRAL SAND HILLS, NE, USA
2.1 Abstract

Mid to late-Holocene climate change is reconstructed from multi-proxy analyses of a lake sediment core from the central Nebraska Sand Hills. A high-resolution diatom record in conjunction with pollen, grain size analyses, and bulk sediment chemistry are used to reconstruct moisture balance fluctuations spanning the last 6500 years. Paleoeocological data from two additional lake sediment cores from a site 60 km to the west were integrated and compared to understand the regional context of climate change. We found evidence that suggests at least six episodes of multi-centennial droughts over the last 6500 cal yr BP. Two distinct wet periods occurred at 5750-5300 cal yr BP and between 3800-1950 cal yr BP. By far the most dramatic climate change, recorded in all sites and accompanied by regional cooling and lake-level rise, occurred between 4000 and 3800 cal yr BP. Several lakes in the western Sand Hills developed during extended arid periods when migrating dunes blocked ancient river beds thereby raising the regional water table. The latest dune blockage occurred prior to 6000 cal yr BP. Our study does not find convincing evidence for a blockage event in the central portion of the Sand Hills region during this time. Although this study shows ample evidence of an extensive drought between 6500-5750 cal yr BP, the evidence suggests predominantly climatically driven lake-level fluctuations, rather than geomorphic influences on basin hydrology.

2.2 Introduction

The Great Plains of North America have been a focal point for many studies addressing Holocene climatic change and the spatial and temporal evolution of drought. The potential for high spatial variability of drought requires the incorporation of multiple
sites in order to describe patterns and to evaluate the mechanisms operating at decadal to millennial time scales. The majority of the published research from the central Great Plains is based on geomorphic reconstructions from eolian dune sands and loess deposits, which are abundant in landscapes such as the Nebraska Sand Hills. These studies suggest episodically recurring drought periods particularly in the Early- to Mid Holocene (e.g. Goble, 2004; Miao et al., 2007). However, they do not portray continuous high-frequency change nor do they reflect the critical moisture thresholds that degrade dune vegetation and allow dune reactivation. Lake sediments, in turn, have the potential for the reconstruction of high-frequency changes in effective moisture and can be used to evaluate the trigger(s) for dune mobilization. In general, variations in lake-level are affected by changes in effective moisture, which, in turn, is driven by climate. However, in some cases lake-levels can be affected by geomorphic processes, such as dune blockages or landslides. In the sediment record climatic versus geomorphic processes can sometimes be hard to discern from one another.

The Sand Hills extend over an area of ~50,000 km² across Nebraska, as well as parts of southern South Dakota, and they represent the largest dune field in the western hemisphere (Swinehart, 1990; Loope and Swinehart, 2000; Nicholson and Swinehart, 2005), with dunes reaching heights of up to 130 m (Swinehart 1990). Most of these dunes were primarily formed by strong NW-SE winds (Ahlbrandt and Fryberger, 1980). Effective moisture (precipitation-evaporation) controls the density of vegetation cover, which is the key limitation on dune mobility (Muhs and Maat, 1993). Today, typically during spring and early summer, heavy southerly-to-southeasterly winds pass over the Gulf of Mexico, transporting sufficient moisture into the central Great Plains (Loope et
al., 1995) to sustain a lush vegetation cover, thereby stabilizing dune fields across the region and preventing activation of the dunes. However, at times during the Holocene, the Sand Hills of Nebraska experienced a series of recurring and long-lasting drought events that killed vegetation and resulted in the remobilization of large portions of the dune field (e.g. Goble 2004; Nicholson and Swinehart 2005). The timing and frequency of these drought events is complex, but recent studies reveal at least four broad periods of increased dune activity occurring at approximately 9000 to 6600 cal yr BP, 3800 ± 300 cal yr BP, 2500 ± 100 cal yr BP, and 850 ± 150 cal yr BP (e.g. Nicholson and Swinehart 2005; Miao et al. 2007). To date, there is no complete chronology of Holocene drought throughout the Sand Hills, and spatial coverage of high-resolution studies is still limited. Lake records can help bridge the gaps between these drought episodes, and they have the potential to further refine periods of drought by providing continuous high-resolution records.

The Nebraska Sand Hills region contains a large number of small and shallow interdunal lakes and ponds, which are very diverse in terms of their chemistry (Gosselin, 2000). A shallow groundwater table is responsible for the presence of extensive lake systems and wetlands occurring in interdunal valleys, which together cover about 10% of this landscape. More than 1000 lakes are located in the western portion of the Sand Hills alone, which represents the driest part of this region. It is hypothesized that during prolonged arid intervals, multiple episodes of dune blockages were largely responsible for the creation of these lakes (Loope et al., 1995; Loope, 2000). In western Nebraska, dune dams resulted in the blockage of two large valley systems, thereby raising the water table of the High-Plains aquifer as much as 25 m over an area of 7000 km². Mason et al
suggest at least two distinct episodes of eolian dune blockage, the earlier occurring prior to 12,750 cal yr BP and the latter occurring before 6000 cal yr BP.

Here we present a high-resolution multi-proxy lake sediment record from Beaver Lake, Nebraska, located in the north central part of the Sand Hills to evaluate the timing and frequency of drought events and whether or not lake-level change is attributable to the process of dune blockage or instead is primarily driven by climate. We also discuss the local and regional hydrologic impact of desertification episodes during the mid to late Holocene by using high-resolution records from another site within the Sand Hills to determine if patterns at Beaver Lake are regionally representative and to provide evidence for the causes of lake-level change.

2.3 Study Sites

Beaver Lake (42°27’35” N, 100°40’08”W) lies within the north-central portion of the Sand Hills in an interdunal valley within immediate proximity to stabilized linear dunes. Beaver Lake has a maximum depth ($z_{max}$) of about 3.5 meters and is hydrologically connected to Rat Lake to the east. Like most lakes in the Sand Hills, it is strongly influenced by groundwater fluctuations, as well as seasonal variability of effective moisture (precipitation minus evaporation, $P-E$).

Located about 60 km to the west of the Beaver Lake site are two small lake basins called East and West Twin Lakes (42°24’30” N, 101°26’20”W). These basins are surrounded by barchanoid dunes, some of which reach heights of more than 60 m. There are roughly 30 similar groundwater-fed wetlands in the area that accumulate peat and lake mud (Steinauer et al. 1996). Presently, East Twin is dry due to artificial drainage.
The combination of strong winds and shallow depth do not promote conditions for seasonal stratification in most Sand Hill lakes, and most lakes are nearly isothermal, regardless of season (La Baugh, 1986). Generally, the 1% level of surface light does not penetrate to the bottom in shallow Sand Hill lakes. Secchi disk transparency is commonly less than 55 cm. Limited water chemistry data are available from Beaver Lake and Rat Lake (Table 2.1).
Table 2.1: Environmental data collected in Fall 2008 from Beaver and Rat Lake.

<table>
<thead>
<tr>
<th></th>
<th>DOC (µg/l)</th>
<th>OP2 (µg/l)</th>
<th>NH₃ (µg/l)</th>
<th>pH</th>
<th>Depth (z_max)</th>
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</thead>
<tbody>
<tr>
<td>Beaver Lake</td>
<td>19355</td>
<td>54.9</td>
<td>231</td>
<td>7.8</td>
<td>3.5</td>
</tr>
<tr>
<td>Rat Lake</td>
<td>20320</td>
<td>18.6</td>
<td>191</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

Figure 2.1: Location of Beaver Lake, Twin Lakes, and the Crescent Lake Wildlife Refuge in relation to the Nebraska Sand Hills (yellow area). White circles indicate approximate coring locations.
2.4 Methods

2.4.1 Field

Beaver Lake was cored with a Wright square-rod piston corer (5 cm diameter) in July 1995 from the deepest part of the basin. Cores from East and West Twin Lakes were obtained by vibracoring between 1999 and 2006. One vibracore was taken from the edge of West Twin, while the cores from East Twin were taken from the center of the lakes (Figure 2.1).

2.4.2 Chronology

Chronology is based on linear interpolation of accelerator mass spectrometry (AMS) radiocarbon dates of terrestrial charcoal, seeds, plant fragments, and bulk sediment. All AMS dates are converted to calendar years BP (see Table 2.2) using CALIB 5.0.1 (Stuiver and Reimer, 1993).
Table 2.2: Radiocarbon ages and calibrated age equivalents used in determining age models for Beaver Lake (BLK), West Twin (WT), and East Twin (ET).

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>14C lab#</th>
<th>Composite depth (cm)</th>
<th>Material</th>
<th>14C age (yr BP)</th>
<th>Age error (yr)</th>
<th>Calibrated range 2 sigma (cal BP)</th>
<th>Midpoint (cal BP)</th>
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<td>CAMS-18863</td>
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<td>Charcoal</td>
<td>1055</td>
<td>35</td>
<td>923-1014</td>
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<td>CAMS-18864</td>
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<td>Charcoal</td>
<td>1310</td>
<td>35</td>
<td>1178-1294</td>
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<td>40</td>
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<td>Charcoal</td>
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<tr>
<td>ET 349-350</td>
<td>OS- 61326</td>
<td>349.5</td>
<td>Bulk sediment</td>
<td>6310</td>
<td>40</td>
<td>7163-7317</td>
<td>7240</td>
</tr>
<tr>
<td>ET 385-386</td>
<td>OS- 60303</td>
<td>385.5</td>
<td>Bulk sediment</td>
<td>7340</td>
<td>40</td>
<td>8023-8212</td>
<td>8117</td>
</tr>
</tbody>
</table>
Figure 2.2: Age-depth models of Beaver Lake and Twin Lakes derived from linear interpolation between calibrated ages. Ages are based on AMS dates of terrestrial grass charcoal and seeds.
2.4.3 Diatoms

Decadal to century-scale diatom analyses were carried out from sediments spanning the mid to late Holocene. The cores were sampled for diatoms in 1-4 cm intervals. For diatom preparation, the samples were homogenized prior to subsampling and processed in hydrochloric acid (10%) to dissolve any accumulated carbonates. Then samples were treated with cold hydrogen peroxide (30%) to digest organic matter, and finally samples were rinsed several times with distilled water until free of peroxide. The final slurries were settled on cover slips and dried before being mounted onto slides with Naphrax®. At least 300 diatom valves from each interval were counted in transects under oil immersion on a Zeiss Axioscop 2 plus light microscope with a 100x objective. Samples were counted every 2 cm for Beaver Lake, for an average resolution between samples of about 35 calendar years. Primary taxonomic references used for all lakes were Patrick and Reimer (1966; 1975) and Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b). Species percent abundances were plotted against the developed chronology to determine changes in species abundances in each site during the last 6500 years.

2.4.4 Multivariate numerical analyses

Diatom zonations were defined based on stratigraphically constraint cluster analysis by incremental sum of squares (CONISS) algorithm and by using the broken-stick method with the software psimpoll 4.10 (Bennett 2002). Prior to analysis, species relative abundance (> 2%) data were square-root transformed, and the resultant dissimilarity coefficient calculated in chord distance.
A diatom inferred water depth curve was established by applying a transfer function generated from diatoms found in surface-sediment communities and depth measurements based on 71 different lakes across Nebraska (Fritz, unpublished data). Depth showed significant independent explanatory power ($r^2=0.81$) for diatom distribution when the measured depths were compared to diatom-inferred depths. The predictive ability of this model was assessed using a weighted-averaging approach with bootstrap error estimation in C2 software (version 1.4; Juggins 2003). The strength of each model was evaluated using the coefficient of determination ($r^2$) and the root mean square error (RMSE). A validation step of bootstrapping with 1000 cycles was used to generate a bootstrapped coefficient of determination ($r^2_{\text{boot}}$) and a root mean square error of prediction (RMSEP), which more realistically portrayed error estimates (Fritz et al. 1999). These models make the general assumption that the depth-community relationship has remained within the range of the modern calibration set throughout the historical period recorded in the lake sediments.

2.4.5 Grain size, percent weight sand, C:N

A grain-size analysis was performed at 2-cm intervals using a Coulter Laser Diffraction unit. At each level 0.5 gram of wet sediment was prepared. If secondary carbonates were present (>0.1 % inorganic carbon by weight), carbonates were removed with a 10% HCl solution. Organic matter was removed by adding 3 ml of concentrated hydrogen peroxide (30 %) to each sample. For the removal of biogenic silica, 10 ml of 1M NaOH was added. The sand samples were separated into five different size fractions.
(D10, D25, D50, D75, and D90). However, for this study the mean grain size was used exclusively.

East and West Twin Lakes were analyzed for total carbon (TC), total nitrogen (TN), and total inorganic carbon (TIC) content from freeze-dried samples. TC and TN were measured by dry combustion analysis, using a Costech Analytical ECS 4010. Prior to analysis, samples were treated with H₃PO₄ (phosphoric acid) to remove all inorganic carbon. TIC content was determined by coulometric titration, using a CM 5012 UIC coulometer, with CaCO₃ as a control standard. To each sediment sample, 5 ml H₃PO₄ (20%) was added to convert TIC into CO₂ gas, which is quantitatively absorbed in the coulometer cell. The generated current during coulometric titration is proportional to the amount of carbon. The linear range was from 0.01 μg to 100 mg C.

2.5 Results

2.5.1 Diatom Profiles

In general, diatoms are very well preserved and abundant throughout most of the core. Planktic fossil diatom assemblages from all lakes are primarily dominated by either Aulacoseira ambiguа or Stephanodiscus minutulus and S. parvus. In a few cases Cyclostephanos dubius, S. niagaraе and A. granulata attain significant percentages locally in the record, but their individual frequencies rarely rise above 20% of the assemblage in any sample. Tychoplanktic diatoms include small Fragilariophyceae, such as Pseudostaurosira sp. and Staurosirella sp. Benthic diatoms are dominated by Fragilaria capucina, Nitzschia amphibia, N. palea, Amphora libyca, Cocconeis
placentula, as well as a variety of species belonging to the genera Gomphonema sp., Navicula sp., Anomoeoneis sp., Cymbella sp. and Encyonema sp.

2.5.2 Diatom-based zonations

Eleven zones were identified based on distinct changes in the diatom assemblages (see Figure 2.3).

B-1 (ca. 6400-5750 cal yr BP) is characterized by conspicuously high concentrations of Nitzschia sp., in particular N. amhibia and N. perminuta. Moreover, high abundances of benthic Gomphonema sp., Amphora sp., Encyonema sp., as well as Anomoeoneis sp. are very common, whereas planktic diatoms are virtually lacking.

B-2 (5750-5300 cal yr BP) features elevated concentrations of S. minutulus and S. parvus in conjunction with relatively high abundances of Achnanthes sp., Navicula sp., as well as Amphora sp.

B-3 (5300-4200 cal yr BP) is distinguished by intermediate to high abundances of tychoplankton (Pseudostaurosira sp. and Staurosira sp.) and Fragilaria capucina (~ 20% on average). The bulk of the diatom composition, however, consists of benthic species belonging to Amphora sp., Cocconeis sp., Nitzschia sp., Gomphonema sp., as well as Cymbella sp. The latter gain dominance between 4430-4700 cal yr BP but remain extremely rare in the record below and above this period. Most other benthic genera undergo a sudden decrease in number at the base of the zone. In contrast, species belonging to the genera Amphora sp. increase dramatically at the top of B-3. S. minutulus and S. parvus obtain intermediate concentrations during this interval.
B-4 (~ 4200-3800 cal yr BP) features an abrupt increase of tychoplanktic species and of *F. capucina*. Moreover, a fairly sudden rise in *Gomphonema sp.* and *Cocconeis sp.* at the top of this zone distinguishes it from other intervals. Planktic species are overall low in abundance, with the exception of a brief spike of *S. minutulus* and *S. parvus* reaching up to 25% occurring between 4100 and 4000 cal yr BP.

Both, B-5 (~ 3800-3300 cal yr BP) and B-6 (~ 3300-1950 cal yr BP) are characterized by high abundances of *S. minutulus* and *S. parvus*, averaging more than 60% over more than 2000 years. The base of zone 5 is characterized by the most dramatic shift from benthic to planktic diatoms in the entire record. Tychoplankton and *F. capucina* decrease at the onset of this zone. The base also features a dramatic drop in *Gomphonema sp.* species, as well as most other dominant benthic groups. In general, benthic diatoms are virtually absent during this time interval with the exception of *Nitzschia sp.*, in particular *N. palea*, representing the most common remaining benthic group.

Zone 6 is characterized by a sharp decline of *Nitzschia sp.* and a simultaneous increase in tychoplankton, while *F. capucina* rarely exceeds 10% in abundance.

The base of B-7 (1950-1180 cal yr BP) is mainly characterized by a shift between the tychoplankton community and *F. capucina*, as well as abundances of *Nitzschia sp.*, which increase at the transition from B-6 to B-7. *S. minutulus* and *S. parvus* persist at high concentrations until midsection (~1700 cal yr BP), when they slightly reduce in number due to the presence of *Aulaceira sp.* and *Cyclotella sp.* species, as well as *Cyclostephanos dubius*. Simultaneously, low concentrations of benthic diatoms such, as *Amphora sp.*, *Encyonema sp.*, *Gomphonema sp.*, and *Navicula sp.*, start to reappear in the
record after having almost completely disappeared for more than 2000 years. The top of this zone is marked by a sudden decrease of *Cyclotella pseudostelligera*.

B-8 (1180-1050 cal yr BP) represents a relatively short-lived transitional zone characterized by a distinct decrease of *S. minutulus* and *S. parvus*, as well as a gradual increase of *Aulacoseira sp*. Also conspicuous is the co-occurrence of *C. dubius* and *S. niagarae*, which attain significant percentages during this interval. The top of B-8 features a drop in the abundances of these two planktic species as well as in benthic diatoms in general.

B-9 (1050-740 cal yr BP) is a zone that is based on low abundances of *S.minutulus/S. parvus* and high percentages of *Aulacoseira sp*.

B-10 (740-70 cal yr BP) is characteristic of intermediate abundances of planktic (43% mean) and benthic species, while small tychoplankton species increase upcore. The transition between B-10 and B-11 is marked by the Dust Bowl event, which is characterized by a sudden increase in the benthic flora.

B-11 (70-0 cal yr BP) is primarily defined by elevated abundance in *S. niagarae*, averaging ~ 63%.
Figure 2.3: Beaver Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yr BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents relative percent abundance, the y-axis age in calibrated years BP.
2.5.3 Pollen profiles

Overall, the pollen diagram (Figure 2.4) is dominated by herbs indicating vegetation in the Sand Hills much like that of today (Watts and Wright, 1966). No pollen data are available from the basal section of the core between 6450 and 6120 cal yr BP. The diatom zonation scheme is used throughout the rest of the paper to correlate synchronous changes between proxies.

Trees

Tree pollen abundance, in particular *Pinus*, gradually increase during B-5 and B-6 between 3700 and ~2000 cal yr BP. Following this period, *Pinus* pollen decrease until the present day.

Herbs

*Poaceae* pollen represents the most common group of the terrestrial plant assemblage throughout the record. Both, B-1 and B-2 are characterized by low abundances of *Poaceae*, whereas B-3 and B-4 represent a time when grasses attain their greatest number. *Artemisia* is at its lowest abundance during B-2 increasing to its peak concentration in the ensuing zone of B-3 and B-4 averaging about 20%. The transition between B-3 and B-4 is characterized by a short drop in number but abundances remain relatively stable during B-4 and B-5. *Chenopods*, in turn, seem to be abundant in particular when *Artemisia* pollen concentrations are lower, as documented during B-1 and B-2. Conversely, when *Chenopods* are not very well-represented in the assemblage, abundances of *Artemisia* are typically greater. During the mid-section of B-4, at around
3900 cal yr BP, the relative abundance of grasses declines to an average of around 25% until the beginning of B-9 (~ 1000 cal yr BP), after which they further decrease to a mean of roughly 20%. Both, *Ambrosia* and *Iva xanthifolia* remain at low concentrations from the basal section upward until the beginning of B-5 at ~3800 cal yr BP, when both simultaneously experience a sharp increase lasting for the entire zone until ca. 3300 cal yr BP. During B-6, abundances of *Artemisia*, *Ambrosia*, and *Iva xanthifolia* decline once more. *Iva xanthifolia* undergoes another short increase at the upper part of B-7 at around 1200 cal yr BP. Overall, *Asteraceae* are low in abundance throughout the record. Subtle increases occur during B-2 and at the beginning of B-5 at around 3800 cal yr BP, similar to the pattern in *Iva* and *Ambrosia*. The beginning of B-8 is marked by a brief drop in *Asteraceae*.

*Aquatic plants*

*Cyperaceae* reach their lowest concentration at the transition between B-1 and B-2. They become more abundant during B-2 and increase overall during the entire record with short-term decreases during B-4, B-7, B-8, and B-11. *Isoetes* is present in low concentrations during B-2, B-8, and B-11 and reaches its peak abundance throughout most of B-6 and B-7. *Myriophyllum*, *Potamogeton*, *Sagittaria*, and *Typha* are very similar in terms of their stratigraphic distribution. All of them occur in highest concentrations between B-2 and B-4, after which they simultaneously decline. They nearly disappear from the record during B-5 and B-6, with the exception of *Typha*, which persists in very low numbers. The onset of B-8 marks a time at which all but *Myriophyllum* experience a
subtle comeback. Particularly, B-11 features a sharp increase in *Myriopyllum* and *Potamogeton. Salsola* is represented exclusively during zone B-11.
Figure 2.4: Beaver Lake pollen stratigraphy plotted against time (cal yr BP). Horizontal lines indicate diatom-based zonation scheme. X-axis represents relative percent abundance (note different scales).
2.5.4 Grain size profiles

Sand transport and deposition are common sedimentary processes in eolian landscapes, such as the Nebraska Sand Hills, particularly during arid episodes, when moisture deficits can lead to the reduction or potential loss of vegetation, thereby exposing dune sand to the elements. In the Sand Hills, present-day winds exceed the threshold velocity for sand entrainment (5 m/sec) about 50% of the time (Muhs et al. 1997). Hence, sand input into a lake basin can provide evidence for reduced local moisture conditions in such landscapes. A direct temporal measure of sand influx into the lake from adjacent dune fields can be determined by a high-resolution grain-size analysis. Increased deposition of particles exceeding 0.2 mm in size indicates wind entrainment by saltation and a severe loss of vegetation of the surrounding uplands and littoral shoreline. The basal portion of the core (B-1) indicates very high sand concentrations of all size fractions over a period of more than 500 years (Figure 2.5). This prolonged high sand input decreases slowly over a period of 200 years, transitioning to zone B-2 where the mean sand size averages ~0.120 mm.

