TAXONOMIC INVESTIGATIONS OF
OKLAHOMA FLORA

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TAXONOMIC INVESTIGATIONS OF
OKLAHOMA FLORA

Thesis Approved:

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[Signatures and titles]

[Signatures and titles]

Dean of Graduate College
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</tr>
</tbody>
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CHAPTER 1

A TAXONOMIC TREATMENT OF THE GENERA AND SPECIES OF THE
SALICACEAE IN OKLAHOMA

INTRODUCTION

Considered by state taxonomists to be one of the more diverse in the United States, the vascular flora of Oklahoma comprises 173 families, 868 genera, and 2,540 species (Tyrl et al., 2003). This diversity of flora is related to the state's ecological and environmental diversity. Across the state, one finds considerable variation in precipitation, temperature, topology, geology, wind, and soils. One finds species representative of the eastern deciduous forest, central grasslands, the Rocky Mountains, the Chihuahuan and Sonoran Deserts, the Gulf Coastal Plain, and the Ozark Mountains.

For three decades, the most commonly used reference for the identification of the vascular plants of Oklahoma was U.T. Waterfall's (1969) *Keys to the Flora of Oklahoma*. As the title implies, it lacks the morphological descriptions of taxa needed to confirm identification of plants. For this information, one had to use descriptions appearing in taxonomic treatments for adjacent areas such as *Gray's Manual of Botany* (Gray, 1950), *Manual of the Vascular Plants of Texas* (Correll and Johnston, 1979), *Flora of the Great Plains* (Great Plains Flora Association, 1986), and *Shinners & Mahler's Illustrated Flora of North Central Texas* (Diggs et al., 1999). In addition, Waterfall's work has
become out dated with respect to revisions in classifications and changes in nomenclature.

This prompted a need for a modern, comprehensive treatment for the vascular plants of Oklahoma. As a result, the non-profit corporation Flora Oklahoma Incorporated was formed in 1983 (Tyrl et al., 2003). Foreseeing the immediate need for students, professionals, and other individuals to use the keys and descriptions that will ultimately be published as Flora of Oklahoma, the project's editorial committee chose to release parts of the Flora as they were written. The key to families, titled Key to the Vascular Plants of Oklahoma, appeared in 1994. Three years later the family descriptions appeared in Key and Descriptions for the Vascular Plant Families of Oklahoma. Recent work has led to keys to the genera of all families as well as keys to many species. Numerous individuals have been asked by the committee to contribute their taxonomic expertise by writing treatments for the families, genera, and species. The treatment presented here is one such contribution.

The Salicaceae, or willow family, is traditionally recognized as consisting of the two genera Salix and Populus, although some taxonomists recognize the segregate genera Chosenia, and Toisusu because they differ greatly in pollen grain morphology from Salix and Populus (Argus, 1997). Absent from Australasia and New Guinea, the family is nearly cosmopolitan in distribution; with the majority of its members inhabiting the northern temperate and arctic regions (Watson and Dallwitz, 2000). These dioecious, spring-flowering trees
and shrubs typically inhabit wet or moist habitats throughout their geographic range. In Oklahoma, *Populus* and *