The beginning of B-3 is characterized by a brief and subtle increase, followed by a gradual decline until about 4700 cal yr BP, after which sand size starts to increase again and exhibits higher frequency variability, lasting for more than 1100 years until the end of B-4. B-4 represents the zone that shows the highest variability throughout the record. Overall, sand size increases during this interval, averaging ~0.15 mm. The end of B-4 and the onset of B-5 (3800 cal yr BP) signify a sharp drop in grain size, and values remain at comparatively low concentrations during most of B-5. In general, B-6 appears to represent more stable conditions, with more gradual changes occurring through time and
less short-term variability. Average grain size increases gradually until 2575 cal yr BP, after which it drops to a low, lasting from ~2300-2090 cal yr BP.
Figure 2.5: Stratigraphic profile of grain size, charcoal, loss-on-ignition (LOI) and estimated CaCO$_3$ plotted against time (cal yr BP). X-axes are split in absolute percent abundance for grain size profiles (red), while other proxies are reported as relative percent abundances. Horizontal lines indicate diatom-based zonations.
Two more intervals, characterized by relatively large size fractions, ensue this time period: 1) ~2090-1870 cal yr BP, and 2) 1500-1400 cal yr BP. A sharp drop occurs at the beginning, as well as the end of B-7. B-8 averages lower values than both B-7 and B-9. The beginning of B-9 shows a rapid increase in grain-size. Moreover, higher values and less variability characterize this period. B-10 shows intermediate grain-size, slightly increasing upcore, with only minor fluctuations. Finally, B-11 commences with a sharp increase that is immediately followed by a sudden drop.

2.5.5 Charcoal profile

Charcoal data are at lower resolution, sampled at an average resolution of ~ 175 years. Nevertheless, they do provide a rough picture of the stratigraphic charcoal distribution reflecting the fire history of the Beaver Lake area. In general, high charcoal abundance coincides with high-frequency variability of sand input and widespread abundance of grasses. Both, B-1 and B-2 are very low in charcoal concentration. The beginning of B-3, however, marks a distinct increase in charcoal, with concentrations persisting through the entire zone. B-4 (5300-3800 cal yr BP) features the highest charcoal concentration over the entire record. B-5 is characterized by very low concentrations increasing gradually during B-6. Intermediate abundance in charcoal characterizes B-7, while the two following zones undergo another decrease. During B-10 concentrations gradually rise again until the onset of B-11, where it resumes to low, modern-day concentrations.
2.5.6 Loss-on-ignition and \(CO_3^-\) concentration

Loss-on-ignition at 550 °C (LOI\(_{550}\)) is a direct measurement of sediment organic matter content, while LOI\(_{900}\) reflects the amount of inorganic carbon (carbonates). High productivity should therefore produce higher concentrations of both indices. In general, high LOI\(_{550}\) values are synchronous with high concentrations of benthic diatoms, in particular epiphytic forms. High percentages of epiphyton reflect an abundance of aquatic macrophytes and hence littoral productivity.

LOI\(_{550}\) values are less than 4% during B-1 and B-2 corresponding to low organic matter input. The amount of organic matter steadily increases during the course of B-3 reaching its maximum value towards the top of the zone. The transition between B-3 and B-4 features a brief drop in organic matter content, which is followed by a steep but brief rise. Overall, LOI values decrease during B-4 and remain at an average of around 10% throughout B-5 and B-6. Organic matter concentrations decrease to values below 3% at the transition of B-6 to B-7. In contrast, the following three zones (B-7 – B-9) are characterized by strong short-term fluctuations showing a general increase in organic matter until about 550-600 cal yr BP. Organic matter concentrations decline during the course of B-10 whereas Zone B-11 features a rise in organic matter reaching about 25%.

Estimation of \(CaCO_3\) as based on LOI\(_{900}\) data is very similar to LOI\(_{550}\) with the exception of the basal section of the core (B-1 through B-3) and the early part of B-8, which is characterized by elevated percentages and short-term excursions in \(CaCO_3\).
2.6 Discussion

2.6.1 Lake-level history

Diatoms preserved in lacustrine sediments can provide excellent paleolimnological records of climate change and can serve as direct evidence of lake-level fluctuations (Brugam et al., 1998). Moreover, short life spans and rapid response times of diatoms to hydrochemical changes make them very useful indicators of high-frequency environmental fluctuations, such as changes in salinity (Fritz et al. 2001) and nutrient dynamics (Brugam, 1983; Leira, 2005). Shifts in the abundance of planktic diatoms relative to benthic near-shore or shallow-water types have been used to infer past lake-level variations (e.g. Schweger and Hickman, 1989; Brugam et al., 1998). However, the relationship between lake-level change and variations in planktic:benthic ratios can be non-linear depending on the complexity of the lake basin morphology (Stone and Fritz 2004), as well as the areal distribution of diatoms by lake currents (Bradbury and Winter, 1976). Hence, potential causes for shifts in planktic:benthic diatom ratios need to be considered carefully. Clearly, applications of this method work best in simple closed-basin systems, such as in many Sand Hill lakes, where lake-level changes are immediately tied to offsets in the planktic:benthic community.

Overall, the diatom record of Beaver Lake oscillates between benthic and planktic dominated assemblages several times over the last 6500 years (Figure 2.3). The planktic diatom assemblage is dominated by *S. minutulus* and *S. parvus*, both eutrophic species (Bradbury, 1975, Brugam and Speziale, 1983). Modern ecological data from surface-sample calibrations consistently show that *S. minutulus* is characteristic of high phosphorus conditions (Bradbury, 1988; Reavie et al, 1995; Brüchmann and Negendank,
Based on the conventional planktic:benthic model, as discussed above, we assume that high abundances of small *Stephanodiscus* species reflect elevated lake-levels and vice versa. We also used a diatom-inferred transfer function based on modern chemistry, depth and diatom data collected from over 70 lakes throughout Nebraska. Because depth represented one of the variables that showed significant links to the variation in the diatom communities across the lakes, we were able to generate a diatom-inferred lake depth curve as illustrated in Figure 2.6. For comparative reasons we included the grain size profile of the coarsest fraction, which serves as independent and direct evidence of drier conditions. In general, the resultant lake-level curve matches well with the small species of *Stephanodiscus*, supporting our assumption of lake-level fluctuations.

The basal section of the core represented by B-1 is dominated by benthic species, such as *Amphora libyca*, *Encyonema silesiacum*, a variety of *Nitzschia* and *Gomphonema* species, as well as *Anomoeoneis sphaerophora*. Most of these species, in particular, *A. libyca*, *A. sphaerophora*, and *N. amphibia* are epipelic and alkaliphilous mainly occurring at pH > 7. They are typically found in littoral zones of water bodies with moderate to high specific conductance (Krammer and Lange-Bertalot, 1998). *F. capucina* is a very common part of the algal flora at the basal section of the core. It prefers circumneutral waters with low to moderate nutrient levels (Krammer and Lange-Bertalot, 1998). In conjunction with a consistently high input of medium sand from the surrounding dunes, we conclude lower lake levels due to a generally drier climate that lasted for more than 600 years. Ensuing this prolonged drought, intermediate to relatively high lake-levels are inferred during B-2 (5800-5300 cal yr BP), based on abundances of *Stephanodiscus sp.* reaching more than 50% and limited sand transportation into the basin. Lake-levels
decrease to low to intermediate depths during B-3, as indicated by a mostly benthic dominated diatom community reflecting a deficit in effective moisture. High abundance, particularly of *Nitzschia, Gomphonema*, and *Amphora* species not only indicates shallower lake levels but also higher concentrations of aquatic macrophytes. *Amphora sp.* is primarily a benthic littoral diatom that sometimes attaches itself epiphytically to other larger diatoms, such as *Nitzschia* species (Hustedt, 1930) or to aquatic macrophytes (Kociolek and Spaulding, 2003). Little is known about specific ecological preferences within the genus of *Gomphonema* other than that they occur on a variety of littoral substratum types (Spaulding and Kociolek, 2003) including aquatic macrophytes (Tanaka, 1986). Although sand concentrations only increase slightly or even decrease at times during the lower two thirds of this section, the upper third indicates much drier conditions. Based on sand input, Zone B-4 (4200-3800 cal yr BP) shows a continuation of the drought conditions characterizing particularly the top portion of B-3. This observation is supported by increased abundances of two diatom groups: 1) *Gomphonema sp.*, averaging ~ 20%, and 2) *Fragilaria sp.*, averaging ~ 50%. Certain species within the *Fragilaria* complex are meroplanktic and can form stellate-shaped colonies, such as the dominant species *F. capucina*. High concentrations of these genera, in combination with relatively high sand influx, suggest dry conditions, with the exception of a brief interval centering around 4000 cal yr BP.

Probably the most dramatic shift of the entire record occurs at around 3800 cal yr BP at the transition from B-4 to B-5, when the abundance of planktic diatoms dramatically increases and persists for the following 2000 years (B-5 and B-6). A very similar scenario, featured by a drastic change from benthic-dominated systems to
planktic-dominated communities, was observed in two nearby lakes (Twin Lakes) located about 60 km to the west of Beaver Lake. Today, these lakes are shallow basins situated in an interdunal valley, much like Beaver Lake. Both records show identical offsets in the planktic and benthic diatom abundance, although occurring slightly earlier between 4100 and 4000 cal yr BP (see Figure 2.6). The difference in timing of this event can be related to various mechanisms, such as differences in location, response rates among lakes themselves (Fritz, 2008), and inherent dating errors of lake sediments.

Dominance of small *Stephanodiscus* species in combination with high concentrations of epipelic *Nitzschia* species, in particular *N. palea*, during B-5 suggest deeper lake levels as supported by the diatom-inferred lake-level curve. Low concentrations of epiphytic diatoms in the assemblage reflect a lack of suitable habitat for aquatic macrophytes. Due to high lake-levels, exposed mudflats may have become scarce, and deeper turbid waters created unfavorable conditions for submerged aquatic plants to survive and reproduce.

B-6 reflects a prolonged period of increased effective moisture as indicated by high percentages of planktic diatoms and a sheer lack of benthic diatoms. The diatom-inferred water depth curve suggests highest lake-levels for the entire record, especially toward the top of the zone between 2400 and 2000 cal yr BP. A brief interval of increased eolian activity, indicated by elevated sand concentrations, occurred at around 2500 cal yr BP. However, the diatom record suggests relatively stable lake-levels characterize zone B-6. The Badain Jaran Desert in western Inner Mongolia of China contains over one hundred hydrologically-closed and spring-fed lakes, some of which are fresh while others are extremely saline (Young et al., 2007). The presence of a large groundwater reservoir
below parts of the desert allows for a comparison to lakes of the Nebraska Sand Hills during extended periods of drought. Despite the lack of vegetation and high rates of evaporation, these lakes persist, similar to conditions observed around Beaver Lake at around 2500 cal yr BP.

Lake-levels gradually fall to intermediate depths during B-7 (~1900-1200 cal yr BP), as shown by decreasing abundances of *Stephanodiscus* and a simultaneous recurrence of benthic species. Elevated abundances of *Aulacoseira* species during this time may be related to more turbid conditions and/or higher Si:P ratios. *A. ambiguа*, is the dominant species within this genus in Beaver Lake. It has been considered to be characteristic of warmer waters (Denys, 1991-1992) and of eutrophic to mesotrophic temperate lakes (Brugam, 1983). The relatively high abundance of *C. dubius* and *S. niagarae* in B-8 may reflect a time of species succession when P was available in excess similar to the situation as discussed below during B-11. *C. dubius* is abundant in many nutrient-rich lakes throughout Europe (Hickel and Håkansson, 1987), and the species has a high optimum for TP (176 µg L⁻¹) in the NW European diatom TP calibration dataset (Bennion et al., 1996). Moreover, it prefers sites with relatively high mean silica and chlorophyll *a* concentrations. Therefore, high abundance of *C. dubius* in paleolimnological records can be interpreted as reflecting eutrophic conditions.

B-8 is further characterized by the lowest sand input for the entire record, reflecting little or no dune activity during this period. Our lake-level model indicates intermediate depths during this period, which is further supported by the relatively high concentration of epiphytic and epipellic diatom assemblage. The bottom section of B-9 features the highest planktic:benthic ratio. However, the dominant species is *Aulacoseira* sp., while
concentrations of *Stephanodiscus sp.* remain relatively low in this section. Bradbury and Waddington (1973) suggest that *A. ambigua* cannot tolerate very eutrophic conditions. Hence, we argue that higher rates of phosphorus sequestration by macrophytes may be responsible for this distribution, or that highly turbid conditions characterized this period. Intermediate planktic:benthic ratios, as observed during B-10, probably reflect a slight deficit in effective moisture. In addition, increased abundance of *Nitzschia sp.* and *Amphora sp.* indicates shallower lake levels and a higher abundance of aquatic macrophytes.

Zone B-11, representing the last 70 years, is characterized by the dominance of the planktic diatom *S. niagarae*, which has been frequently reported as common in eutrophic lakes in the northern United States and Canada (Theriot and Stoermer 1981; Theriot 1987; Häkansson and Kling 1989). Anthropogenically induced eutrophication of the lake during the recent past are likely responsible for elevated P concentrations which, conversely, seems to be tied to the dominance of *S. niagarae*. Furthermore, it was shown that *S. niagarae* is predominantly found in shallow, eutrophic prairie lakes in Minnesota characteristic of low transparencies and comparatively high levels of sulfate (Brugam, 1983).
Figure 2.6: Diatom-inferred lake-level history of Beaver Lake compared with the Planktic:Benthic diatom ratio and grain-size profile. The vertical line on the depth curve indicates current lake depth. Note the highstand during most of B-5 and B-6.
Figure 2.7: Simplified diatom stratigraphy from East Twin Lake and West Twin Lake located about 60 km southwest of Beaver Lake. The dotted red line indicates a major reorganization in diatom assemblages similar in magnitude and timing as observed in Beaver Lake.
2.6.2 Vegetation, Fire, and Moisture Regime

The vegetation of the Sand Hills incorporates a mixture of many different types of vegetation that moved into the area during and after the last glacial maximum (Kaul, 1998). Today, about 670 native species of vascular plants inhabit this area. Although the plant diversity seems low compared to other grassland areas, a shallow groundwater table and moderate rainfall make it a relatively diverse ecosystem versus other prairies with similar sandy and infertile soils (Kaul, 1998). According to Küchler (1964), the modern vegetation of the Sand Hills is dominated by a combination of *Andropogon* and *Calamovilfa* grass species. In general, it is important to differentiate between topographic sites within the region. For instance, the most species-rich areas in the Sand Hills are typically found on the dunes themselves, as opposed to the wetter and more fertile interdunal valleys (Kaul, 1998). Warm-season grasses and other species with deep roots are typically found on the dune tops, whereas dry interdunal valleys are dominated by cool-season grasses and plants with shallower root systems. Marsh communities vary considerably in their species composition depending upon their soil, depth, water supply and quality (Kaul, 1998). Moreover, many plant species show a restricted geographic distribution which may be tied to a suite of factors: 1) variable precipitation patterns across the Sand Hills; 2) amount of below ground moisture availability; 3) interspecies competition; and 4) fire regime.

Records of vegetational history of much of the Great Plains are relatively sparse, and only a few datasets extend as far back as the early Holocene (Grimm, 2001). Accordingly, Holocene paleoecological studies from the Sand Hills are limited, and the sparse literature shows vegetational changes associated with drought that often produced
widespread dune remobilization (Watts and Wright, 1966; Wright et al. 1985). A relatively recent wetland study located about 65 km to the west of Beaver Lake revealed a vegetation assemblage that was dominated by grasses and aquatic sedges (i.e. *Scirpus* and *Carex*) during the mid- to late Holocene (Nicholson and Swinehart, 2005).

The basal portion (B-1: 6400-5750 cal yr BP) of the Beaver Lake record is very low in submerged aquatic plant diversity (Figure 2.4). In conjunction with the dominance of terrestrial *Chenopodiaceae*/*Amaranthaceae* it suggests an overall drier climate with high annual to decadal variability in precipitation and a high rate of disturbance (Grimm, 2001). In fact, Baker et al. (1990) suggest that low concentrations of *Ambrosia* in combination with high percentages of *Chenopodiaceae*/*Amaranthaceae* are characteristic for playas and shallow lakes that frequently dry out in prairie regions. Barnosky (1989) argued that high amounts of *Chenopodiaceae*/*Amaranthaceae*, *Artemisia*, and *Poaceae* (grasses) pollen in eastern Montana are indicative of xeric grasslands and a climate drier than present. *Poaceae*, although comparatively low in abundance during this period, comprise a significant portion of the vegetation throughout the entire record. A drier climate as indicated by vegetation assemblages is supported by the dominance of benthic diatoms, as well as a continuously high sand input from the surrounding dunes during B-1. Early to Mid-Holocene aridity has been reported over most of North America with temperatures ranging 1-2°C higher than at present (Webb et al., 1993; Dean et al., 1996). Eolian activity during the Early to Mid-Holocene has also been documented from a suite of sites in the Sand Hills (i.e. Goble et al., 2004; Miao et al., 2007) and immediately south of the Sand Hills, where sustained aridity occurred between 12 000 to 6500 years ago (Miao et al., 2005).
The lower half of B-2 (5750-5300 cal yr BP) is almost identical in terrestrial pollen stratigraphy, suggesting similar conditions to B-1. Similarly, LOI_{550} remains at low values indicating little organic matter deposition, because of low concentrations of aquatic vegetation. However, grain-size analysis reveals reduced deposition of all grain sizes into the basin at the onset of B-2 (5800 cal yr BP), suggesting increasingly humid conditions. Moreover, a rapid increase of planktic diatoms at the beginning of B-2 signifies higher lake-levels throughout the zone creating potential habitat for a variety of plants along the shoreline. Vegetation of the upper half of B-2 indicates a transition from drier to wetter conditions with declining Chenopodiaceae/ Amaranthaceae and increasing aquatic species, such as Potamogeton. Rising percentages of Cyperaceae (sedges) support the overall trend of higher effective moisture at around 5500 cal yr BP. Both, B-1 and B-2 do not show any significant amounts of charcoal that would indicate fire due to high fuel load.

Grasses attain their highest abundance during B-3 (5300-4200 cal yr BP) and most of B-4 (4200-3800 cal yr BP), suggesting conditions conducive for the growth of warm-season grasses on the surrounding dune fields. The overwhelming presence of grasses and a concomitant decline of Chenopodiaceae/ Amaranthaceae suggest lower annual to decadal variability in precipitation favored by many prairie grass species. Charcoal concentrations increase along with the rise of grasses, supporting the notion of dense vegetation and perhaps warmer and possibly drier summers. Slightly drier summers would account for the increased abundance of Artemisia, a large and diverse genus of herbs and shrubs that typically favors dry or semi-arid habitats. Diatom stratigraphy shows that benthic species, in particular epiphytic taxa, dominated throughout most of B-
3 and B-4, supporting an inference of lower lake-levels relative to the present. The increased abundance of epiphytic diatoms is supported by increasing concentrations of aquatic species, such as emergent taxa of *Sagittaria* and *Typha*, as well as submersed taxa of *Potamogeton* and *Myriophyllum*. *Cyperaceae* may have established along the shorelines during the more humid phase of B-2, blocking coarser sand from entering the basin during the ensuing drier zone of B-3. Even drier conditions characterize most of B-3, which led to a further decline of water levels allowing the proliferation of aquatic plants in the shallower or partially exposed areas of the basin.

A prolonged arid period between 4200 and 3800 cal yr BP likely caused a long-term exposure or development of a shallow sandy shoal separating Beaver Lake from Rat Lake, thereby increasing suitable habitat for submersed vegetation along the shorelines. Aerial photographs of Beaver- and Rat Lake illustrate differences in lake-level during the Dust Bowl Drought compared to present-day lake-levels (Figure 2.8). It shows the complete detachment of both basins during major drought and supports the assumption of lake separation during earlier Holocene drought episodes. Short-term more humid phases separated periods of destabilization during this overall arid period, as evidenced at around 4100 cal yr BP, when low sand influx coincided with the highest abundances of *Poaceae* pollen and a concomitant peak in charcoal. This relatively wet interval is also characterized by an intermediate peak of the small diatom genus *Stephanodiscus* *sp*. This short-lived wet interval is followed by a sharp decline of grass pollen giving rise to increasing concentrations of *Iva* and *Ambrosia*. *Iva xanthifolia* (giant sumpweed) is commonly found on disturbed areas, such as exposed mudflats. *Ambrosia*, on the other hand, is a very abundant perennial ragweed in Sand Hills grasslands today. Increased
abundances of this group do not necessarily signify instability or bare sand (Wedin, pers. comm.) as proposed in other studies (Clark et al., 2001; Laird et al., 1998). Rather *Ambrosia* may in fact be indicative of wetter and colder conditions with extended long growing seasons (Grimm, 2001).

A rapid and large shift in the benthic:planktic diatom ratio at around 3800 cal yr BP suggests a rise in water level and higher effective moisture. Epiphytic diatoms decrease between the transition of B-4 and B-5 due to the decline of submersed aquatic macrophytes. The loss of macrophytes and the increase of planktic diatoms are likely caused by rising lake-levels limiting shallow habitat across the embankment between Beaver Lake and Rat Lake. A rise of lake-level at this time is supported by the lack of medium-sized sand and submersed vegetation. Water tables of the Twin Lakes also show a dramatic rise at around 4000 cal yr BP (Figure 2.7).

Increasing abundance of pine tree pollen during B-5 (3800-3300 cal yr BP) and B-6 (3300-1950 cal yr BP) presumably denotes regional rather than local cooling as pine tree forests expanded along bluffs to the west of the Sand Hills (Wright et al., 1984) and in the Black Hills area of South Dakota. Reduced abundance of *Chenopodiaceae/Amaranthaceae* after 4000 cal yr BP suggests undisturbed prairie grassland with *Poaceae* reaching an average of about 30%. Increasing concentrations of *Cyperaceae*, i.e. *Scirpus* and *Carex*, after 4000 ka are indicative of wetland and marsh expansion. Moreover, *Isoëtes* (quillworts), which occur extensively during B-6 and B-7 (1950-1180 cal yr BP), are aquatic or semi-aquatic and typical of clear ponds and slow-moving streams (Taylor and Hickey, 1992). Conditions associated with higher lake levels stayed fairly stable throughout most of B-6 and B-7 spanning nearly 2000 years. One
exception occurred at around 2500 cal yr BP, when lake-levels dropped to near modern
day levels as indicated by a temporary loss of Isoëtes and increased medium-sized sand
influx. Dune activity at around this time has been reported from several sites across the
Sand Hills (Goble et al., 2004, Miao et al., 2007).

Rising concentrations of grasses during B-7 accompanied by higher charcoal
percentages, and a decrease of aquatic species indicate somewhat drier conditions lasting
until about 1300 cal yr BP. Sand flux during this interval shows high-frequency
variability. Immediately following this time, grasses slightly decrease, while aquatic
species attain somewhat higher abundances. The upper portion of B-7 (1300-1200 cal yr
BP) is becoming wetter, as confirmed by the presence of Cyclotella and Cyclostephanos.
Water levels at this time were likely close to the present. B-8 (1180-1050 cal yr BP)
features a minor drop in Asteraceae and Cyperaceae in conjunction with subtle increases
in Poaceae and Artemisia. We infer slightly drier conditions during this interval despite
very low concentrations of sand.

B-9 (1050-740 cal yr BP) shows a subtle increase in
Chenopodiaceae/Amaranthaceae and a reduction of grasses similar to conditions during
B-1 and B-2, except less drastic. Cyperaceae in particular, rise to their highest
concentration, while diatoms are dominated by Aulacoseira sp., which necessitate turbid
waters and high Si:P ratios. Sand deposition was high compared to the previous 150 years
but lower on average during the wet intervals of B-6 and B-7. B-9 spans a time period
between 1050-740 cal yr BP equivalent to the Medieval Warm Period (MWP). A severe
multidecadal drought has been reported from multiple sites across the Sand Hills during
this interval (Miao et al., 2007; Nicholson and Swinehart, 2005; Goble et al., 2004). The
proliferation of *Cyperaceae* may suggest optimal water depth conditions, including frequently exposed mudflats that created suitable habitat during fluctuating lake levels.

The most obvious features during B-10 (740-70 cal yr BP) include the reduction of *Chenopodiaceae/ Amaranthaceae* and the rise of *Myriophyllum*. Herbs, such as *Artemisia* and *Ambrosia*, increased slightly in abundance, while grasses remained relatively steady comprising about 20% of the total vegetation. Charcoal and sand concentrations are intermediate and diatom-inferred water depth suggests slightly lower lake-levels compared to today.

### 2.6.3 Discrepancies among proxies and OSL ages

Dating of dunefield sediments is a valuable tool and can provide rich stratigraphic records of both temporal and spatial variation of Holocene climate change (Mason et al., 2004). Geomorphic studies in the Sand Hills have generated unequivocal evidence of eolian activity related to drought, based on both OSL ages from sand and loess sediment, as well as from radiocarbon ages from paleosols. Results from the most comprehensive Holocene climate study of upland dune records and loess deposits (Miao et al. 2007) are compared to the lake record of this study (Figure 2.9). Although OSL results are in large part consistent with the grain-size analysis of Beaver Lake, the diatom based lake-level curve is in many intervals distinct, especially between 3800-2200 cal yrs BP. The presence of dune activity at times of elevated lake-levels evident from the lake record suggests that drought magnitude may not be the critical, or at least the sole, cause of dune reactivation. Thus, the precondition for dune destabilization may be some critical combination of drought frequency, duration, and seasonality. In fact, it appears that high variability in drought frequency between 4500-3600 cal yr BP, as apparent from grain
size analysis, coincides with a drop in lake-levels reflected by a major shift in the diatom assemblage. Discrepancies among these records also may arise because data from geomorphic studies are oftentimes discontinuous providing only snapshots of time. In turn, paleolimnological studies can, in many cases, reveal continuous records at much higher resolution.

Many lacustrine deposits have the advantage that may include multiple proxies, but differences in responses of proxies can lead to complications and perhaps misinterpretations, if not considered carefully. As in the case of this study, some proxies provide counterintuitive signals, in particular during B-2 through B-4 (Figure 2.10). A range of explanations are possible. First of all, individual proxies may inherently show non-linear response times to changes in moisture regime (Fritz, 2008). For instance, closed lakes with strong groundwater connectivity may respond more slowly relative to climate change than some terrestrial vegetation, particularly aquatic species and relatively short-lived prairie species. Moreover, records with lower resolution (such as pollen and charcoal data) may portray an unrealistic picture of the extended time periods between samples. In addition, planktic to benthic-ratios in Beaver Lake may be non-linear with respect to lake-level change. Stone and Fritz (2004) have shown that in some lakes with a complex morphology, benthic diatoms can actually increase with rising water table and vice versa. The deepest portion of Beaver Lake is located on the eastern side close to the shallow platform that separates Beaver Lake from Rat Lake. Today, macrophytes (in particular *Cyperaceae*) inhabit this shallow area. Falling lake-levels, such as during the Dust Bowl drought, expose this shallow bank, initially turning it into a mudflat and eventually, if drought persists, it becomes completely barren (Figure 2.8). Loss of benthic
habitat could shift the P:B ratio by artificially increasing the relative abundance of planktic species during lake-level fall while flooding of the embankment due to lake-level rise would increase benthic habitat.

Potential explanations that led to the deposition of coarse sand during B-6 (in particular between 2700 and 2350 cal yr BP) include either increased aridity or the lack of blocking vegetation fringing the littoral area around the lake. Raised lake-levels during this zone may have limited suitable habitat for emergent plants, allowing sand to be transported freely into the basin. On the other hand, increased dune activity around 2500 cal yr BP has been reported from the central Sand Hills (Goble et al. 2004; Miao et al. 2007).

The shallow nature of the High Plains Aquifer that underlies the Sand Hills forms a significant portion of the water budget. It can act as a buffer during droughts keeping water tables of most lakes relatively stable at least on shorter timescales. However, as shown in the aerial photographs of Figure 2.8, short-term droughts, such as the recent Dust Bowl, had a considerable effect on lake-level drawdown. Both basins, presently connected by a narrow channel, became separated within a matter of a few years. Therefore, water-level changes can respond over relatively short time scales. In contrast, large-scale megadroughts, lasting multiple decades and longer, would clearly lead to even lower lake-levels, potentially to complete desiccation, resulting in drastic changes of lake chemistry and biota.

Seasonal shifts towards higher winter precipitation and reduced summer precipitation may explain disagreement of proxies observed during B-2 through B-4.
high inputs of runoff during snow melt and lower rates of evaporation, while plants like *Ambrosia* and *Poaceae* respond to growing-season moisture during the summer time. In the Sand Hills, approximately 75% of the average annual precipitation occurs during the April-to-September growing season, sustaining vegetation that stabilizes the extensive dune fields (i.e. Wilhite and Hubbard, 1998; Loope et al., 1995; Sridhar et al., 2006). Winter precipitation is usually through snow ranging from 56 to 115 cm. Snowmelt increases soil moisture and acts as an important source of moisture for early plant growth (Wilhite and Hubbard, 1998). Snow cover also shields the dune sands from wind erosion by providing a temporary cover during winter storms. In fact, the top 10-15 cm of the dune sand is oftentimes frozen, protecting the sand dunes from additional erosion (pers. comm. Swinehart, 2009). Precipitation is the ultimate source of water for lakes and wetlands in the Sand Hills directly by rain- or snowfall and indirectly by recharging the groundwater reservoir (Bleed and Ginsberg, 1998). Lake net evaporation rates (evapotranspiration minus precipitation) exceed precipitation rates throughout much of the year, making the presence of a large groundwater supply essential for the existence of most Sand Hills lakes (Wilhite and Hubbard, 1998).
Figure 2.8: Comparison of aerial photographs from Beaver Lake and Rat Lake. The left picture shows the modern lake size, the right picture shows the lake during the Dust Bowl Drought. During drought the two lakes become separated from each other by the exposure of a shallow bank.
Figure 2.9: OSL dune and loess records compared with results from Beaver Lake. The top graph (a) illustrates a qualitative interpretation of drought intervals based on the well-known 900-700 year drought. The dotted red line indicates grain size of 125 µm. (b) Bar graph of OSL drought records based on results in (d). (c) Beaver Lake lake-level curve. Red line in box indicates present-day lake-level (3.5 m). Levels below 3 m are interpreted to represents arid periods.
Figure 2.10: Qualitative comparison of changes in effective moisture between major proxies from Beaver Lake, as well as from Jumbo Valley (after Nicholson and Swinehart, 2005) and East Twin Lake. The first graph from the left shows a diatom-inferred lake-level curve measured as depth in meters; the second graph illustrates results from the grain-size analysis, while the center graph reflects shifts in moisture based on pollen analysis. Red lines represent qualitative interpretations of significant thresholds that indicate changes in effective moisture. For regional comparison we included the weight percent sand stratigraphy from Jumbo Valley, as well as planktic diatom abundance from East Twin, both located about 60 km west of Beaver Lake (2 graphs on left).
2.6.4 Dune blockage versus climatic factors

Running water is the dominant geomorphic agent on Earth’s surface. Eolian processes can, however, gain importance in climatically arid regions, where vegetation is sparse, and abundant sand is available for transport. Boundaries between fluvial-dominated and eolian-dominated systems can shift with climate change as was shown by Loope et al. (1995) in the Nebraska Sand Hills. Their work in the Crescent Lake Wildlife Refuge (see Figure 2.1d) provided evidence of multiple episodes of dune blockage events. Extended arid periods in the latest Pleistocene and middle Holocene were shown to be responsible for the mobilization of eolian dune sand, which blocked two large valley systems in the region. These blockages raised the local water table of the High Plains aquifer as much as 25 m over an area of 7000 km² and created over one thousand lakes (Loope et al., 1995). At Beaver Lake, dune blockage as reported from the Crescent Lake area was most likely not responsible for major shifts in lake-level during the last 6500 years. No immediate geomorphic evidence from topographic maps and satellite images is apparent around the periphery of the catchment area that would indicate signs of blocked ancient river beds. In addition high-resolution records of the Twin Lakes, 60 km to the west of Beaver Lake, show a similar lake-level rise occurring around 4000 cal yr BP. The similarity in timing (within ~200 years) and lack of geomorphic clues suggest climatically driven controls.

The East and West Twin records extend back nearly 9000 and 10,000 cal yr BP, respectively. Diatoms are abundant for the entire record indicating that a lake existed throughout the Holocene. If a dune blockage had cut off a nearby stream at any time during the Holocene, we would expect to see a coherent rise in local lake-levels.
However, a wetland study conducted in Jumbo Valley (Nicholson and Swinehart, 2005), located less than a mile to the west of the Twin Lakes shows no immediate evidence of water table fluctuations that match the Twin Lake record. Given the high number of lakes found in relatively small pockets across certain areas of the central Sand Hills, we can, however, not entirely exclude that smaller streams may have been blocked by migrating dunes during extended arid phases causing a local rise in groundwater. In fact, the existence of most, if not all Sand Hills lakes, is the result of dune blockages of ancient rivers and streams at some point in latest geologic history. We were, however, unable to find immediate evidence for dune-blockage during the Mid- and Late Holocene. Therefore, we conclude that the significant driver of effective moisture fluctuations during the Holocene in the central Sand Hills region studied here were directly related to regional climate changes operating on decadal- to centennial time scales.

2.6.5 Major climate change between 4200-3800 cal yr BP

Booth et al. (2005) described a severe centennial-scale drought affecting mid-continental North America between 4300-4100 years ago. Studies that indicate such widespread abrupt climate change are abundant and have been recorded from eastern Wyoming (Stokes and Gaylord, 1993), several sites across Minnesota (i.e. Dean et al, 1996; Brugam and Swain, 2000; Booth et al., 2004), the Nebraska Sand Hills (Loope et al., 1995; Stokes and Swinehart, 1997; Mason et al., 1997; Goble et al., 2004; Miao et al., 2007), and northeastern Iowa (Denniston et al., 1999). Moreover, Baedke and Thompson (2000) reported falling water levels of Lake Michigan between 4500 and 4000 years ago that far exceeded the rate of isostatic rebound. Severe droughts at or near 4200 years have
also been documented from multiple mid-latitude and subtropical sites on all other 
continents of the Northern Hemisphere (Booth et al., 2005). Our high-resolution study of 
Beaver Lake shows a clear signal of regional climate change spanning the central portion 
of the Sand Hills between 4200 and 3800 cal yr BP. Drought conditions persisted in this 
area for at least several centuries interrupted only by a single brief humid interval at 
~4000 cal yr BP. By far the most dramatic change occurred at ~3800 cal yr BP based on 
major shifts in the diatom community, a rapid decline of local sand deposition, charcoal, 
and LOI₅₅₀, as well as the loss of aquatic macrophytes. The Twin Lake records are 
characterized by identical abrupt shifts in the diatom assemblage centering at ca. 4050 cal 
yr BP transitioning for less than a century from dry to wetter conditions.

Our records of a major climate change, centering around 4000 cal yr BP, are in 
agreement with many sites across the Sand Hills of Nebraska and with other records of 
the Great Plains. Our results suggest a transition from drier to wetter conditions at this 
time. OSL ages from dune sands of many locations throughout the Sand Hills show 
evidence of drought between 4000-3100 years BP (Miao et al, 2007), whereas other areas 
do not show any eolian activity (Figure 2.9). Accordingly, sites and proxies differ in their 
sensitivity, response time and temporal resolution, making it difficult to pinpoint the 
exact timing and regional extent of this major climate shift.

2.7 Conclusions

A combined analysis of diatoms, pollen, grain size, and bulk sediment chemistry 
from Mid- to Late Holocene lake sediments reveals multiple changes in effective 
moisture in the central Sand Hills of Nebraska. Significant overlaps in most intervals 
allow for reasonable interpretations of lake-ontogeny and hydrologic budget, as well as
related changes of the surrounding dune landscape. The few cases where combined
datasets show asynchronous results are likely due to differences in resolution, sensitivity
and response times among proxies.

Aerial photographs from the Dust Bowl Drought provide evidence that support the
notion that lower lake-levels are a manifestation of dry conditions. We established a high-
resolution diatom-based lake-level reconstruction that indicates two distinct wet intervals
(5750 – 5300 and 3800 – 1750 cal yr BP), as well as two prominent drought periods
(6400 – 5750 and 5300 – 3800 cal yr BP). Grain-size analysis reveals four additional
multi-centennial drought episodes (3100 – 2300, 2000 – 1800, 1500 – 1400, and 900 –
700 cal yr BP) allowing for further refinement of the climate record. However, some of
these episodes featuring increased sand input did not seem to have a strong affect on
lowering the local lake-level.

The basal portion of the record (6400 – 5750 cal yr BP) represents a severe
centennial-scale drought spanning at least 700 years. This interval complies relatively
well with studies from the upland dune record, which document extensive eolian activity
between 9000-6000 years BP. It is followed by a comparatively wet period (5750 – 5300
cal yr BP) featuring high lake-levels that lasted nearly 500 years. Between 5300 and 3800
cal yr BP lake-levels were predominantly low reflecting drier conditions in the area. The
most distinct climate change, accompanied by regional cooling and lake-level rise,
occurred at ~3800 cal yr BP. This major climate perturbation was also observed in the
Twin Lakes located about 60 km west of Beaver Lake suggesting a regional impact.
Elevated lake-levels persisted for the next 2000 years until about 1650 cal yr BP. Based
on our grain size analysis and from results of previous studies, significant multi-
centennial drought periods occurred around 3800, 2500, and 1900 cal yr BP. These events did not, however, have serious effects on lake-levels. The last 1650 years were characterized by intermediate lake-levels and featured three longer-term droughts: 1) ~1600-1400 cal yr BP; 2) ~900-700 cal yr BP, as well as 3) ~250-150 cal yr BP. The 900-700 BP drought corresponds with the well-documented drought episode on dune data.

Our results suggest that dune mobilization, as evidenced from recent geomorphic studies, can coincide with elevated lake-levels at times. Therefore, drought magnitude may not always be the sole cause of dune reactivation. Rather, a specific combination of factors may be necessary, such as drought frequency, duration, and changes in seasonality.

2.8 Acknowledgements

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Chapter 3

A REGIONAL-SCALE LACUSTRINE CLIMATE RECONSTRUCTION OF THE LAST 4000 YEARS FROM THE NEBRASKA SAND HILLS, USA.
3.1 Abstract

We compared high-resolution paleohydrological reconstructions of five shallow lakes in
the Nebraska Sand Hills across an east-west transect in order to 1) determine whether
long-term droughts of the past 4000 years were spatially and temporally coherent across
the region, 2) distinguish local variation in climate or hydrology from regional patterns of
change, 3) compare the paleolimnological results with the existing dune records, and 4)
assess the frequency of variation among the sites. We reconstructed diatom-inferred lake-
level curves for all sites and compared these with other proxies, including upland sand
input and bulk sediment chemistry. Our findings indicate frequent alterations between
high and low lake-levels during the past 4000 years, which suggests that shifts between
dry and wet periods were prevalent across the Sand Hills. Extended multi-decadal to
centennial-scale droughts were more common prior to 2000 years BP, while the last two
millennia were hydrologically more complex, and climate shifts alternated on shorter
timescales. Despite some discrepancies among the five records, we were able to refine
the Holocene drought history of the Nebraska Sand Hills, particularly between ~2200 and
4000 yr BP. Many of these drought events were contemporaneous with severe droughts
documented at sites in the northern Great Plains and Rocky Mountains, lending support
for the severity and regional significance of these events in western North America.

3.2 Introduction

Droughts represent one of the most common and disastrous natural hazards in the
Great Plains region of North America today (Riebsame et al., 1991) and can have
deleterious effects on society, as evidenced by the Dust Bowl of the 1930’s and major
droughts of the 1950’s and 1980’s. The continental interior of North America hosts a large number of drought-sensitive eolian landscapes, and drought reconstructions from these active or episodically active areas can provide insight into the natural variability and magnitude of past drought (Foreman et al., 2001).

The Nebraska Sand Hills represent the largest contiguous grass-stabilized dune region in North America, extending over an area of more than 50,000 km² (Swinehart, 1990; Loope and Swinehart, 2000; Nicholson and Swinehart, 2005). Sand dunes can reach heights of up to 130 m (Swinehart, 1990) and were primarily formed by prevailing NW-SE winds (Ahlbrandt and Fryberger, 1980). Effective moisture (precipitation-evaporation) is the key driver of vegetation density, which, in turn, is responsible for the stability of the sand dunes (Muhs and Maat, 1993). Today, typically during spring and early summer, heavy southerly-to-southeasterly winds pass over the Gulf of Mexico, transporting moisture into the central Great Plains (Loope et al., 1995), which sustains lush and dune-stabilizing vegetation. However, in the recent past, extensive drought has killed the grass cover, resulting in widespread dune migration (Stokes and Swinehart, 1997; Loope and Swinehart, 2000).

A critical component of this landscape that distinguishes it from many other dune fields is the presence of interdunal lakes and wetlands, which together cover an estimated area of more than 700 km² (Rundquist, 1983). Many of these water-dominated environments are hydrologically connected to the underlying groundwater system of the High Plains Aquifer (Timer, 2003), and their water budget is a manifestation of the height of the local water table. Other basins are isolated and respond to climate variation (P-E) more rapidly (Zlotnik et al., 2007).
Holocene paleoclimatic evidence from the Nebraska Sand Hills region is predominantly derived from paleosols and eolian sediments (Mason et al., 2004; Goble et al., 2004; Miao et al., 2007), as well as from a limited number of studies of wetland and marsh systems (Nicholson and Swinehart, 2005). Optically stimulated luminescence (OSL) dating of sand and loess deposits, in conjunction with radiocarbon dates from paleosols interspersed between dune deposits, provides evidence of the timing of droughts that destabilized the dunefields in the past. OSL results suggest that the Sand Hills of Nebraska experienced a series of recurring and long-lasting drought events over the course of the Holocene (Goble et al., 2004; Nicholson and Swinehart 2005; Miao et al., 2007). The timing and frequency of these drought events is spatially variable, but a synthesis of the eolian data suggests at least three periods of increased dune activity during the Mid and Late Holocene: 3800 ± 300 yr, 2500 ± 100 yr, and 850 ± 150 yr (Nicholson and Swinehart 2005; Miao et al., 2007). Presently, high-resolution studies of Holocene dune activity throughout the Sand Hills are limited spatially, and thus, it is unclear whether major droughts were regionally coherent or whether dune activation was spatially variable. Today, the Sand Hills region is characterized by a large precipitation gradient, ranging from about 400 mm yr\(^{-1}\) in the west to more than 600 mm yr\(^{-1}\) in the eastern part (Wilhite and Hubbard, 1998). Whether this gradient was similar in the past is unknown, and it is unclear how climate variation across the region might have influenced dune activity.

Although geomorphic studies have provided an impressive record of regional drought, their temporal resolution is limited, and they only provide a record of landscape destabilization, not of the previous conditions that triggered that response. Lake and
wetland studies can provide higher temporal resolution and have the potential to provide
evidence of the magnitude and duration of the droughts that led to dune activation. Lake
and wetland sediments also represent another aspect of the broader landscape response to
drought that can complement the eolian record.

Here we present a high-resolution study of five late-Holocene climate records from
lakes that span an east-west transect across the Nebraska Sand Hills. In particular, we
attempt to focus on the following four key questions:

1) Are there common intervals of change among the five study sites? If so, do
they show coherent changes or site-specific responses?

2) Are there common frequencies of variation among the sites?

3) How do these lake sites compare with other regional records of climate change,
particularly to eolian records?

4) How do these records relate to other records from the Great Plains and western
U.S., and what does this suggest about environment and climate?

This study is both spatially more continuous and at a much higher temporal
resolution than previous work available from this region.

3.3 Study Sites

Large portions of Cherry County, Nebraska host a number of small groundwater-
fed wetlands and lakes that accumulate peat and lake mud (Steinauer et al. 1996). Lakes
and wetlands are especially abundant along ancient channel beds that drained either
southeastward into the North Loup River or northeast into the Niobrara River. All study
lakes except Swan Lake are located in Cherry County. All occur in interdunal valleys in
between linear or barchanoid dunes, which can reach heights of more than 60 m. Most lakes in the Sand Hills are strongly influenced by groundwater fluctuations, as well as seasonal variability of effective moisture. The topographic relief and relative location of lakes to the groundwater flow system can be of great importance in terms of their hydrologic and chemical variability (Gosselin et al., 2006). Lakes in this region also vary in their chemical composition. For instance, Gosselin (1997) observed that Total Dissolved Solids (TDS) ranged from 200 mgL\(^{-1}\) to more than 100,000 mgL\(^{-1}\) in a relatively small area of the Sand Hills. Moreover, Schnagl (1980) reported alkalinity varying from ~0 to more than 90,000 mgL\(^{-1}\). Much of this spatial variation in ion chemistry is a product of the role of groundwater in the water budget (Zlotnik et al., 2007; Bennett et al., 2007), as well as the age of the lake (Gosselin, 1997).

The westernmost of the five study lakes (Figure 3.1) is Round Lake (42°25'48" N, 101°33'34" W; elev. 1064 m), which is approximately 2.5 m deep (\(z_{\text{max}}\)) in the center of the basin (Daniels, 2000), and its shoreline length is about 4.5 km. Alkalinity was recorded during the summer of 1957 by McCarraher and was ~170 mgL\(^{-1}\) (McCarraher, 1977). Round Lake is situated about 9 km west of the Twin Lakes (see below).

The Twin Lakes (42°24'30" N, 101°26'20"W; elev. 1045 m) consist of two small lake basins (each ca. 3.5 km in shoreline length) that are surrounded by giant barchanoid dunes. Presently, East Twin is without water due to artificial drainage. Alkalinity measurements were recorded by McCarraher for East Twin Lake (1205 mgL\(^{-1}\)) in December of 1959 (McCarraher, 1977).
Located about 60 km to the east of the Twin Lakes is Beaver Lake (42°27′35″ N, 100°40′08″W; elev. 905 m). It is situated in an interdunal valley within immediate proximity to stabilized linear dunes. Beaver Lake is similar in size to Round Lake. It is ~3.5 m deep and hydrologically connected to Rat Lake to the east.

Swan Lake (42°09′55″ N, 99°02′06″W; elev. 702 m) is about 140 km to the east of Beaver Lake, near the eastern boundary of the Sand Hills. Dunes in the eastern part of the Sand Hills are smaller overall, and the relief is generally not greater than 40 m. Swan Lake is a closed-basin system, with a maximum depth of ~3.5 m. With a shoreline length of ~5 km, it represents the largest lake among the five study sites.

In most Sand Hill lakes, the combination of strong winds and shallow depth do not promote conditions for seasonal stratification. Vertical temperature profiles collected from a number of shallow lakes show nearly isothermal conditions regardless of season (La Baugh, 1986). Usually, the 1% level of surface light does not penetrate to the bottom in Sand Hill lakes deeper than ~1 m, because of the high turbidity. As a result, Secchi disk transparency is commonly less than 55 cm. A linear relationship between phosphorus (P) and nitrogen (N) has been documented in some Sand Hill lakes (LaBaugh, 1986), although other studies suggest seasonal and spatial variation in nutrient dynamics (Salm et al., 2009).
3.4 Methods

3.4.1 Field

Round Lake was cored from two inflatable boats during the summer of 1999. A 230 cm Nesje piston core and a 25 cm Glew core were retrieved from near the center of Round Lake within 2 m of each other. Beaver Lake was cored in July 1995 with a Livingstone-Wright square-rod piston corer (5 cm diameter) at the deepest part of the basin. Sediment cores from West Twin (1999) and East Twin (2006), as well as Swan Lake (2007), were obtained by vibracoring. The vibracore of West Twin Lake was taken from the edge of the lake basin, while the cores from East Twin Lake and Swan Lake were taken from the center of the lakes.

3.4.2 Chronology

In most cases, the chronology for the cores is based on linear interpolation of accelerator mass spectrometry (AMS) radiocarbon dates of terrestrial charcoal, seeds, plant fragments, and bulk sediment (Table 3.1). All AMS dates were calibrated to calendar years BP using CALIB 5.0.1 (Stuiver and Reimer, 1993) and are presented with two sigma error ranges.

The top 30 cm of the Round Lake core was sampled in 5 cm increments for \(^{210}\text{Pb}\) dating (Table 3.2). Prior to analysis samples were dried and homogenized. The dates were obtained by using the Constant Rate of Supply (CRS) model on the activity data. This method is useful for determining ages of less than approximately 150 years (Blaise et al., 1995).
In addition to radiocarbon dating, we sampled a stratigraphic section of the dune field immediately north of East Twin Lake and another dunefield north of the North Platte River in the south-central Sand Hills for optically stimulated luminescence (OSL) dating, using 90-150 μm quartz grains under the Single Aliquot Regenerative protocol (Murray and Wintle, 2000). A second vibracore was obtained from Swan Lake at approximately the same location as the other core in order to date two conspicuous sand intervals (Table 3.3). The OSL ages from the lake sediment core were integrated in constructing the chronology of Swan Lake (Figure 3.3). OSL ages reflect the time elapsed since quartz grains were last exposed to sunlight during periods of increased aridity when sand is being entrained and transported by strong winds. Previous studies in the Sand Hills have shown that OSL ages from dunes are consistent with radiocarbon dates of neighboring paleosols (Stokes and Swinehart, 1997, Goble et al., 2004).
Figure 3.1: (a) Map of the Nebraska Sand Hills highlighting locations of the four study sites and topographic maps of individual sites (b-e). Red circles indicate approximate coring locations.
Table 3.1

Radiocarbon ages and calibrated age equivalents used in determining age models for Round Lake (AZ & CO), Beaver Lake (BLK), West Twin (WT), East Twin (ET), and Swan Lake (SL).

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<th>Sample ID</th>
<th>¹⁴C lab#</th>
<th>Mean depth (cm)</th>
<th>Material</th>
<th>¹⁴C age (yr BP)</th>
<th>Age error (yr)</th>
<th>Cal. range 2 sigma (cal BP)</th>
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<td>Seeds</td>
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<tr>
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<td>423-670</td>
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<td>346.5</td>
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</tr>
<tr>
<td>SL VC1 347-348 OS- 72014</td>
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<td>Bulk Sediment</td>
<td>3390</td>
<td>35</td>
<td>3556-3721</td>
<td>3638.5</td>
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</tr>
</tbody>
</table>
Table 3.2

$^{210}\text{Pb}$ results of the top 30 cm of the Round Lake record (Daniels, 2000).

<table>
<thead>
<tr>
<th>Depth at top of section (cm)</th>
<th>$^{210}\text{Pb}$ activity (Bq/g)</th>
<th>Activity standard deviation (%)</th>
<th>Age at top of section (yr BC)</th>
<th>Age standard deviation (years)</th>
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<tr>
<td>0</td>
<td>0.209</td>
<td>3.4</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>5</td>
<td>0.191</td>
<td>3.5</td>
<td>9.8</td>
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<td>10</td>
<td>0.185</td>
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<td>15</td>
<td>0.134</td>
<td>2.7</td>
<td>39.9</td>
<td>1.9</td>
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<tr>
<td>20</td>
<td>0.098</td>
<td>3.3</td>
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<td>25</td>
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<td>0.035</td>
<td>5.0</td>
<td>118.3</td>
<td>15.1</td>
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</table>

Table 3.3

Field and laboratory data, as well as OSL results, from three sites: 1.) UNL 1595-1596: sand dune at Tom Hansen Ranch north of the Platte River; 2.) UNL 1597-1600: sand dune north of East Twin Lake; 3.) UNL 2194, 2198, 2202: sand intervals of Swan Lake core.

<table>
<thead>
<tr>
<th>Sample #</th>
<th>Depth (m)</th>
<th>In situ moisture content (%)</th>
<th>K$_2$O (%)</th>
<th>Th (ppm)</th>
<th>U (ppm)</th>
<th>$D_{\text{cosmic}}$ (Gy a$^{-1} \times 10^{3}$)</th>
<th>$D_{\text{total}}$ (Gy a$^{-1} \times 10^{3}$)</th>
<th>$D_e$ (Gy ± 1σ)</th>
<th>Aliquots (n)</th>
<th>Age (a ± 1σ)</th>
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</thead>
<tbody>
<tr>
<td>UNL 1595</td>
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<td>0.61</td>
<td>1.5</td>
<td>3.9</td>
<td>0.7</td>
<td>0.1983</td>
<td>1.97±0.08</td>
<td>1.23±0.04</td>
<td>18</td>
<td>628±37</td>
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<tr>
<td>UNL 1596</td>
<td>6.7</td>
<td>8.74</td>
<td>1.63</td>
<td>4.3</td>
<td>0.8</td>
<td>0.0976</td>
<td>2.02±0.08</td>
<td>5.37±0.08</td>
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<tr>
<td>UNL 1597</td>
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<td>1.36</td>
<td>4.9</td>
<td>0.8</td>
<td>0.1866</td>
<td>1.91±0.08</td>
<td>1.48±0.06</td>
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<tr>
<td>UNL 1598</td>
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<td>5.1</td>
<td>0.8</td>
<td>0.1530</td>
<td>1.82±0.08</td>
<td>1.43±0.08</td>
<td>13</td>
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<tr>
<td>UNL 1599</td>
<td>4.7</td>
<td>0.29</td>
<td>1.32</td>
<td>4.5</td>
<td>1</td>
<td>0.1298</td>
<td>1.88±0.08</td>
<td>1.60±0.03</td>
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<td>853±46</td>
</tr>
<tr>
<td>UNL 1600</td>
<td>6.7</td>
<td>3.97</td>
<td>1.33</td>
<td>4.5</td>
<td>1</td>
<td>0.1053</td>
<td>1.90±0.08</td>
<td>1.65±0.04</td>
<td>16</td>
<td>868±47</td>
</tr>
<tr>
<td>UNL 2194</td>
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<td>25</td>
<td>2.01</td>
<td>3.64</td>
<td>0.73</td>
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<td>1.73±0.09</td>
<td>5.90±0.10</td>
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<td>3411±217</td>
</tr>
<tr>
<td>UNL 2198</td>
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<td>25</td>
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<td>1.54±0.08</td>
<td>6.10±0.10</td>
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<tr>
<td>UNL 2202</td>
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<td>1.95</td>
<td>4.33</td>
<td>1</td>
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<td>1.81±0.09</td>
<td>1.21±0.04</td>
<td>30</td>
<td>668±44</td>
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</tbody>
</table>
3.4.3 Diatoms

Diatom analyses at decadal to multi-decadal resolution were carried out from lake sediments of all five sites. All cores were sampled for diatoms in 1-4 cm intervals. Diatom samples were prepared according to techniques outlined in Battarbee (1986). At least 300 diatom valves from each interval were counted in transects under oil immersion on a Zeiss Axioscop 2 plus microscope with a 100 x objective. Primary taxonomic references used for all lakes were Patrick and Reimer (1966; 1975) and Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b). Species percent abundances were plotted against the developed chronology to reconstruct limnological change at each site.

3.4.4 Multivariate numerical analyses

In order to compare the five records with each other, we defined diatom zonation schemes at each site on the basis of stratigraphically constrained cluster analysis. The software PSIMPELL 4.10 (Bennett, 2002) was used, which applies an incremental sum of squares (CONISS) algorithm. Prior to analysis, species relative abundance (> 2%) data were square-root transformed, and the resultant dissimilarity coefficient is chord distance.

We performed multitaper method (MTM) spectral analysis (Mann and Lees, 1996) on individual diatom species, groups of species, and diatom indices in order to identify significant frequencies of variation in each of the lake sites. Prior to spectral analysis, records were re-sampled to create uniformly spaced time series and normalized to unit variance using the program Analyseries (Paillard et al., 1996). The re-sampled time series have a uniform spacing of 20.4 yr in Round Lake, 12 yr in West Twin, 43.4 years in East
Twin, 53.3 yr in Beaver Lake, and 32.8 yr in Swan Lake. Spectral analysis (SA) is based on the Fast Fourier transform method of Blackman and Tukey (1958). It assumes that a time series is composed of periodic curves of different periodicities (Davis, 1973). SA identifies periodic signals and determines the magnitude (power) of each of the spectral components and their statistical significance.

Diatom-inferred water-depth curves were established by applying a transfer function generated from modern diatom samples and depth data from 71 different lakes (Figure 3.2) across Nebraska (Fritz, unpublished data). Depth showed significant independent explanatory power ($r^2 = 0.81$ to 0.84) in terms of diatom distribution when the measured lake depths were compared to diatom-inferred depths. The predictive power of this model was assessed using a weighted-averaging approach with bootstrap error estimation in C2 software (version 1.4; Juggins 2003). The strength of each model was evaluated using the cross-validated coefficient of determination ($r^2$) and the root mean square error (RMSE). A validation step of bootstrapping with 1000 cycles was used to generate a bootstrapped coefficient of determination ($r^2_{\text{boot}}$) and a root mean square error of prediction (RMSEP), which more realistically portrayed error estimates (Fritz et al. 1999). Prior to analysis, depth measurements were log-transformed to ensure normal distribution of the data. These models make the general assumption that the depth-community relationship has remained within the range of the modern calibration set throughout the historical period recorded in the lake sediments. According to Birks et al. (1990b), there is no definite and simple way to evaluate the reliability of an organism-based reconstruction in paleoecology. However, the implication of multiple evaluation approaches together may provide a good means to evaluate the accuracy of the inferred
values. First, the statistical performance of the inferred model in terms of the coefficient of determination ($r^2$) and the root-mean-square error of prediction (RMSEP) serves as an indication of the general predictive power of the transfer model. Furthermore, the dominant taxa are well-represented in the calibration set and thus provide good estimates of species optima from which the depth estimates are based.
Figure 3.2: CCA sample biplot of the diatom surface samples and measured environmental variables. Lake depth and Secchi depth explain the largest proportion of the variability in diatom distribution.
3.4.5 Grain-size, percent weight sand, C:N, bulk density, loss-on-ignition (LOI_{550})

A grain-size analysis was performed at 2-cm intervals on the Beaver Lake core using a Coulter Laser Diffraction unit. 0.5 gram of wet sediment was prepared for every sample. If present, secondary carbonates were extracted with a 10% HCl solution. Organic matter was removed by adding 3 ml of concentrated hydrogen peroxide (30 %) to each sample. 10 ml of 1M NaOH were added for the removal of biogenic silica. The sand samples were then separated into five different size fractions (D10, D25, D50, D75, and D90). From these five size fractions, we calculated the mean grain-size and compared it with other proxies. For the Swan Lake and East Twin records, sand concentrations (expressed in % dry weight) were measured in 4-cm increments. Samples were treated with HCl (hydrochloric acid) and H₃PO₄ (phosphoric acid) to remove carbonates and organic matter, respectively. Diatom frustules were subsequently removed by wet sieving through a 0.062 mm sieve and treating the remaining sand fraction with 3% HF for 1 minute. The samples were then decanted, washed three times, and finally dried.

East and West Twin, as well as Swan Lake were analyzed for total carbon (TC), total nitrogen (TN), and total inorganic carbon (TIC) content from freeze-dried samples. TC and TN were measured by dry combustion analysis, using a Costech Analytical ECS 4010. Prior to analysis, samples were treated with H₃PO₄ (phosphoric acid) to remove all inorganic carbon. TIC content was determined by coulometric titration, using a CM 5012 UIC coulometer, with CaCO₃ as a control standard. To each sediment sample, 5 ml H₃PO₄ (20%) were added to convert TIC into CO₂ gas, which is quantitatively absorbed in the coulometer cell. The generated current during coulometric titration is proportional
to the amount of carbon. The linear range was from 0.01 µg to 100 mg C. TOC was calculated as the difference between TC and TIC.

Bulk Density (BD) was performed on the Round Lake sediment core, and Loss on Ignition (LOI550) was carried out on Beaver Lake and Round Lake as a measure of organic content. BD measurements were done on 10 cm³ samples taken every 5 cm. LOI analysis was performed at 1 cm resolution throughout the core. The samples were dried at 105°C for 12 hours, weighed, baked at 550°C for 2 hours, and weighed again (Dean, 1974). The weights at 105 and 550°C were compared and the percentage of loss was calculated.

3.5 Results
3.5.1 Chronology

Age models suggest that Round Lake and East Twin Lake have relatively simple depositional histories (Figure 3.3). Beaver Lake and West Twin Lake, on the other hand, had relatively slow depositional rates between 3300-1500 cal yr BP. A similar break in sedimentation (~2900-1700 cal yr BP) has been reported from wetland records of Jumbo Valley and is thought to represent a decrease of organic matter accumulation caused by climate or removal of peat by fire (Nicholson and Swinehart, 2005). The age of the lower section in the Swan Lake record, particularly the thick sand deposit, is uncertain, because of three conflicting ages. The mid-point of the lower OSL age deviates by more than a hundred years from the two carbon ages below, making a linear correlation between these ages impossible. However, the large age errors inherent in the OSL date allows for the
correlation of its lowest age with the oldest age range of the carbon date below (Figure 3.3). This age model represents a better fit compared with the other lake records based on simultaneous changes in diatom stratigraphy.

3.5.2 Diatom analysis and zoning of core data

The diatom records of all five Sand Hills lakes are broadly similar in terms of community structure and dominant taxa. Benthic (near-shore shallow-water) diatom assemblages are generally dominated by *Nitzschia* spp. (*N.amphibia*, *N. palea*, *N. frustulum*), *Gomphonema* spp., *Navicula* spp., *Fragilaria capucina* sensu lato, and *Fragilaria tenera*. Tychoplankton include *Pseudostaurosira brevistriata*, *Staurosira construens* sensu lato, and *Staurosirella pinnata* sensu lato. Strictly speaking, tychoplanktic diatoms are small benthic *Fragilariaceae* that are circumstantially carried into the plankton by turbulence. Because shallow Sand Hills lakes are exposed to strong winds year-round, small chain-forming tychoplanktic diatoms are frequently entrained in the water column. In all lakes, the planktic (deeper open-water) flora is dominated by either *Aulacoseira ambigua* or small *Stephanodiscus* spp. (*S. minutulus*, *S. parvus*, *S. hantzschii*). Other significant planktic diatoms include *Aulacoseira distans*, *Aulacoseira granulata*, *Stephanodiscus niagarae*, and *Cyclostephanos dubius*. 
Figure 3.3: Age-depth models of all lakes derived from linear interpolation between calibrated $^{14}$C, OSL, and $^{210}$Pb ages. Calibrated radiocarbon ages are based on AMS dates of terrestrial grass charcoal and seeds and error bars represent 2 sigma. The dotted line in the Swan Lake age model represents the best correlation fit between the oldest OSL and carbon dates.
Round Lake (Figures 3.4 & 3.5)

122 diatom slides were counted from the top 191 cm of Round Lake, resulting in an average resolution of ~20 years between samples. Preservation of frustules was generally good, with minor evidence of breakage or dissolution (Daniels, 2000). Only few diatoms were present at a depth of 80 cm, coinciding with a peak in sand concentration (Daniels, 2000). Elevated LOI$_{550}$ values are generally synchronous with high concentrations of benthic diatoms, in particular epiphytic taxa. Increased percentages of epiphyton likely reflect high concentrations of aquatic macrophytes and hence littoral productivity. Nine diatom assemblage zones were identified based on major changes in the diatom composition.

Zone 1 (2450-2350 cal yr BP) is primarily dominated by *Nitzschia frustulum*, with abundances ranging between 10% to almost 40%. *Rhopalodia gibba* reaches its maximum abundance, while *Aulacoseira ambigua* and *A. granulata* are virtually absent from this interval. Bulk density values decreased substantially compared to the sandy base of the record.

Zone 2 (2350 – 1750 cal yr BP) represents the longest interval of the entire record. It features *A. ambigua* and *A. granulata* as the most significant species of the assemblage, reaching up to 50% in the bottom portion of the zone and ensued by a gradual but steady decline. A distinctive increase in the small tychoplanktic species *Staurosirella pinnata* and *Fragilaria virescens* characterizes this interval, along with high abundances of *Cocconeis placentula* var. *lineata* and moderate abundances of *Nitzschia frustulum*. 
Planktic and tychoplanktic species are nearly absent at the onset of Zone 3 (1750 – 1480 cal yr BP) and remain at very low concentration during the entire zone. The genus *Gomphonema*, in turn, is the dominant diatom group during this interval. Moreover, *Fragilaria capucina var. mesolepta*, *Synedra radians*, as well as *Eunotia parallela* increase markedly in number. Benthic species present in Zone 2 also occur throughout Zone 3 in more or less the same concentration. A very strong but short-lived peak in LOI550, occurring at ~1600 cal yr BP, is characteristic for this zone and coincides with generally high abundances of benthic diatoms (Figure 3.4).

Zone 4 (1480 – 1300 cal yr BP) is primarily dominated by *N. frustulum*, whereas abundances of *Gomphonema* are lower compared with the previous zone. *Aulacoseira distans* increases significantly, especially in the upper third of the zone. In fact, this planktic species becomes the dominant diatom during the entire interval of Zone 5 (1300 –900 cal yr BP). All benthic species common in the previous zones decrease dramatically at the transition to Zone 5. Overall, zones 1 through 4 are dominated by benthic diatoms, with the exception of the onset of Zone 2 at 2350 cal yr BP. The top portion of Zone 5 also features a short increase in *S. pinnata* and a rapid decline in *A. distans*.

The bottom part of Zone 6 (900 – 760 cal yr BP) is still dominated by plankton. It is characterized by a brief spike of *A. ambigua* plus *A. granulata*, followed by a short rise in *A. distans*, and an increase in *Asterionella formosa*. The upper half of the zone, in turn, features a significant loss of plankton, while benthic species become more abundant. The bulk density profile reveals increased values corresponding to high sand concentrations.
Zone 7 (760 – 610 cal yr BP) returns to a planktic-dominated stage predominantly composed of *A. ambigua/A. granulata*. *S. pinnata* becomes very abundant during the mid section of the zone, and benthic species are rare.

Both Zone 8 (610 – 125 cal yr BP) and Zone 9 (125 cal yr BP – present) are dominated by planktic diatoms, in particular *A. ambigua/A. granulata*. The youngest section of the core is characterized by increasing abundances of *Stephanodiscus niagarae*.

*West Twin Lake (Figures 3.6 & 3.7)*

310 diatom slides were counted for the 315 cm of the record, resulting in a mean resolution of 12 years between samples. The top section of the core (88 cm), which represents ca. 260 yr of the record, was lost during core recovery. Preservation of frustules is good throughout the section. Diatom stratigraphy was split in eight characteristic zones. Planktic diatoms are well represented, averaging 41%; however, they are less abundant overall compared to the East Twin Lake record. On the other hand, benthic and small tychoplanktic diatoms are more common in West Twin Lake, averaging 25% and 34%, respectively. Benthic species generally show less variability in abundance than benthic assemblages in East Twin Lake.

Zone 1 (4000 – 3870 cal yr BP) features high abundances of *S. pinnata* and *A. ambigua*, while the main characteristic of Zone 2 (3870 – 3580 cal yr BP) is a further increase in *A. ambigua* and declining *S. pinnata*, as well as a distinctive appearance of *S. niagarae*. Both zones are similar to Zone 1 and Zone 2 of East Twin Lake based on
diatom stratigraphy and age. TC and TN values are low in Zone 1 and increase during Zone 2.

Although the timing of Zone 3 (3580 – 3400 yr BP) matches relatively well with its counterpart in East Twin Lake, West Twin Lake has a distinctive peak in small tychoplanktic taxa (in particular *P. brevistriata* and *S. construens* var. *binodis*), reaching over 80% of the total population at times.

Zone 4 (3400 - 3370) is defined by brief spikes in *A. ambigua* and *Stephanodiscus medius*, as well as in the genus *Cyclorella*. Total carbon (TIC and TOC) and nitrogen (N) concentrations are highest during this zone.

Zone 5 (3370 – 1020 cal yr BP) represents the longest interval, spanning more than 3000 years. It is defined by relatively high abundance of the small plantkic *Stephanodiscus* species, which show very little variability. This single zone is the equivalent to 4 zones of the East Twin Lake record, which are subdivided based on fluctuations of the major planktic species. Carbon and nitrogen concentration decrease during this interval and remain at relatively low values for the remainder of the record.

Zone 6 (1020 – 650 cal yr BP) features a drop in small *Stephanodiscus* spp. and a concomitant increase in *A. ambigua*.

The main features of Zone 7 (720 – 500 cal yr BP) include the first relevant occurrence of *Aulacoseira distans* and a strong influx of various species within the genus *Achnanthes*. All planktic diatoms previously dominant decreased significantly in abundance during this zone.
During Zone 8 (500 – 375 cal yr BP) *A. ambigua* and small *Stephanodiscus* spp. increase and then drop down again at the transition to Zone 9 (375 – 260 cal yr BP).

The sand profile shows peak concentrations between the uppermost portion of Zone 1 through 3, as well as during Zone 5.
Figure 3.4: Round Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yrs BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents percent abundance, the y-axis age is calibrated years BP.
Figure 3.5: Bulk density and Loss-on-ignition data from Round Lake compared to planktic, benthic, and tychoplanktic diatom distribution.
Figure 3.6: Bulk sediment chemistry (C and N) compared to planktic, benthic, and tychoplanktic diatom distribution from West Twin Lake.
East Twin Lake (Figures 3.8 & 3.9)

70 diatom slides were counted between 34-173 cm depth, equal to an average resolution of 48 years between samples. The top section of the core, which represents more than 680 years, was lost during core recovery. Preservation of frustules is excellent. Seven zones were identified based on major changes in diatom stratigraphy. The majority of the core is dominated by the planktic *A. ambigua* and small *Stephanodiscus* species, which together make up nearly 65% of the assemblage for the entire record. Benthic diatoms, in turn, are chiefly composed of *N. palea*, *N. amphibia*, and *N. gracilis*. They constitute roughly 10% of the assemblage. Tychoplanktic diatoms reach a mean of ~25%.

The oldest section, represented by Zone 1 (4000 – 3800 cal yr BP), features a high abundance of tychoplanktic species, such as *S. pinnata*. Sand concentration range at ~50%, and both C and N concentrations are relatively low.

Zone 2 (3800 – 3500 cal yr BP) is mainly characterized by the presence of *S. niagarae*, as well as higher abundances of *A. ambigua*. Tychoplanktic and benthic diatoms are less common. Two peaks in sand (> 80%) occur in this zone, while C and N concentrations remain low.

Zone 3 (3500 – 3260 cal yr BP) is characterized by a high abundance of *Nitzschia* spp. and a rapid decline of *S. niagarae* at the onset of this interval. Sand concentration drops significantly but rises during the upper half of the interval. Both C and N show increased concentrations.

A brief and sharp rise in small *Stephanodiscus* spp. marks the bottom of Zone 4 (3260 – 2730 cal yr BP). Tychoplanktic species are more common, whereas benthic diatoms undergo a gradual decline. Sand concentrations drop below 40% during the
lower half and fluctuate in the upper portion. Concentrations of C and N continue to climb, but decrease toward the top.

Small *Stephanodiscus* spp., averaging roughly 50% of the assemblage, characterize Zone 5 (2730 – 2500 cal yr BP). *N. amphibia* shows a brief peak in abundance towards the very top of this section. Sand influx is low during this interval, whereas C and N concentrations both increase for a short period before concentrations decline again.

Zone 6 (2500 – 2020 cal yr BP) is characterized by the highest concentration of planktic diatoms in the entire record. The dominant planktic species are primarily *A. ambigua*. In contrast, *S. minutulus, S. parvus, and S. hantzschii* undergo a sharp decrease during this phase but seem to recover towards the top of the zone. Benthic species generally are very poorly represented. The sand concentrations for this interval start out low but increase toward the top, accompanied by high-frequency variability. C and N concentrations are low at the bottom and top section of the interval, while the mid-section is characterized by a brief rise.

Zone 7 (2020 cal yr BP – present) is by far the longest interval and exhibits relatively stable conditions in the diatom flora. The first ~250 years of this zone features comparatively high abundances of *N. amphibia* and *N. palea*. Otherwise, *A. ambigua* and small *Stephanodiscus* species are the dominant planktic diatoms. Resolution of this interval is relatively coarse for weight % sand and bulk-sediment-chemistry data. However, the lower half of the interval shows comparatively low amounts of sand input, which are followed by a continuous increase. C and N concentrations are relatively high for most of the interval, with the exception of the last 250 years (1000-750 cal yr BP). In general, sand concentration appears to be negatively correlated with benthic diatoms and
positively correlated with planktic diatoms (Figure 3.7). In other words, high amounts of sand generally correlate well with low benthic and high planktic abundances.
Figure 3.7: Bulk sediment chemistry (C and N) and weight % dry sand compared to planktic, benthic, and tychoplanktic diatom distribution of East Twin Lake.
Beaver Lake (Figures 3.10 & 3.11)

115 slides were counted for Beaver Lake, with an average resolution of 35 years between samples. Included in the analysis are grain-size and LOI$_{550}$.

Zone 1 (~4000-3800 cal yr BP) features abundant tychoplanktic species, especially *S. pinnata*. Benthic diatoms including *F. capucina*, *Gomphonema* spp., and *Cocconeis* spp. are also common. Planktic species are low in abundance overall, with the exception of a brief spike of *S. minutulus* and *S. parvus* at the very bottom of the zone. Zone 1 marks a time of elevated sand input, as reflected by the relatively large average grain-size. Moreover, sand stratigraphy shows high-frequency variability, which generally seems to be correlated with higher LOI$_{550}$ and charcoal values.

Both, Zone 2 (~3800-3300 cal yr BP) and Zone 3 (~3300-1950 cal yr BP) are characterized by high abundances of *S. minutulus* and *S. parvus*, averaging more than 60%. The base of Zone 2 is characterized by a sudden shift from benthic to planktic diatoms. Tychoplankton also decrease at the onset of this zone. In general, benthic diatoms are absent during this time interval, with the exception of *N. palea*. The bottom of Zone 2 is marked by a sharp decrease in sand size, followed by an overall grain-size increase throughout the interval.

Zone 3 is characterized by a sharp decline of *Nitzschia* spp. and a simultaneous increase in tychoplankton, while *F. capucina* rarely exceeds 10%. Sand size increases until about mid-section of Zone 3 and then commences to decrease. LOI$_{550}$ increases slightly during this interval.

The base of Zone 4 (1950-1180 cal yr BP) is characterized mainly by a shift between the two tychoplankton communities, as well as abundances of *Nitzschia* spp.,
which increase at the transition from Zone 3 to Zone 4. This diatom community shift is coincident with elevated sand size. *S. minutulus* and *S. parvus* persist at high concentrations until midsection (~1700 cal yr BP), when they decline slightly as a result of increased *Aulacoseira* spp., *Cyclotella* spp., and *Cyclostephanos dubius*. Simultaneously, low abundances of benthic diatoms, such as *Amphora* spp., *Enyconema* spp., *Gomphonema* spp., and *Navicula* spp., start to reappear in the record after being almost completely absent for nearly 2000 years. The top of this zone is marked by a sudden decrease of *Cyclotella pseudostelligera*. The upper half of Zone 4 features increased grain-size, in addition to high concentrations of LOI$_{550}$.

Zone 5 (1180-1050 cal yr BP) represents a relatively short-lived transitional zone, characterized by a distinct decrease of *S. minutulus* and *S. parvus*, as well as a gradual increase of *Aulacoseira* spp. Also distinctive is the co-occurrence of *C. dubius* and *S. niagareae*, which attain significant percentages during this interval. The top of Zone 5 features a decrease in the abundances of these two planktic species, as well as benthic diatoms in general. Sand size is at its lowest during this zone.

Zone 6 (1050-740 cal yr BP) is an interval that is based on low abundances of *S.minutulus/S. parvus* and high percentages of *Aulacoseira* spp. It is also characterized by increasing sand particle size and rising levels of LOI$_{550}$.

Zone 7 (740-70 cal yr BP) is characteristic of intermediate abundances of planktic and benthic species, while small tychoplankton diatoms increase. Sand influx is low, as indicated by a relatively small average grain-size, and LOI$_{550}$ remains at high concentrations.
The transition to Zone 8 (70-0 cal yr BP) begins at the onset of the Dust Bowl event, which is reflected by a sudden rise in the benthic flora and rise in grain-size. Zone 8 is defined primarily by elevated abundance of *S. niagarae*. 
Figure 3.8: West Twin Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yrs BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents percent abundance, the y-axis age in calibrated years BP.
Swan Lake (Figures 3.12 & 3.13)

Overall, 122 diatom slides were counted in 2-cm intervals. However, most of the lower section (~1 m) is sandy and barren of diatoms; only a few organic laminae within the sand deposit were sampled and counted. Average resolution of the first 240 cm, representing 3250 years, is ~27 years between samples. As in previous sites, diatom preservation in this core is pristine. Ten zones have been identified based on major changes in the diatom stratigraphy.

Zone 1 (3730 – 3625 cal yr BP) is characterized by generally high sand concentrations and predominantly benthic diatoms, dominated in the lowermost section by *Nitzschia* spp., *Hantzschia* spp., and a variety of *Navicula* spp. Diatoms are missing for the following ~30 years due to sand deposition. Two thin organic sections further up section contain diatoms, which again are comprised of benthic-dominated assemblages. However, one sample contained 37% of the planktic diatom *S. minutulus*.

Zone 2 (3625 – 3300) is characterized primarily by unstructured sands. Only two thin organic sections of this zone contained diatoms. Most of these sections are dominated by benthic diatoms, except for the lowermost sample, which contains 37% of the planktic diatom *S. minutulus*.

The bottom and top portions of the following Zone 3 (3250 – 2930 cal yr BP) feature a relatively high abundance of the planktic diatom *A. ambigua*. Otherwise this interval is strongly dominated by benthic diatoms, such as *Fragilaria* spp. and *Gomphonema* spp. Sand is still very abundant, averaging more than 80%. Due to the high sand concentration in the sediment, C and N concentrations are very low.
Zone 4 (2930 – 2500 cal yr BP) exhibits a drastic change in the assemblage due to the occurrence of *A. granulata* and small *Stephanodiscus* spp. as the major diatoms. Benthic diatoms that dominated in earlier zones decreased drastically. Sand input decreased slightly in contrast with the previous zone, averaging ~70%. Accordingly, C and N values increase also but remain at low concentrations.

Zone 5 (2500 – 2050 cal yr BP) starts out with the rapid loss of *A. granulata* and small *Stephanodiscus* spp. The entire interval is characterized by the dominance of the planktic *A. ambigua* and the lowest representation of benthic taxa overall. Sand deposition remains relatively steady at ca. 50%. The transition to Zone 6, however, is characterized by a short increase of sand input and a concomitant change in the dominance of tychoplanktic species.

Zone 6 (2050 – 1250 cal yr BP) starts out with a rapid increase of the tychoplanktic *Staurosira construens*, which peaks in abundance around 1900 cal yr BP. Rising concentrations of benthic genera, in particular *Fragilaria tenera*, ensue the brief peak of tychoplankton. Sand concentrations are generally decreasing until 1600 cal yr BP and increase between ~1600 1300 cal yr BP. In general, C and N values increase during this interval.

Zone 7 (1250 – 850 cal yr BP) signifies a strong decline of *A. ambigua* and a concomitant increase of *A. distans*. At the same time, benthic genera become the most abundant group. Benthic diatoms remain relatively abundant for the following two zones, whereas tychoplanktic species generally decrease. Overall, planktic diatoms become the most abundant group for the remainder of the record. Sand input reaches its lowest average concentration, while C and N concentrations attain their highest values.
Zone 8 (850 – 600 cal yr BP) exhibits elevated abundances of small *Stephanodiscus* spp. and *Aulacoseira* spp. The youngest part of this zone is a barren section, due to relatively high sand concentrations. C and N concentrations decrease accordingly.

Zone 9 (600 – 150 cal yr BP) differs from the previous zone by higher abundances of *Nitzschia* spp., *Cocconeis plancentula* var. *lineata*, and *Amphora* spp. At the same time, tychoplanktic species reach their lowest concentration. The bottom of the zone displays a marked decrease in sand influx, which is soon after followed by another increase. The upper portion of Zone 8 marks a prolonged drop in sand concentration until the transition to Zone 9.

Zone 10 (150 cal yr BP – present) has a return of small tychoplankton, as well as *A. granulata*, while a significant percentage of *S. niagarae* appears in the record for the first time. Initial sand influx marks the bottom of Zone 10, after which it steadily decreases. C and N are at relatively low concentrations during the final two zones.
Figure 3.9: East Twin Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yrs BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents percent abundance, the y-axis is calibrated years BP.
Figure 3.10: Beaver Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yrs BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents percent abundance, the y-axis is calibrated years BP.
Figure 3.11: Loss-on-ignition, charcoal abundance, and grain-size analysis compared to planktic, benthic, and tychoplanktic diatom distribution of Beaver Lake.
Figure 3.12: Bulk sediment chemistry (C and N) and weight % dry sand compared to planktic, benthic, and tychoplanktic diatom distribution of Swan Lake.
Figure 3.13: Swan Lake diatom stratigraphy and diatom-based zonations plotted against time (cal yrs BP). Zonations are based on CONISS algorithm with significant clusters identified by the broken-stick method. The x-axis represents percent abundance, the y-axis is calibrated years BP. Gray bars indicate discrete sand layers.
3.6 Discussion

3.6.1 Paleohydrological reconstructions of individual sites

Diatom-inferred water-depth curves (Figure 3.14) were generated to identify common versus localized water-level change among all sites, as well as to aid in our interpretation of environmental conditions for each study lake.

One issue with the reconstruction of depth in some sites is that *A. distans* occurs in fairly elevated numbers in Round Lake, and to a lesser degree in West Twin, and Swan Lake between ca.1400-400 cal yr BP. However, it has not been found in any of the 71 lake surface sediment samples that make up our training set. *A. distans* is typically common in low-alkalinity bogs and wetlands (Brugam and Swain, 2000), with mean alkalinites between 31.7 and 19.1 meq/L (Davis *et al.*, 1994). Therefore, we equate high abundances of this planktic species with lowered lake-levels that likely produced a wetland, similar to the fens that are common in the Sand Hills region nearby.
Figure 3.14: Diatom-inferred lake-level histories of all lakes. Vertical lines delineate critical depths based on reconstructed level during the Dust Bowl drought for sites that have 20th century sediment (see arrows). For the Twin Lakes, the vertical lines represent mean depth, as both records lack the top portion. Lake-depths to the left of the lines represent low effective moisture (drought); everything to the right side of the line reflects higher effective moisture and wetter conditions.
3.6.1.1 Round Lake

In general, Round Lake indicates somewhat contrasting signals compared with the other lake records and also the upland drought history.

The base of the Round Lake core (2800-2300 cal yr BP) is characterized by unstructured sands, as reflected in the bulk density profile. The sands may be the result of a dune blockage that caused the formation of Round Lake as a result of a gradual rise of the local water table at around 2500 yr BP. Similar scenarios of dunes blocking ancient riverbeds have been documented in the western Sand Hills (Loope et al., 1995).

The diatom record in the uppermost part of this section is largely characterized by periphytic species, including *N. frustulum*, *Gomphonema* spp., and *Navicula* spp., attesting to shallow water conditions between ~2500-2300 cal yr BP. *N. frustulum* has a wide salinity tolerance (0.35-620 gL⁻¹) with an optima centered ~16.5 gL⁻¹ (Wilson et al., 1996). Elevated abundances of this species were also found in surface samples from Sand Hills lakes that have high conductivities and alkalinitities (Fritz, unpublished data). Moreover, high abundance of the alkalibiontic diatom *Rhopalodia gibba* indicates relatively high pH (>7). A sharp increase of *A. ambigual/ A. granulata* at around 2300 cal yr BP and a concomitant decline of *N. frustulum* and *R. gibba* marks a brief increase in lake-level and effective moisture that lasted about half a century. Both, *A. ambigua and A. granulata* are common planktic species and often occur during turbulent mixing (Anderson, 2000), when light availability is low and Si:P ratio is high. *A. ambigua* also is characteristic of eutrophic to mesotrophic temperate lakes (Brugam, 1983). *A. ambigua* decreases and almost disappears at ~1750 cal yr BP. Benthic diatoms dominate the system between 2250-1350 cal yr BP, suggesting decreased lake-levels and low effective
moisture. The diatom-inferred lake-level reconstruction suggests particularly low stands between \( \approx 1500 \) and \( 1300 \) cal yr BP (Figure 3.14). OSL ages of adjacent dunes of Round Lake and nearby Cottonwood Lake suggest drought conditions centering around \( 1390 \pm 130 \) yr (Forman et al., 2005), which coincides with our reconstructed low lake-level curve. The following period (1350-900 cal yr BP) is characterized by the dominance of \( A. \) distans (\( \approx 60\% \) of the assemblage). The replacement of \( N. \) frustulum and other common benthic diatoms by this species suggests distinct ecosystem changes or perturbations, but it does not necessarily indicate lake-level rise. As noted above, \( A. \) distans is a wetland species (Brugam and Swain, 2000) and in this context probably represents episodes of lake-level fall and low alkalinity because of reduced groundwater. The inferred drought in the lowermost part of the Round Lake record corresponds with the regional eolian synthesis, but the period from \( \approx 2200 \) to \( 1000 \) cal yr BP is roughly the time when dunes were relatively stable according to Miao et al. (2007). Some eolian activity has been reported at the onset of this period from Jumbo Valley (2100-1800 cal yr BP) (Nicholson and Swinehart, 2005). Jumbo Valley is an interdunal wetland, only about 7 km to the east of Round Lake and 1 km west of the Twin Lakes. Drought intervals common among these three sites should be representative of trends for that region of the north-central Sand Hills.

The diatom stratigraphy suggests generally higher lake-level in the upper part of the core. The time period from 950 to 880 cal yr BP likely spans a brief lake-level rise, as indicated by the replacement of \( A. \) distans by \( A. \) ambigua and \( A. \) formosa. The diatom inferred lake-level reconstruction suggests a relatively quick increase to unprecedented heights. Diatom reorganization following this episode suggests a short low lake stand
ensuing this wet period until around 770 cal yr BP. This period is known for its eolian activity throughout the Sand Hills region (Nicholson and Swinehart, 2005; Miao et al., 2007) and coincides with the Medieval Climatic Anomaly (MCA).

The last 770 years of the Round Lake record is dominated by *A. ambigua*/*A. granulata* and suggests a return to relatively high lake-levels and higher effective moisture. This overall stable period is interrupted by a single brief drought episode at around 700 yr BP, based on a short spike of small tychoplankton and eolian activity recorded in adjacent dunes of Round Lake and Cottonwood Lake (Forman et al., 2005). No evidence was found that would suggest drought conditions occurring at 470±40 yr as reported by Forman et al. (2005).

### 3.6.1.2 Twin Lakes

The records of these two lakes are in good agreement, in particular the coincident occurrence of *S. niagarae* at the bottom, the rise of small *Stephanodiscus* spp. ~3300 cal yr BP, the dominance of *Aulacoseira* spp. and *Stephanodiscus* spp. from 3300 to 1400 cal yr BP, and the rise of *Achnanthes* spp. at the top.

Overall, however, the fluctuations in diatoms differ in magnitude between the two lakes and some intervals show divergent signals. Discrepancies in the diatom distribution pattern and in the magnitude of individual diatom responses are likely a manifestation of coring location in relation to shoreline proximity. The West Twin Lake vibracore was obtained from the edge of the lake, while East Twin Lake was cored at the lake center. Therefore, the diatom community of West Twin Lake consistently shows a much stronger
benthic signature in contrast to the diatom composition of the East Twin Lake core and is less variable than the East Twin Lake core from the lake center.

The planktic diatom community in both records is dominated by *A. ambigua* and small *Stephanodiscus* spp. Modern ecological data from surface-sample calibrations indicate that *S. minutulus, S. parvus, and S. hantzschii* are characteristic of high phosphorus conditions (Bradbury, 1988; Reavie et al., 1995; Cumming et al., 1995).

According to the diatom-inferred depth reconstruction, lake-level was relatively low between 4000-3800 cal yr BP, as suggested by the large populations of small tychoplanktic alkaliphilic Fragilariaceae. These taxa have been found in a wide range of environments (Westover et al., 2005), but the most important factors controlling their distribution may be light and tolerance of physical disturbance (Anderson, 2000). In the Twin Lake records, elevated sand influx, as determined from weight % sand data, generally coincides with lower abundances in these species. A rise in *A. ambigua* and *S. niagarae*, and a concomitant decrease in tychoplankton, suggest rising lake-levels between 3800-3500 cal yr BP. *S. niagarae* is common in eutrophic lakes in the northern United States and Canada (Theriot and Stoermer 1981; Theriot 1987; Håkansson and Kling 1989). In shallow, eutrophic prairie lakes in Minnesota, it is characteristic of low transparencies and relatively high concentrations of sulfate (Brugham, 1983).

Large increases in tychoplankton and benthic *N. palea* and *N. amphibia* indicate falling lake-levels between 3500-3300. The following period (3300-1400 cal yr BP) is generally characterized by rising lake-levels interrupted by two brief dry intervals (~2500 and ~1900 cal yr BP), as indicated by high abundances of *N. amphibia*. The dominance
of *A. ambigua*, in particular in East Twin Lake, suggests turbid conditions driven by strong winds. Between ~1400 and 1000 cal yr BP, diatom assemblages indicate modest lake-level decline evident in the increase in tychoplanktic species at West Twin Lake and to a lesser degree in East Twin Lake.

Between ~1000 and 700 cal yr BP, the depth reconstruction of East Twin Lake suggest increasing levels, as indicated by abundant small *Stephanodiscus* spp. and very few benthic diatoms. At the same time, a rapid decrease in small *Stephanodiscus* spp. and benthic diatoms in combination with increasing numbers of *A. ambigua* in the littoral area of West Twin Lake either suggests lower lake-levels or perhaps low-light conditions. This interval coincides with the well-documented regional drought that has been reported from many sites in the Nebraska Sand Hills. In fact, four OSL dates obtained from the top 7 m of the sand dune immediately northwest of East Twin Lake ranged between 900-720 years BP, attesting to eolian activity during this period (Table 3.3). Moreover, weight % sand concentrations from both, East Twin Lake and Jumbo Valley (Nicholson and Swinehart, 2005), reveal increased sand influx. Possible explanations that could support the offsets in results from both proxies could lie in a higher water table at East Twin Lake, or the destruction of suitable habitat of benthic diatoms in the littoral area (i.e. loss of macrophytes, diatom burial) due to high sand input during eolian activity. Therefore, in spite of generally lower lake-levels during drought, planktic diatoms may be abundant. On the other hand, uncertainties in the age model of both lakes could explain asynchronies in the timing of drought. However, this seems unlikely as both age models were shown to be in good correlation with each other.
The uppermost record is absent in East Twin Lake but in West Twin Lake, the period between 700-400 cal yr BP is characterized by a distinctive increase of epiphytic *Achnanthes* spp., reflecting low lake-levels. The sudden occurrence of these diatoms post-dates the MCA and coincides with the onset of the Little Ice Age. A megadrought during the first half of the 1500's has been documented from tree-ring based studies spanning the bulk of North America (Stahle et al. 2000) including west of the Sand Hills (Weakly, 1962), and the latter part of this interval may be correlative with the 16th century megadrought. In addition, eolian activity, occurring at around 470±40 yr BP, has been reported from Round Lake and Cottonwood Lake (Foreman et al., 2005). The period between 400-250 years suggests a return to wetter conditions as evidenced by a spike in the planktic diatom *A. ambigua*.

3.6.1.3 Beaver Lake

High abundances of *Gomphonema* spp. (averaging ~ 20%) and *Fragilaria* spp. (averaging ~ 50%), combined with relatively high sand influx suggest dry conditions and low lake-stands from 4200 and 3800 cal yr BP, with the exception of a brief interval centering around 4000 cal yr BP.

A dramatic reorganization in the diatom flora occurs at around 3800 cal yr BP, evidenced by a sudden increase of planktic diatoms. Dominance of planktic small *Stephanodiscus* species persists for the following 2000 years suggesting high lake-levels.

Lake-levels gradually fall to intermediate depths between 1800 and 1100 cal yr BP, as shown by decreasing abundances of *Stephanodiscus* spp. and a simultaneous
recurrence of benthic species. Elevated abundances of *Aulacoseira* species during this time suggest turbid conditions and/or higher Si:P ratios. Relatively high abundance of *Cyclostephanos dubius* and *S. niagarae* during this period suggest a time when P concentrations are elevated. *C. dubius* is abundant in many nutrient-rich lakes throughout Europe (Hickel and Håkansson, 1987), and the species has a high optimum for TP (176 µg L⁻¹) in the NW European diatom TP calibration dataset (Bennion et al., 1996).

The period from 1100-1000 cal yr BP is characterized by very low sand input reflecting little or no dune activity during this period. Relatively high concentrations of epiphytic and epipelic diatom assemblages for most of this interval indicate low lake-levels, excepting a peak in planktic:benthic ratio occurring at around 1050 cal yr BP.

1050 cal yr BP – present: Grain-size analysis reveals an increase in sand size at ~900 cal yr BP, coinciding with the MCA reported from the other study sites. Intermediate planktic:benthic ratios probably reflect a slight deficit in effective moisture during most of this period. In addition, increased abundance of *Nitzschia spp.* and *Amphora spp.* suggest shallower lake-levels and a higher abundance of aquatic macrophytes. The last ~130 years of the record are characterized by anthropogenically induced nutrient enrichment reflected in a concomitant rise of *S. niagarae*.

3.6.1.4 Swan Lake

The bottom 15 cm of the Swan Lake vibracore consists of sand-rich peat. Above sit dune-derived sands with few thin organic laminae. These deposits are more than 90 cm thick, representing 450 years in time (3710-3260 cal yr BP), and provide unequivocal
evidence for eolian activity related to drought. Diatoms were found only in two organic layers at ~3650 cal yr BP and consisted mainly of benthic Naviculoids. Examination of the diatom assemblage and weight % sand profile above the sand unit indicate that dry conditions prevailed for the following ~400 years, although water availability increased and the lake itself was established during this time. This interval is characterized by the only significant occurrences of *F. capucina mesolepta* and *Hantzschia amphioxys*. The former is alkaliphilous and mainly occurs at relatively high pH (>7) (Krammer and Lange-Bertalo, 1988), while the epipelic *H. amphioxys* often extends into the subaerial habitats of soils (Round et al., 1990). The occurrences of these species suggest very shallow conditions or perhaps an ephemeral wetland. After 3300 cal yr BP, lake-levels became consistently higher and, by 2900 cal yr BP, the diatom community reflects freshwater conditions with plankton averaging nearly 50%. At around 2500 cal yr BP, sand concentrations decreased to about 50% and continued to decline until about 1600 cal yr BP. Another reorganization of the diatom community marks the beginning of Zone 4 (2500 cal yr BP), when the abundance of benthic diatoms dropped significantly, lasting until about 1900 cal yr BP. The planktic community, averaging 60% of the entire assemblage, is predominantly made up of *A. ambigua*, indicating low light conditions and high Si/P ratios. *A. granulata* and *S. minutulus*, in turn, both disappear, and tychoplanktic species become more prominent between 2150 and 1600 cal yr BP. *S. minutulus* is a diatom with high nutrient requirements, in particular phosphorus, while *Fragilaria tenera* is extremely efficient under low-phosphorus conditions (Interlandi et al., 1999). This shift in the diatom community suggests lower phosphorus recycling from the sediments either due to weaker winds and/or elevated water depth. Overall, benthic diatoms, mainly *F.*
tenera and Gomphonema spp., become the dominant group between around 1600-850 cal yr BP. A relatively brief interval, between 1350-1250 cal yr BP, is characterized by high abundances of A. ambiguа, signifying higher effective moisture during this time. Otherwise conditions were probably drier than previously and macrophytes became more abundant. Moreover, the appearance of relatively high numbers of A. distans, in conjunction with low sand influx from the surrounding dunefields, suggests low alkalinites and shallow water, while local dune activity has decreased. This counter-intuitive trend is similar to conditions observed in the Twin Lake records where offsets in results may be related to availability of suitable habitat for benthic diatoms. Habitat in the littoral area seems to be correlated with the amount of sand input from the surrounding dunes. Hence, low sand input produces more suitable habitat for benthic diatoms, despite overall higher effective moisture conditions.

At around 850 cal yr BP, sand input increased drastically due to regional eolian activity related to the MCA. OSL ages of a discrete sand layer further upsection date to 670±45 yrs BP. This event coincides with very low diatom diversity and abundance suggesting low effective moisture conditions.

3.6.2 Are there common intervals of change among the five study sites? If so, do they show coherent changes or site-specific responses?

In order to determine significant regional changes among the five study sites, we made use of the diatom-based zoning scheme (Figure 3.15), summarized synchronous drought events of Beaver Lake and Swan Lake (Figure 3.16), and visually correlated
deviations from mean lake-depths (Figure 3.17), even if changes were pointing in the opposite direction (Fritz et al., 2000; Laird et al., 2003). Using P:B ratios to relate common intervals of change proved to be difficult, because of different basin morphologies among the sites (Stone and Fritz, 2004), which can produce conflicting shifts with respect to the P:B ratio during same climatic conditions.

The five lakes investigated in this study are within a uniform physiographic region, but, at the same time, they span a strong regional gradient in effective moisture, which can have a great impact on the triggers of local drought patterns. Mean precipitation records from 1971-1990 for climate stations closest to each of the lakes indicate a difference of more than 100 mm between Swan Lake (597 mm) and Round Lake (479 mm) (http://www.nebraskaclimateoffice.unl.edu/). Effective moisture may have been always higher in the wetter eastern part of the Sand Hills during the Holocene and may have played a key role in terms of individual lake-responses across this region. However, trends and internal stratification of linear dunes in the Sand Hills have recorded large-scale wind shifts during the MCA, whereby moist southerly flow was replaced by dry southwesterly winds (Sridhar et al., 2006). As a result, the predominant moisture source was removed from the region, and the modern E-W precipitation gradient may have been severely reduced or interrupted completely. Similar shifts may have occurred at other periods of time.

The reconstructions from all sites indicate that the climate of the last 4000 years was hydrologically complex, with large oscillations in lake-levels. The sites show a moderate degree of coherency in magnitude and pattern of change. For example, the Twin Lakes and Round Lake indicate localized patterns of change based on combined
low lake-stands (Figure 3.16) in comparison to Beaver and Swan Lake. These differences are probably related to changes in the local groundwater flow-regime, which is strongly correlated to the dune topography (Gosselin et al., 2006). Localized dune migration(s) at these closely-spaced sites might have changed the depth to groundwater and/or directional patterns of groundwater flow causing the differential changes in lake-level. Because of these localized differences in hydrology, we excluded these westernmost sites from our regional lake-level comparison in Figure 3.16.

Overall, we found nine major correlative events based on a minimum of two synchronous diatom zones (Figure 3.15). In turn, based on synchronous low lake-stands (Figure 3.16) of Beaver- and Swan Lake we were able to identify 10 common intervals of drought: ca. 4000-3850, 3750-3250, 3150, 2800, 1550, 750-500, 350, 125, 80, and 50 cal yr BP. However, both of these approaches do not reconcile the inherent differences in the chronologies among each site. Slight shifts in the time-scale at various points could either improve the inter-correlation of depth trends, or result in inverse properties. Therefore, we tried to look for common behavior of the depth curves themselves to correlate regional drought events. Twelve intervals are thought to be correlative with this approach, while each basin shows individualized fluctuations of varying degrees (Figure 3.17). In general, it is difficult to reconcile the fine-scale (decadal to multi-decadal) behavior of the records, in part because of differences in resolution and age-models. Nevertheless, the most noticeable common interval among all lake records, representing relatively low lake-levels, occurs between 4000-3800 cal yr BP. A short period characteristic of higher moisture defines the time between ca. 3800-3700 cal yr BP. Another time period of sustained drought occurred between ca. 3700-3300 cal yr BP,
ensued by relatively elevated lake-levels between ca. 3300-2500 cal yr BP. Shorter periods of low lake-level and inferred drought that are common in all sites are evident at approximately 2500 cal yr BP and 1500 cal yr BP. Prior to 2100 cal yr BP, depths at Swan Lake indicate shallower conditions in contrast to Beaver Lake, but both are generally low after 1000 cal yr BP. In turn, the Twin Lakes show increasing lake-stands between 900-500 cal yr BP, although common directional changes towards lower lake-levels are apparent in all lakes during the MCA at ~750 cal yr BP. The Little Ice Age interval cannot be easily identified with respect to moisture conditions as both wet and dry periods alternated within each. Our records indicate dramatic differences in duration of lake-level highs and lows among sites. These differences are likely a manifestation of discrepancies in response time due to primarily groundwater, lake size and depth, as well as longitude.

Sand influx into a basin is independent of these factors and a comparison of lake-depth with sand input may depict instances where lake-level change is directly related to moisture balance fluctuations. Figure 3.18 illustrates this relationship. No clear correlation between the two proxies is apparent in the Beaver Lake and East Twin records, although most major lake-level highs correspond to more or less synchronous decreases in sand influx. Swan Lake, in turn, shows a relatively linear relationship between the two proxies, where high sand input is correlated with low lake-levels and vice versa. Although sand input is a direct result of local or regional dune activity, it can be difficult to interpret in lake cores, partly because of the influence of littoral macrophytes that act as a barrier by trapping sand. The wind carries sand primarily by saltation, a process whereby grains bounce typically less than 1 m above the surface
(Fryberger, 1979). However, littoral vegetation common to these lakes and wetlands, such as *Typha* and *Scirpus*, grow generally much taller and can form thick stands that have the potential to block bouncing sand even during drought episodes. Drought duration and magnitude, as well as fire intensity and frequency, are among the most crucial factors affecting the density of macrophytes, and consequently determine the amount of sand that gets deposited in the basin. The orientation and distance of dunes relative to individual lake basins can vary tremendously and therefore impact the amount of sand deposition, as well. Finally, discrepancies between the two proxies are inherently problematic due to differences in temporal resolution and age models.

Observed discrepancies in behavior among our study lakes suggest either differences in local climate or differences to hydrological response to environmental variability. Droughts of the last century have been spatially heterogeneous even within a relatively small geographic area, and regional droughts such as the Dust Bowl have been infrequent (Oladipo, 1986). However, despite modern differences in precipitation patterns across our sites, it seems unlikely that strong climatic differences would occur over longer time periods especially between relatively closely-spaced sites of ~200 km or less. We suggest that other mechanisms, in particular altered groundwater flow patterns (Gosselin, 1999), are responsible for shifts in hydrologic behavior of individual lake systems. The influence of ground water on individual lakes in the Sand Hills can vary tremendously even on a local scale (Gosselin et al., 2006). While groundwater is the primary source of water in Sand Hills lakes, the specific hydrologic details are determined in large part by local topographic relief and slope discontinuities (Gosselin et al., 1999) as well as lake location in relation to the groundwater flow path (Gosselin et
al., 2006). Similarly, a high resolution palaeohydrologic synthesis of Fritz et al. (2000) showed that variability in behavior among three lake sites in North Dakota are produced by differing hydraulic responses of the lakes.

In general, identifying common intervals of change among a number of geographically discrete sites can be a challenging task. We have mentioned a few scenarios that can produce divergent lake responses to related climatic intervals. As noted above, individual age-depth models can be out of phase, because of complex depositional histories of certain basins. In addition to differential influences of groundwater on individual lakes, dune blockages can raise the water table and lake-levels during extended drought periods (Loope et al., 1995; Mason et al., 1997) in areas where the geomorphology is suitable. Consequently, hydrologic changes are not always directly caused by a decrease in effective moisture (Digerfeldt et al., 1993; Fritz et al., 2000; Telford & Lamb, 1999), and it is necessary to carefully examine multiple sites, as well as calibrate and model basin responses in order to better constrain the nature of lake response to climate (Fritz, 2008).
Figure 3.15: Comparison of diatom zones across all sites. Common intervals of change are represented by the horizontal dashed red bars.
Figure 3.16: Common intervals of drought of Round Lake and East Twin and Beaver- and Swan Lake (red bars). Orange bars indicate individual lake responses. Localized differences between the two groupings are probably related to changes in local groundwater settings and do not reflect regional coherency. The West Twin record was omitted in this analysis, because of differences in diatom responses due to coring location.
Figure 3.17: Z-scores of diatom-inferred lake-level histories of all lakes with 20-year interpolated sample spacing of the entire 4000 year record. Vertical lines depict mean depths. Lake-depths to the left of the lines represent low effective moisture (drought); everything to the right side of the line reflects high effective moisture and wetter conditions. Shaded intervals represent times of drought, and unshaded intervals indicate wetter periods. Vertical red bars on the right signify common drought intervals based on deviations from mean lake depth. Arrows represent coherent changes according to diatom zones.
Figure 3.18: Diatom-inferred lake-level histories compared with sand influx. Prior to analysis data points were interpolated at 20-year intervals. Red lines indicate weight% sand or grain-size and the green curves depict lake-level.
3.6.3 Are there common frequencies of variation among the sites?

Understanding the dynamics of a climate system at longer time scales for a given region, involves relating climate variation inferred from proxy records to large-scale drivers, such as variability of sea-surface temperature (Stone and Fritz, 2006; Ekdahl et al., 2008) or solar forcing (Bond et al., 2001). However, these comparisons can be difficult to assess at high temporal resolution, because of dating uncertainties (Fritz, 2008). One way to facilitate this problem is to use spectral analysis, which identifies common natural periodicities among records, which in turn, can be compared to periodicities of forcing functions.

Time-series analysis of diatom relative abundance, DCA, and P:B ratio shows statistically significant (>99% confidence interval) centennial and multi-decadal variation in all lakes, but only a few common peaks. Differences in resolution between each site result in distinctive temporal periodicities. For instance, both, West Twin and Beaver Lake, show pronounced decadal periodicities, whereas East Twin and Swan Lake exhibit centennial variability only. Some of the multi-decadal to centennial-scale peaks may be interpreted as multiples of lower frequency signals. However, the differential patterns of response among all sites make it too difficult to recognize which signals are regionally representative and how they might be related to forcings.
Figure 3.19: MTM power spectra plotted against individual diatom species and diatom indices. Red and green lines signify 99% and 95% confidence intervals, respectively. Y-axis is power.
3.6.4 How do these lake sites compare with other regional records of climate change, particularly to eolian records?

Overall, our records are in broad agreement with the existing upland dune record of the Sand Hills (e.g. Miao et al., 2007) as illustrated in Figure 3.20. However, diatom-inferred lake-level curves in conjunction with sand influx suggest higher frequency variability in the regional climate. Between 4000 and 2200 cal yr BP, our study suggests five distinct drought events of multi-decadal to multi-centennial scale, while other studies report only two major arid episodes during this time (Nicholson and Swinehart, 2005; Miao et al., 2007). Periods in between these arid events suggest equally long discrete wet phases. Several multi-decadal-scale droughts, occurring at ca. 2000, 1800, 1500, and 1250 cal yr BP, occur during a period of overall higher lake-levels and effective moisture between 2200-1200 cal yr BP. The last 1200 yr of the record generally suggest higher frequency variability in the climate record. We identified at least three drought episodes (Figure 3.17) in addition to eight common intervals representing lower lake-levels across most sites (Figure 3.16), in addition to a concomitant increase in sand. It appears that drought intervals at Swan Lake bear most resemblance to the existing upland OSL ages. While the general directional pattern in the Beaver Lake record is broadly similar to Swan Lake and the upland drought record, it seems to be less sensitive to drought in comparison with all other lakes. Perhaps lake-levels at Beaver Lake are stabilized by the proximity to the Niobrara River ca. 35 km north, or some of its tributaries. Additional lake cores from nearby need to be studied in order to test this hypothesis. Nevertheless, between 2250 and 3750 cal yr BP, lake-levels in Beaver Lake remain high and sand input is low as opposed to the regional OSL signal, which shows extensive and long-term
aridity during most of this period. On the other hand, both Swan- and Beaver Lakes suggest low lake-levels at around 1500 and 1250 cal yr BP. Only a few OSL dates have been published that register drought during this time period in the Nebraska Sand Hills (Goble et al., 2004). Mostly these dates stem from sands within paleosols that are exposed in blowouts and have age errors typically range around ±100 yr. A period of eolian activity at approximately this time has also been recorded from western Kansas (Forman et al., 2008) and attests to the regional context of these events. The combined Twin Lake records generally resemble the existing OSL drought records with additional local aridity occurring between 2000-1800 cal yr BP and multiple short-term droughts during the 750-250 cal yr BP. Evidence supporting these additional drought records exists from nearby Jumbo Valley where droughts occurred between 2100-1800 and 950-700 cal yr BP (Nicholson and Swinehart, 2005).

3.6.5 How do these records relate to other records from the Great Plains and western U.S., and what does this suggest about environment and climate?

The dominant common moisture fluctuations documented in this study appear to have affected a large portion of the continental U.S over the last 4000 years. The widespread geographic extent is especially apparent for droughts that occurred between 4000-3000, ~1500, ~1200, and 1000-700 yr BP (Figure 3.20). In general, prior to 3800-4000 years BP, the mid-continent was more arid and warmer than today (Kutzbach and Ruddiman, 1993; Dean et al., 1996). After the mid-Holocene warm period, climate became overall cooler and more humid (Webb et al., 1993). Despite generally cooler and wetter conditions, a variety of proxy-climate records indicate that droughts affected much
of the western United States and the Northern Great Plains (e.g. Daniels and Knox, 2005; Cook et al., 2004; Forman et al., 2000; Laird et al., 1996, 1998; and Woodhouse and Overpeck, 1998, Laird et al., 2007). For example, widespread and extensive dune activity has been reported from multiple sites across the Great Plains (Forman et al., 2000). Diatom-inferred salinity reconstructions and ostracode–Mg/Ca ratios from lake sediments in the northern Great Plains also suggest brief episodes of low lake-level between 900 and 600 BP (Laird et al., 2003; Shapley et al., 2005). Increased influx of eolian-derived clastic material is evident in sediments of Elk Lake in north-central Minnesota prior to 3800 yr BP and centering around 800 yr BP (Dean et al., 1996). Radiocarbon ages from paleosols of the Minot Dune Field in North Dakota places the oldest recognized dune event just prior to 1300-1100 cal yr BP, and two subsequent younger dune migration events at ca. 1000 and 600 cal yr BP (Muhs et al., 1997). Lake-level reconstructions of Lake Michigan are in broad agreement with our results for the last 2300 cal yr BP (Baedke and Thompson, 2000). The Lake Michigan record suggests the following drought periods: 600-500, ~750, 1100-1000, 2000-1900, 2300-2100, 3500-3300 cal yr BP. In other Midwestern regions, such as in southwestern Kansas, drought intervals have been documented at ~1490 yr BP based on OSL ages of eolian sand (Forman et al., 2008). Droughts between 1000 and 700 yr BP also extended across much of the western United States, where tree-ring records have clearly documented four multi-decadal drought events (Cook et al., 2004). Moreover, paleosols found within eolian sands of northeastern Colorado provide evidence for eolian activity at around 1400, 1050, and 900 cal yr BP (Madole et al., 1995; Muhs et al., 1997) very similar to our findings. On the other hand, a high-resolution record of drought variability from a lake sediment core at
Foy Lake in eastern Montana suggests consistently lower lake-levels between 2300-1300 cal yr BP with no cyclicity and generally higher lake stands with cyclical drought patterns between 1300 cal yr BP to the present (Stevens et al., 2006). Similarly, Crevice Lake at Yellowstone National Park indicates drier conditions between 2100 and 800 cal yr BP, followed by higher effective moisture (Bracht et al., 2008). Although these findings are substantially different from our results with respect to the direction of lake-level and effective moisture, they do show similar temporal fluctuations. The eastward extent of these western drought events is not entirely understood, because of the relatively few existing drought-sensitive records of multi-decadal resolution from eastern North America.

Similarities in duration and frequency of diatom-inferred hydrologic events between Sand Hills lakes and other records of the Great Plains are apparent, and we can propose correspondence of major climatic events in the regional record with some confidence.

The mechanisms behind these climatic fluctuations are believed to be related to changes in the Pacific and/or Atlantic sea-surface temperatures that altered atmospheric circulation patterns across America (McCabe et al., 2004; Seager et al., 2007). The east- or southward migration of the North Atlantic subtropical high-pressure ridge (“Bermuda High”) was believed to be responsible for the replacement of moisture-laden southerly winds from the Gulf of Mexico with dry southwesterly winds in the Sand Hills during the MCA (Sridhar et al., 2006), and it is likely that similar changes in wind regimes played a key role in earlier Holocene droughts across the Great Plains.
Figure 3.20: Summary figure showing diatom-inferred lake-level curves from all study sites, sand influx, and the resultant common intervals of change (gray bars). Our data are compared with a compilation of the newest OSL results from the Nebraska Sand Hills (Mason et al., 2003; Goble et al., 2004; Miao et al., 2005, 2007), as well as with a number of other regional and continental paleoclimatic records.

3.7 Conclusions

The synthesis of multiple sites across the Nebraska Sand Hills indicates that droughts of varying intensity and frequency have been a common feature in this region for at least the last four thousand years. Our study shows that most large-scale multi-centennial shifts seem to exhibit regional coherency, albeit of varying magnitude and duration. Locally confined droughts are predominantly a manifestation of local fluctuations/changes in the groundwater hydrology, which in turn, is primarily the result of changing dune morphology and precipitation. Centennial-scale droughts with equally long intervals of stability were more frequent prior to 2000 cal yr BP, while the last 2000 years exhibit higher frequency variability with generally shorter drought periods. Spectral analysis from all sites did not reveal any unequivocal evidence for common periodicities among the sites, nor did they show well-defined frequencies related to climate forcing. Overall, our findings refine the existing upland drought record in the Sand Hills and improve our understanding of late-Holocene climate variability across the region. At the same time, this study raises awareness of the oftentimes complex hydrologic settings in the Sand Hills lakes and their intimate relationship to the stability of the surrounding dune landscape.
3.8 Acknowledgement

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Chapter 4

DIATOM DIVERSITY TRENDS AND THEIR RELATION TO GEOCHEMICAL GRADIENTS IN NATURAL AND MAN-MADE LAKES OF NEBRASKA, USA.
4.1 Abstract

Diatom diversity trends were analyzed for a suite of Nebraska lakes, including natural lakes, reservoirs, and sand pits to evaluate the sensitivity of diatom communities to various chemical and physical gradients. Diatom diversity of natural lakes shows the strongest correlation with total nitrogen, turbidity, and conductivity, whereas in reservoir lakes, diversity is predominantly driven by phosphorus (TP and OP2), nitrate-nitrogen, turbidity, and pH. Sand Pits are very similar to reservoir lakes with respect to diversity-chemistry relationships, where diversity is primarily a function of TP, TN, and pH. Our findings suggest that differences in diversity trends among the three lake types are primarily a manifestation of nutrient and light availability, which in turn, is dependent on the physical and geographic properties that characterize each lake system. Moreover, this work highlights the necessity of integrating multiple environmental variables beyond nutrient concentrations when studying algal biodiversity.

4.2 Introduction

Understanding the factors controlling species richness in local habitats is a central concern in modern ecology. In aquatic ecology, Hutchinson’s classic work identified the paradox of the plankton, which spurred exploration of how diversity in form, function, and identity can persist in seemingly homogenous habitats, such as the pelagic zones of lakes.

McCune (2002) defines species richness as the number of species in a sample unit, but in a broader sense it refers to the number of different species of a given area. The
dominant controls on species diversity can be divided on two classes of influence. The local or deterministic view of species richness focuses on biological interactions, such as predation and competition effects, as well local physical and chemical influences as the principal control of diversity. The regional or historical view, on the other hand, emphasizes the importance of species differentiation and movement at the regional level, as well as the interactions between local and regional processes. For instance, strong inverse correlations exist between species richness and latitudinal/ altitudinal gradients, because of a concomitant decrease or increase of suitable habitats. Most modern studies in ecology incorporate both of these ideas in a hierarchical perspective over time and space (Ricklefs & Miller, 2000).

Lakes are ideal model systems for studying relationships between species richness and primary productivity as was demonstrated by Dodson et al. (2000). The main reasons for utilizing lakes include direct $^{14}$C measurements of primary productivity, well-defined community structures particularly in closed-basin lakes, and, finally, the availability of large data sets of species communities across taxonomic groups, as well as of primary productivity. Diatoms, in particular, share important qualities that make them powerful biomonitors of environmental change (Stoermer & Smol, 1999). Not only are they often the most abundant algal group in many freshwater systems, they are also very diverse, with an estimated $10^4$ species, each of which possesses characteristic environmental optima and tolerances.

Local and regional processes that affect or influence aquatic species richness, in particular, include physical forcings, such as daily and seasonal light fluctuations (Litchman & Klausmeier, 2001), lake size and morphology, as well as underlying
geology. Dodson (1992) showed that an increase in lake area of 10 orders of magnitude is coupled with an increase of zooplankton species richness of about one order of magnitude. Stone & Fritz (2004) showed that lake morphology can impact planktic and benthic habitat area, which is manifested in species shifts that can potentially affect diatom biodiversity. Moreover, climate creates indirect effects on species richness through fluctuations in precipitation and evaporation, which form the major control on lake-level changes in closed basin systems. Lehman et al. (2002) identified groups of phytoplankton taxa that respond in similar ways to key environmental variables, such as temperature, stratification, light intensity, nutrients, and/or zooplankton, which provide a unique glimpse of the complex drivers that are imposed on the plankton.

Modern ecological thinking is increasingly concerned with how ecological dynamics are affected by processes occurring at larger scale (Leibold & Norberg, 2004; Cardinale et al., 2000). Large-scale spatial surveys suggest that species richness varies in a unimodal fashion with nutrient availability and hence primary productivity (Dodson et al. 2000), whereas short-term experiments, have identified both positive and negative relationships (Downing & Leibold, 2002). Rusak et al. (2004) note the lack of a temporal perspective between species richness and ecosystem functioning. They suggest that temporal controls of diversity-function relationships over millennia or centuries may be fundamentally different from those operating on smaller timescales.

McNaught (2002) underscores how little is still known about the factors that control species exchange across a landscape or even the extent of spatial variation in planktonic biodiversity within a lake region. There are many unknown variables controlling species richness, so the key is to consider multiple perspectives and tease out
those factors that best explain variation. This study focuses on the correlations between diatom species richness and geochemical variables (nutrient concentration, conductivity, pH, and turbidity) in lake systems, including natural lakes, reservoirs, and sand pits, across Nebraska. Nutrient concentration, in particular phosphate and nitrate, is highly correlated with productivity, which, in turn, is related to lacustrine species richness and has therefore been of long-standing interest in ecology. Previous studies suggest that the shape of the relationship between productivity and species diversity is highly variable (Mittelbach et al. 2001), albeit predictable. Multiple studies propose that lakes between the two extremes of primary productivity generally exhibit the highest species richness (Dodson, 1992). Conductivity/salinity, as well as pH, can influence biodiversity, because these variables can pose physiological stresses on organisms at extreme ends of the gradient. Individual diatom taxa have characteristic ranges of tolerance and optima for salinity and pH (Fritz et al., 1993). pH affects the solubility of many elements, as well as the speciation of nutrients, including changes between the harmless ammonium ion (NH4+) and the toxic undissociated ammonia (NH3) (Lampert & Sommer, 1997). Salinity concentrations may directly influence diatom physiology, i.e. by exerting osmotic stress, or they may directly or indirectly interact with other factors and therefore affect species composition (Saros and Fritz, 2000). The goal of this work is to test how diatom diversity is correlated with nutrient concentrations (phosphorus and nitrogen), conductivity/salinity, turbidity, and pH.
4.3 Methods

Surface sediment samples were obtained between 2000 and 2004 from a survey of lakes across Nebraska. Diatom counts from 41 natural lakes (NL), 18 reservoirs (R), and 12 sandpits (SP) were used to calculate species diversity. A total of 240 diatom taxa were identified across all sites. However, to reduce the influence of rare species, only diatoms that had a relative abundance of at least 2% were retained for statistical analysis. Matching environmental data were available for 17 natural lakes, 18 reservoirs, and 12 sandpits (Figure 4.1). For diatom preparation, the sediment surface samples were homogenized and processed in hydrochloric acid (10%) to dissolve any accumulated carbonates. Afterwards samples were treated with cold hydrogen peroxide (30%) to digest organic matter and finally rinsed several times with distilled water until free of peroxide. The resulting slurries were settled on cover slips and dried before being mounted onto slides with Naphrax®. At least 250 diatom valves were counted in transects under oil immersion on a Zeiss Axioscop 2 plus microscope with a 100 x objective, with the exceptions of Border Lake (NL), Upper Harrison Lake (NL), Big Indian Lake (R) and Clatonia Lake (R). Primary taxonomic references used for all lakes were Patrick and Reimer (1966; 1975) and Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b). Those samples with fewer counted individuals were not incorporated in the numerical analysis. We used alpha diversity as the basis for our analysis, which, in this case, reflects the diatom diversity per individual sample unit. Diversity indices, in particular Shannon diversity (H’) and Simpson Index (1-D), were calculated using the software package Past.
Simpson original index (1/D2) is a measure of dominance ($\lambda$) rather than diversity (McCune and Grace, 2002). It represents the likelihood that two randomly chosen individuals will be the same species. It varies inversely with diversity and ranges from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely):

$$\lambda = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

where $S$ is the number of taxa and $p_i$ is the fraction of all organisms which belong to the $i$-th species. The complement of the Simpson’s index of dominance is:

$$1 - \sum_{i=1}^{S} p_i^2$$

It is a measure of the 'evenness' of the community or the likelihood that two randomly chosen individuals will be different species. This index is only little affected by addition or loss of rare species and it emphasizes common species. It is therefore relatively stable with sample size.

Shannon index ($H'$) is based on information theory (Shannon and Weaver, 1949):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$
in units per individual per unit volume or area, where pi is estimated from ni/N as the proportion of the total population of individuals (N) belonging to the i-th species (ni) and using logarithms to the base 2. Communities with only a single taxon have a zero value, as opposed to communities comprised of many taxa, each with few individuals, which have higher values accordingly. H’ measures the diversity in a multiple-species community (Wetzel, 2001).

The diversity indices described above were chosen, because they are the most commonly used in the literature. In addition, correlations of the Shannon index with the other implemented indices provided by Past are highly correlated (R > 0.9). The Shannon diversity index was used to evaluate patterns and trends among the data based on a principle components analyses (PCA) using the software R (R Development Core Team. 2006).

Water chemistry is highly variable in Nebraska lakes. Natural lakes of the Sand Hills range from dilute freshwater to hypersaline, whereas reservoirs and sand pits are commonly freshwater with salinity concentrations below 0.5 g l⁻¹ (Bennett et al., 2007). Most lakes range in pH between 7.5 to 8.5, and nutrient levels are typically high, in particular in Sand Hills lakes and reservoirs. Due to the skewed distribution of the chemical data, log- or square-root transformations were performed on the environmental data (except for pH) prior to analyses. Principal components analysis (PCA) was employed to identify variables that have the strongest influence and to test for major trends in biodiversity in relation to environmental data (in particular pH, conductivity (µScm⁻¹), alkalinity (mgL⁻¹ CaCO₃), turbidity (NTUs), nitrate (NN₂, µgL⁻¹), total phosphorus (TP, µgL⁻¹), total nitrogen (TN, µgL⁻¹), and orthophosphate (OP₂, µgL⁻¹).
Moreover, simple regression plots of diversity along individual chemical gradients were tested for each lake type alone and combined to identify the significance of those relationships.

Because diatoms assimilate large quantities of silica (Si) in their frustules they require high concentrations of its soluble form (> 5 mg L\(^{-1}\)), which is derived from the weathering of silicate minerals, such as quartz (Wetzel, 2001). In many lacustrine systems Si can be a limiting nutrient, and its availability can have a strong influence on diatom diversity and productivity (Tilman et al., 1982). Si data are not available from any of the sites in this study. However, Si concentrations from eight other Sand Hills lakes have an average of 43 mg L\(^{-1}\), and all but one lake had concentrations greater than 5 mg L\(^{-1}\). Therefore, we do not expect Si limitation in most Nebraska lakes, particularly in Sand Hills lakes, because of high inputs from the silica-rich dune sands.

### 4.4 Study area and sites

The state of Nebraska is characterized by two major physiographic regions. The extreme eastern portion of the state is part of the Central Lowlands, while the remainder of the state forms part of the Great Plains. The Great Plains regions itself is further subdivided into the High Plains, the Sand Hills, the Loess Hills and Canyons, as well as the Loess Plains based on differences in surficial geology and topography. Nebraska has a continental climate featuring eight climatic divisions based on NOAA/NCDC Climate Division maps. Mean January temperatures range from -7 to -2°C southwest to northeast, and average July temperatures across the state center around 23°C. Nebraska is
characterized by a large precipitation gradient, with mean annual precipitation of 360 mm in the northwest to more than 800 mm in the southeast. 50-75% of the precipitation falls during the summer months, while winter precipitation shows more limited spatial variation (Wilhite and Hubbard, 1998). Nebraska sits above the High Plains Aquifer, which extends under eight states in the central and southern Great Plains. According to Bleed and Flowerday (1998), 65% of the High Plains Aquifer underlies the Sand Hills alone. Most of Nebraska’s native pre-settlement vegetation was grassland dominated. The eastern and southern portions of the state were primarily characterized by tall-grass prairie, whereas the Sand Hills area is predominantly characteristic of mixed-grass prairies.

Nebraska features more than 2000 natural lakes, as well as hundreds of man-made reservoir lakes and sand pits (Bennett et al., 2007). The semi-arid Nebraska Sand Hills contain many interdunal-valleys that hold wetlands, marshes and lakes. These natural lakes tend to be rather shallow (< 4 m) and highly turbid systems (mean turbidity ~60 NTU). Depths of natural lakes vary between ~0.7 m and ~2.1 m. Reservoir depth measurements range between 1.3 m to 10.5 m. No depths are available from sand pits. However, these types of lakes often tend to be deeper compared with natural lakes. Sand pits and natural lakes generally lack any surface in- or outflows, and are sustained primarily by groundwater. The reservoirs and sand pits in this study are situated outside of the Sand Hills area itself (Figure 4.1).

Chemical characteristics vary tremendously among lakes. Alkalinity (Table 4.1), for instance, ranges from 75.5 mgL⁻¹ to 4,627 mgL⁻1. Sand pits and reservoirs exhibit lower values, averaging ~ 200 mgL⁻¹, whereas the Sand Hill lakes average ~860 mgL⁻¹.
Similar variation can be seen among lakes in the conductivity data (166-9680 mgL\textsuperscript{-1}). Salinity varies from freshwater (72 mgL\textsuperscript{-1}) to moderately saline conditions (5,495 mgL\textsuperscript{-1}). pH values are all alkaline and range from 7.9 to 10.3. Nutrient concentrations, in particular TP and TN, are, on average, lowest for sand pits lakes, followed closely by reservoirs. Highest values occur in natural lakes. TN is about seven times higher in natural lakes (7105 mgL\textsuperscript{-1}) than in reservoirs and sand pits, while TP concentrations are nearly 4 and 13 times higher in reservoir and sand pits. The high nutrient content is in part a function of the relatively shallow depth of these lakes, in which sediments are easily mixed into the water column by strong winds. This is corroborated by the generally higher turbidity in natural lakes as opposed to sand pits and reservoirs.
Figure 4.1: Digital elevation map illustrating locations of individual lake sites. The yellow area represents the Nebraska Sand Hills.
Table 4.1: Summary of diatom diversity indices and environmental variables for sampled sites: (NL) – Natural lakes, (SP) – Sand pits, (R) – Reservoir lakes.

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<th># Individuals</th>
<th>Dominance</th>
<th>Shannon</th>
<th>Evenness</th>
<th>pH</th>
<th>TN (µgL⁻¹)</th>
<th>NN₂ (µgL⁻¹)</th>
<th>TP (µgL⁻¹)</th>
<th>OP₂ (µgL⁻¹)</th>
<th>Conductivity (µScm⁻¹)</th>
<th>Alkalinity (mgL⁻¹ CaCo₃)</th>
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<td>Evenness</td>
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<td>800.40</td>
<td>100.00</td>
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<td>20.55</td>
<td>751.53</td>
<td>180.56</td>
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<td>291.82</td>
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<td>920.00</td>
<td>692.76</td>
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<td>20.00</td>
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4.5 Results and Discussion

To evaluate whether diatom diversity is primarily correlated with nutrient availability, we performed PCAs to identify the main directions of variation within the species data and how it is correlated with measured environmental gradients. Principal components analysis is an objective method that combines the original variables into linear combinations (eigenvectors) and concentrates the primary patterns of variation among all variables within the first few components, while it leaves the least coherent aspects for the last few components.

4.5.1 Natural Sand Hills Lakes

Diversity trends from diatom counts of all 41 natural lakes in the Sand Hills show that the species richness varies tremendously, from as low as 3 species (Reno Lake, Whitehead Lake, and Bean Lake) to up to 31 species (Dewey, Dry, and Duck Lake). On average, 17.5 species are present. The Simpson index of dominance in low-diversity lakes ranges between 0.65 and 0.92, indicating dominance by a few species, and evenness ranges between ~0.08 and 0.55, reflecting relatively uneven distributions of the taxa (see also Table 4.1). No chemistry data are available for Bean, Reno, and Whitehead lakes to interpret the low diatom diversities in these systems. Nevertheless, all three of these basins contain high abundances of the species *Aulacoseira ambiguа*, which is indicative of low light conditions and high Si/P concentrations. Furthermore, *A. ambiguа* is generally common during isothermal mixing and is often found in turbid waters (Anderson, 2000). The other dominant species in Whitehead Lake is *Campylodiscus*
This taxon is known to thrive in brackish or saline environments, and it is restricted to pH greater than 7 (Krammer and Lange-Bertalot, 1988). Thus, the low diversity observed in these lakes is likely the result of turbid, hypersaline or saline conditions where only a limited number of species are able to survive. All three lakes are located in the Crescent Lake Wildlife Refuge in the western portion of the Sand Hills, where saline to hypersaline lakes are common (Bennett et al, 2007).

To evaluate whether diversity is predominantly correlated with nutrient concentration, we first compared the Shannon diversity index with all environmental variables, including conductivity, turbidity, and pH. Overall, results reveal that in most natural lakes high diatom diversity appears to be related to low to intermediate nutrient concentrations, as well as low or average turbidity and conductivity. More specifically, increased diversity occurs at low or average turbidity and conductivity, TN, NN2, OP2 and TP concentrations, as well as relatively high pH.

Turbidity, TN, and conductivity are highly correlated with each other. Together, these three variables explain most of the observed variation, as they all plot in direction of the first ordination axis, which has an Eigenvalue of 43% (Figure 4.2). However, at closer examination, TN turns out to be the most significant variable among the three and explains the majority of the observed diversity distribution (Figure 4.3). TP and OP2 both point in similar directions relative to ordination axes 1 and 2, more or less orthogonal to NN2 (Figure 4.2). In contrast, a PCA plotting phosphorus and nitrogen species independently reveals that both nutrients explain approximately similar degrees of variation with respect to diatom diversity (Figure 4.4). Nevertheless, highest diversity predominantly occurs in average TP and OP2 concentrations, although I-00 and D-00 and
D02 show opposite trends. Regression analysis does not show a significant correlation between diversity and turbidity even after outliers are removed (Figures 4.5 & 4.6). TN, on the other hand, has a much better correlation to diversity without consideration of outliers. Although conductivity does show a relatively good correlation with diversity including outliers, it increases significantly when they are deleted from the analysis (Figure 4.6). In general, lakes with highest diversity show lower dominance, usually ranging between ~ 0.07 and ~ 0.18, and a higher evenness between 0.81 and 0.93. However, simple regression plots indicate no significant relationship between Shannon diversity index and TP, TN, conductivity, and turbidity if all natural lakes are considered (Figures 4.5 & 4.6). Removing two outliers (BA-02 and TC-04) from the calculations, improves the significance of the relationship tremendously with respect to total nitrogen (r² = 0.43, p-value = 0.0079), while it is not significant statistically with those lakes included. Figure 4.4 illustrates that phosphorus and nitrate/nitrogen roughly explain the same amount of variation, albeit no significant relationship (r² = 0.064) is apparent between TP and Shannon diversity index, both, with or without the two outliers.
Figure 4.2: PCA plotting all variables against diatom diversity within natural lakes. Circle size corresponds to diversity. Bigger circles indicate higher diversity of individual sites and vice versa. Arrows point in direction of maximum rate of change of a particular variable across the diagram. Length of arrows indicate relative rate of change in that direction. Origin represents the average value for each variable.

Fig. 4.3: Relationship between conductivity, turbidity and TN variables in relation to Shannon diversity index.
Fig. 4.4: PCA of nutrient variables plotted against Shannon diversity index for natural lakes of the Sand Hills.
Figure 4.5: Linear regression plots between Shannon diversity index versus conductivity (upper left), turbidity (upper right), total phosphorus (lower left), and total nitrogen (lower right) across all natural lakes.
Figure 4.6: Above left: Correlation matrix between Total Nitrogen and Turbidity of Natural Lakes

Bottom: linear regression models between Shannon Diversity Index and selected environmental variables with two outliers removed for natural lakes of the Sand Hills. Statistical relevance improved significantly among all relationships.
Analysis of the data indicates that conductivity and total nitrogen have the strongest influence on diversity in the natural lakes. Highest diversity generally occurs at average to low concentrations. Although turbidity has a strong correlation, as well, regression analysis does not show any significant relationship to diversity, even after outliers were removed. High diversity is also related to low to intermediate nutrient concentrations and vice versa.

4.5.2 Reservoir lakes

Species richness is generally higher for reservoir lakes than natural lakes of the Sand Hills, possibly because they are more strongly influenced by groundwater and surface water inflow, which results in shorter residence times compared to other lake types (Bennett et al., 2007). The average species abundance is 24, which means that they are almost one third more diverse in comparison with diatom communities of natural lakes. None of the reservoir lakes investigated exhibits such low diversities as found in some of the Sand Hills lakes. Turbidity, TP, NN2, and OP2 show the strongest influence on diversity in reservoir lakes based on PCA’s. Similar to natural lakes, highest diversity is commonly established at low to average concentrations and relatively high pH.

Highest diatom diversity is found in Kilpatrick Lake (35), Carter P. Johnson Lake (34), and Wellfleet Lake (33). For these lakes, Evenness ranges between 0.95 and 0.93, Dominance between 0.05 and 0.07, and the Shannon diversity index ranges between 3.2 and 3.1, respectively. Kilpatrick Lake not only exhibits the highest diversity, but it also
features the highest pH, very low phosphorus, and below average nitrogen concentrations.

Lowest diversity is recorded in Oxbow Trails Lake, with only 9 counted species. Its Evenness is 0.78, Dominance is 0.23, and Shannon diversity index equals 1.7. The other lakes have at least 17 species present. Cub Creek South Lake has the highest nutrient content, as well as lowest conductivity and alkalinity measurements.

Figure 4.7 plots all chemical data against diversity. Ordination axis 1 (PC1) explains about 64% and axis 2 (PC2) 16%, such that pH, OP2, TP, NN2, and turbidity exert the greatest amount of influence on observed species composition in the figure. Conductivity is strongly correlated with PC2. The graph demonstrates that highest indices occur at low to average TP, OP2, and NN2 concentrations and turbidity measurements, as well as intermediate pH. Conductivity, in turn, shows high diversity at all ranges, except for the highest concentrations. Figure 4.7 illustrates the relationship between diversity and nutrient concentrations alone. All variables are intercorrelated and more or less point in the direction of PC1, which explains 81% of the variance. The influence of each component on the variation is highest for TP, followed by NN2 and OP2. However, the length and direction of arrows indicate nearly identical influences. It is apparent from the graph that highest diversity occurs at below average values of OP2, NN2, and TP - similar to the pattern observed for natural lakes where generally highest diversity was shown to appear at average to low concentrations. Highest diversity indices occur at low to intermediate TN concentrations. The correlation of diversity with pH, turbidity, and conductivity is illustrated in Figure 4.8. Increased values of pH, in addition to low and intermediate turbidity and conductivity, relate to high diatom diversity similar to
observations made in Figure 4.7 above. High turbidity and conductivity values, as well as low pH, appear to be correlated to lower diatom diversity.

To test whether the principal components analyses carried out above are statistically significant, a regression analysis between Shannon diversity index versus conductivity, turbidity, TP, and TN was performed. The results indicate a significant relationship ($r^2$ of 0.44, p-value 0.005) with total nitrogen only (see Figure 4.10). Conductivity, turbidity, and total phosphorus, in turn, are not statistically significant. Similarly, regressions performed on a number of species versus conductivity, turbidity, TP, and TN reveal a strong correlation for TN only. Simpson’s index of evenness shows statistically significant correlations with turbidity and TP, in addition to TN (Figure 4.10).
Fig. 4.7: PCA of all variables plotted against diatom diversity in reservoir lakes.

Fig. 4.8: All nutrient variables plotted against diatom diversity.
Fig. 4.9: PCA plotting all non-nutrient variables – pH, turbidity, conductivity – against diversity.
Fig. 4.10: Linear regression plots between Shannon diversity index vs. conductivity, turbidity, total phosphorus, and total nitrogen across reservoir lakes.
In contrast to natural lakes, turbidity, TP, NN2, and OP2 explain most of the variation observed in the diatom diversity of reservoir lakes. Similar to natural lakes, highest diversity is commonly established in low to average concentrations of all geochemical variables, with the exception of pH. Most of these relationships are not statistically significant, however. High and statistically significant correlation was found only between diversity and total nitrogen.

4.5.3 Sand Pit lakes

On average, Sand Pits have the highest diatom diversity among all three lake types, with approximately 28 species per site. Overall, TP, TN, and pH explain most of the variation with respect to diatom diversity, but also turbidity is strongly correlated with diversity (Figure 4.11). Generally, highest diversity occurs at low to intermediate conductivity and nutrient concentrations, as well as low to intermediate pH.

The highest diversity is found in West Gothenburg Lake (WGEg-02) with 39 species, in contrast with War Axe Lake (WAXe-02), which has 20 species. West Gothenburg exhibits the lowest conductivity values and below average nutrient values. Its Shannon index is ~3.2 and Evenness ~0.94, in contrast with War Axe Lake, which has a Shannon index of ~2.3 and Evenness of ~0.8. The latter has elevated nitrate concentrations and above average conductivity measurements.

TP, OP2, TN, and pH have the most significant influence (ca. 48.5 %) relative to the observed variation of diatom diversity. Similar to the other lake types, highest diversity relates to low to intermediate conductivity levels, as well as to low to
intermediate turbidity, pH and nutrient concentrations. Low diversity is again correlated with elevated concentrations of each variable.

A closer examination of diatom diversity based on the nutrient components only, generally reveals a similar pattern (see Figure 4.12). Highest diversity is almost exclusively found at low to intermediate concentrations of TN, NN2, TP, and OP2. Blue Hole Lake (BHOe-02) is the only exception to this trend, with a Shannon diversity index of 2.8 and 29 different taxa. Fig. 4.13 shows the relationship of diversity to pH, turbidity, and conductivity. In this graph, the first ordination axis explains 53.5 % of the variation seen, while PC2 explains approximately 35 %. Turbidity has the strongest influence of all three variables (Figure 4.13). Highest species diversity seems to be the result of low to intermediate pH and relatively low turbidity values. Conductivity is different in the sense that low diversity is neither found at high nor at low concentrations. On the other hand, it seems that at low concentrations, diversity is particularly high (COZd-02 & WGEg-02) and high diversities occur at intermediate and average concentrations of conductivity.
Fig. 4.11: All nutrient components plotted against diatom diversity across sand pits.

Fig. 4.12: PCA illustrating nutrient components against diversity.
Fig. 4.13: PCA plot demonstrating the relationships between diversity versus pH, turbidity, and conductivity.

Fig. 4.14: Linear regression plots of Shannon diversity index vs. conductivity, turbidity, total phosphorus, and total nitrogen across reservoir lakes. Significant relationships exist between for conductivity and turbidity.
Sand pits are the most species rich lake type among all three, with an average of 28 species per site. TP, TN, and pH explain most of the observed variation of diatom diversity. However, also turbidity plays an important role. Generally, highest diversity occurs at low to intermediate conductivity and nutrient concentrations, as well as low to intermediate pH. In contrast to natural and reservoir lakes, pH has the opposite effect on diatom diversity in Sand pits. Regression analyses of Shannon diversity index and individual chemical variables, as illustrated in Figure 4.16, suggest two significant correlations – the first between diversity and conductivity (R² = 0.2885; p-value = 0.0717) and the second between diversity and turbidity (R² = 0.259; p-value = 0.0911).

4.5.4 All lakes combined

If the relationships between diatom species richness and environmental variables are investigated with all lakes combined, patterns may be stronger due to longer environmental gradients. On the other hand, it may aid in our understanding of how individual variables exert different patterns and distributions regarding diatom diversity in each lake system. Overall, TP, OP2, TN, and turbidity have the strongest influence on the variability in diversity among Nebraska lakes. Sand pits are the least variable lakes and almost exclusively plot at low concentrations of the variables with the strongest influence. Reservoir lakes are similar, except that NN2 has a greater influence on diatom diversity. Natural lakes are highly variable but primarily occur on the negative portion of PC2. In these systems, highest diversity occurs at intermediate pH, nutrient components, and turbidity.
Figure 4.15 illustrates all variables plotted against diatom diversity. Turbidity, total nitrogen, total phosphorus, as well as ortho-phosphorus show the strongest influence on the observed variability (Appendix 1). Natural lakes exhibit the greatest range of values regarding diversity and chemical variability. In contrast, sand pits show little variation. The latter, more or less, form a cluster on the positive side of PC2, with the exception of Cochran Lake (Coch-02). Reservoir Lakes are somewhere in between Sand Hill Lakes and Sand Pits, with low diversity occurring at high conductivity, intermediate to high NN2 and turbidity, as well as intermediate OP2 and low to very low pH. Natural lakes, in turn, plot primarily on the negative side of PC2. Therefore, all lakes, apart from Big Alkali (BA-02), have above average concentrations of turbidity, OP2, TP, TN, and conductivity, with a tendency of decreasing diversity at higher concentrations and vice versa. Moreover, highest diversity in natural lakes primarily relates to intermediate pH and low NN2 concentrations, although DB-00, I-00, and BA-02 are obvious outliers to this generalization. Total phosphorus and ortho-phosphorus show the strongest influence in terms of diversity, if nutrients are considered alone. The majority of the lakes of each group plot in a very similar manner as in the previous example where all environmental components were considered. While sand pits plot primarily on the positive side of PC2, natural lakes occupy most of the negative side. Reservoirs, on the other hand, are somewhere in between the two. Overall, highest diversity occurs at low to intermediate nutrient concentrations in all of the three lakes. Sand pits and reservoirs with increased nutrient concentrations have generally low diversities, whereas in natural lakes the distribution is disordered, such that low diversity waters (SH-02) plot next to species rich lakes. Moreover, BA-02 shows correlations to low nutrient conditions, while TC-04
correlates with intermediate nutrient concentrations. Turbidity features the greatest influence on the observed diversity distribution along gradients in pH, conductivity, and turbidity (Figure 4.17). PC1 accounts for approximately 42% of the variability. Conductivity has a greater impact on diversity than pH. Nevertheless, low conductivity and turbidity gradients, as well as low to average pH, is correlated with high diversity within sand pits. Diversity in reservoir lakes shows a similar pattern, with highest diversity in low conductivity and turbidity, as well as to low and/or intermediate pH. In contrast, low diversity is correlated with very low pH and intermediate conductivity. In natural lakes, high diversity occurs at low to average conductivity and turbidity in addition to low to intermediate pH. The dispersal of natural lakes with low diversity, in particular TC-04 and BA-02, appears random. Therefore a sound interpretation remains difficult. Other gradients, such as nutrients, seem to be better indicators with a higher influence to discern and evaluate the distribution.

The relationship between the Shannon diversity index and total nitrogen, total phosphorus, conductivity, and turbidity is illustrated in Figure 4.18. All correlations are highly significant, although the correlation coefficients ($r^2$) are relatively low. Likewise, testing the significance between the number of species and the same environmental factors suggests highly significant correlations. Less significant relationships are found between correlations of the Simpson’s index of evenness and TN, TP, conductivity, and turbidity. Only conductivity and total nitrogen are significant.
Table 4.2: Eigenvalues for the first three unconstrained axes:

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<th>PC2</th>
<th>PC3</th>
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<td>1.045</td>
</tr>
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<td>nutrient components</td>
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<td>0.536</td>
<td>0.324</td>
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<td>1.259</td>
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Fig. 4.15: PCA plotting the relationships between diatom species richness and all chemical variables across the three lake types. Natural lakes = black; Reservoirs = red; Sand pits = green.
Fig. 4.16: PCA plotting the correlations between diatom species richness and nutrient variables across the three lake types.
Fig. 4.17: PCA demonstrating the relationships of diatom diversity vs. conductivity, turbidity, and pH across all types.
Fig. 4.18: Linear regression plots of Shannon diversity index vs. conductivity, turbidity, total phosphorus, and total nitrogen across all three lake classifications. Significant relationships exist for all correlations.
Of all variables, total phosphorus, ortho-phosphorus, total nitrogen, and turbidity have the strongest influence on the variability in diversity when all lakes are considered together. Sand pits are the least variable lake groups and almost exclusively plot at low concentrations of the variables with the strongest influence. For reservoir lakes this pattern is similar, except that NN2 exerts a greater influence on the diatom diversity. Natural lakes are highly variable but primarily occur on the negative portion of PC2. Highest diversity occurs at intermediate pH, nutrient components, and turbidity. Conductivity plays a less significant role with respect to diversity trends, in particular when considered alone. Nevertheless, lower salinities are generally preferred environments for increased diatom diversity. Overall, the significance of the relationships increases when all lake types are plotted as a function of environmental variables. Moreover, results reveal that diatom communities of individual lake types require different concentrations of nutrients, as well as pH etc. in order to reach maximum diversity. This phenomenon is likely the result of a variety of factors, such as differences in overall physical properties (depth, area, and temperature), magnitude of groundwater inflow and residence time, and geographic location. Generally, low to intermediate concentrations of nutrients, pH, and turbidity form the ‘best’ environment for high diversity, while elevated concentrations of any chemical species has the opposite effect.
Diatoms require multiple nutrients for growth, and nitrogen and phosphorus are commonly thought to limit phytoplankton production (Downing, 1997). Recent studies show that primary productivity often saturates with species richness within single trophic levels (Mittelbach et al., 2001). The relationship between nutrients and diversity is commonly reported to be ‘hump-shaped’ at a local scale. However, Chase & Leibold (2002) report that this pattern becomes linear when considered at regional scales (among watersheds). This study confirms a humped-shaped diversity distribution, with increasing species richness at low to intermediate nutrient concentrations across all lake types and for each lake type individually. Therefore, no differences between local and regional scales in terms of nutrient-diversity relationships are apparent. Other physiochemical components such as pH, conductivity, and turbidity also play an important role in diatom species richness. For instance, turbidity is a crucial parameter in natural lakes of the Sand Hills primarily by controlling light availability. Moreover, turbidity and total nitrogen are closely correlated for this region (Appendix C) due to the shallow nature of the Sand Hills lakes and the relatively strong winds occurring in this region, which together cause the lakes to mix and prevent stratification. The mixing, in turn, redistributes dissolved nutrients to organisms. High diversity is more or less always related to low to intermediate turbidity measurements across all lakes and individual lake types. In addition, conductivity and salinity are closely correlated and have the potential to limit diatom distribution and abundance. For each scenario, high diatom diversity is almost always related to low to intermediate conductivity/salinity concentrations. Conductivity seems to play a principle role only for natural lakes of the Sand Hills, whereas for reservoirs and sand pits this variable is not significant in terms of diversity likely because
the range of values is relatively small. The impact of salinity/conductivity on diatom
distributions and/or richness does not necessarily reflect salinity in a system, however. It
could also be driven by indirect effects on nutrient uptake that are caused through salinity
or some other physiological process (Fritz, 1999).

4.6 Conclusions

Our study provides insight in the intricate relationship between diatom diversity
and various chemical and physical gradients in natural and man-made lakes across
Nebraska. Although planktonic diversity may be profoundly influenced by other factors,
such as interactions between species, interactions across taxonomic levels, local
environment, geographic location, etc., this work highlights the importance of integrating
multiple environmental variables beyond nutrient concentrations when studying
biodiversity.

Natural lakes are the most variable lakes and TN, turbidity, and conductivity show
the strongest correlation with diatom diversity. Diversity in reservoir lakes, on the other
hand, is primarily correlated with OP2, TP, NN2, turbidity, and pH. Sand Pits are very
similar to reservoir lakes with respect to diversity-chemistry relationships, where
diversity is primarily a function of TP, TN, and pH.
4.7 Acknowledgements

I am grateful to Johannes M. Knops for providing the research idea. Thanks goes to S. Fritz for revising the manuscript and for offering her extensive Nebraska lake database, which contains the diatom counts and environmental data. I thank Dr. Danuta Bennett, who organized the database and made the diatom counts; John and Aris Holz for sharing their water chemistry data, and finally, thanks to Dr. Steve Juggins, who offered assistance with the statistical analyses.

4.8 References


Chapter 5

SUMMARY
5.1 Summary and Conclusions

Climate change remains a central concern to our society, in particular in drought sensitive regions, such as the Nebraska Sand Hills, where landscape stability affects hundreds of cattle ranches and the recharge of one of the world’s largest groundwater sources - the High Plains Aquifer. 65% of the groundwater stored in this vast aquifer occurs in Nebraska, and over half of that lies under the Sand Hills (Bleed, 1998). Because of a high groundwater table, interdunal valleys in the Sand Hills are filled with complexes of lakes, wetlands, and natural sub-irrigated wet meadows.

Previous geomorphic and wetland studies have shown that the Sand Hills experienced a series of severe and long-lasting drought episodes over the course of the Holocene, which destroyed the vegetation and remobilized the dunes (Mason et al., 2004; Miao et al., 2007). The mechanisms that caused drought in this region are relatively well understood (Shridar et al., 2006; Miao et al., 2007), however, the lack of high-resolution records does not provide sufficient evidence of the preconditions that triggered drought responses. Lake and wetland studies can offer records of higher temporal resolution, and they have the potential to reveal clues about magnitude and duration of drought events that led to dune activation. Moreover, the synthesis of multiple sites across a larger area can shed light on the regional extent of past droughts among various sites.

Diatoms were used as a primary means to identify changes in the effective moisture at the five study sites. Because diatom distribution and abundance are intimately tied to ionic- and nutrient composition, as well as to the light and temperature regime of a lake, we investigated the relationship that affects diatom diversity along a suite of environmental gradients.
The second Chapter of this dissertation is a combined paleolimnological study of mid- to late Holocene lake sediments of the central Nebraska Sand Hills using diatoms, pollen, grain size, and bulk sediment chemistry. Significant overlaps of these proxies in most intervals allow for reasonable interpretations of lake-ontogeny and hydrologic budget, as well as related changes of the surrounding dune landscape. A high-resolution diatom-based lake-level reconstruction suggests two distinct wet intervals (5750 – 5300 and 3800 – 1750 cal yr BP) as well as two prominent drought events (6400 – 5750 and 5300 – 3800 cal yr BP). Grain size analysis provides evidence for four additional multi-centennial drought episodes (3100 – 2300, 2000 – 1800, 1500 – 1400, and 900 – 700 cal yr BP) allowing for further refinement of the climate record. The few cases where combined datasets show asynchronous results are likely the result of differences in resolution, sensitivity and response times among proxies. Aerial photographs from the Dust Bowl Drought provide evidence that support the notion that lower lake-levels are a result of dry conditions. Dune mobilization, as evidenced from recent geomorphic studies, can coincide with elevated lake-levels during some periods of time, and therefore, drought magnitude may not always be the sole cause of dune reactivation. Rather, a specific combination of factors may be necessary, such as drought frequency, duration, and changes in seasonality.

Chapter 3 is a synthesis of multiple sites across the Nebraska Sand Hills including the Beaver Lake site from Chapter 2. Results indicate that droughts of varying intensity and frequency have been a common feature in this region for at least the last four thousand years. Most large-scale multi-centennial shifts seem to exhibit regional coherency, albeit of varying magnitude and duration. Locally confined droughts are likely predominantly a manifestation of local fluctuations/changes in the groundwater hydrology, which in turn, is primarily the result of changing dune morphology and precipitation. Centennial-scale droughts with equally long
intervals of stability were more frequent prior to 2000 cal yr BP, while the last 2000 years exhibit higher frequency variability with generally shorter drought periods. Spectral analysis from all sites did not reveal any unequivocal evidence for common periodicities among the sites, nor did they show well-defined frequencies related to climate forcing. Overall, our findings refine the existing upland drought record in the Sand Hills and improve our understanding of late-Holocene climate variability across the region.

Diatom diversity trends were analyzed for a suite of Nebraska lakes, including natural lakes, reservoirs, and sand pits in Chapter 4. The goal was to evaluate the sensitivity of diatom communities to various chemical and physical gradients. Diatom diversity of natural lakes shows the strongest correlation with total nitrogen, turbidity, and conductivity, whereas in reservoir lakes, diversity is predominantly driven by phosphorus (TP and OP2), nitrate-nitrogen species, turbidity, and pH. Sand Pits are very similar to reservoir lakes in terms of diversity-chemistry relationships, where diversity is primarily a function of TP, TN, and pH. Our findings suggest that differences in diversity trends among the three lake types are primarily a manifestation of nutrient and light availability, which in turn, is dependent on the physical and geographic properties that characterizes each lake system. Moreover, this work highlights the necessity of integrating multiple environmental variables beyond nutrient concentrations when studying algal biodiversity.

5.2 Suggestions for Further Research

This research has identified mid- to late Holocene hydrological changes in the Sand Hills region and investigated the relationships of modern diatom diversity trends to measured environmental gradients across Nebraska lakes. The results refine, and in parts revise, some of
the conclusions of previous studies and provide a complimentary line of evidence for deciphering changes in the Sand Hills hydrologic systems, as well as for providing insight into the interconnections of diversity and environmental gradients.

The high resolution diatom records incorporated in this dissertation proved to be very useful indicators of shorter-term hydrologic changes. However, observed discrepancies of proxies derived from the surrounding upland, such as sand input or pollen stratigraphy, raise questions about the relationship among these proxies, and how each variable operates individually during fluctuating climate.

Groundwater plays a significant role in a lake’s response to changes in effective moisture in the Nebraska Sand Hills. Future research needs to focus more on the groundwater connection of individual lakes in a given area, in order to account for changes in fluctuations over time. For instance, Beaver Lake consistently showed the highest lake-levels among all sites, whereas Swan Lake, which is similar in depth and size, fluctuated much more over time. Is this phenomenon a unique trend or do other lakes close by show similar patterns? Does the relative position of a lake(s) to the nearest river/stream cause these differences? What does lake history and geomorphology tell us about how these streams might have changed position over time? Moreover, it is important to understand the potential of littoral vegetation of blocking dune-derived sand. Do exposed mudflats create more suitable habitat for denser growth of littoral vegetation during falling lake-levels?

The aerial photographs shown in Chapter 2 of this dissertation clearly show that Beaver Lake becomes detached from its neighboring basin during times of drought (Figure 2.8). Based on our multiple proxy study we did not find convincing evidence that suggest a dune blockage
within the last 6500 years. However, OSL ages obtained from the sand bank that separates the two lake basins would provide unequivocal evidence of when and how this sand body encroached upon the lakes. This, in turn, could potentially be correlated to dune blockages events occurring in the western portion of the Sand Hills.

Overall, a more complete study of the mechanisms that link the flow of water from upland dunes to lakes and wetlands to groundwater will help to refine our understanding of the history of the Sand Hills.
APPENDIX
<table>
<thead>
<tr>
<th></th>
<th>Kilpatrick</th>
<th>Oxbow Trails</th>
<th>Average</th>
<th>West Gothenburg</th>
<th>War Axe</th>
<th>Average</th>
<th>Dewey</th>
<th>Whitehead</th>
<th>Average</th>
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<td><strong>Individuals</strong></td>
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<td>264</td>
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<td>272</td>
<td>285</td>
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<td>300</td>
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<td>0.06</td>
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<td>0.07</td>
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<tr>
<td><strong>Shannon</strong></td>
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<td>2.28</td>
<td>2.64</td>
<td>2.91</td>
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<tr>
<td><strong>Evenness</strong></td>
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<td>0.86</td>
<td>0.94</td>
<td>0.82</td>
<td>0.88</td>
<td>0.93</td>
<td>0.31</td>
<td>0.77</td>
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### Chemical data Summary

<table>
<thead>
<tr>
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<th>Reservoirs</th>
<th>Sand Pits</th>
<th>Natural Lakes</th>
</tr>
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<tr>
<td><strong>pH</strong></td>
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<td>Lowest</td>
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<td><strong>NN2</strong></td>
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<tr>
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<tr>
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<tr>
<td><strong>Alkalinity</strong></td>
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<tr>
<td><strong>Turbidity</strong></td>
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<td>65.1</td>
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</table>
Correlation matrices of diatom diversity in Natural Lakes of the Sand Hills
Correlation matrices of diatom diversity in Sand Pits

**Correlation matrix between Ortho-Phosphate & Total Phosphorus**

```
20 40 60 80 100 120 140
500 1000 2000 5000
```

**Correlation matrix between Nitrate & Total Nitrogen**

```
20 50 100 200
400 600 800 1000
```

**Correlation matrix between pH & Conductivity**

```
5.0 e+08 1.0 e+09 1.5 e+09 2.0 e+09
400 600 800 1000
```

**Correlation matrix between TP & Turbidity**

```
20 50 100 200
20 50 100 200
```

Correlation matrices of diatom diversity in Sand Pits
Correlation matrices of diatom diversity in Reservoirs

Correlation matrix between Ortho-Phosphate & Total Phosphorus

Correlation matrix between Nitrate & Total Nitrogen

Correlation matrix between pH & Conductivity

Correlation matrix between TP & Turbidity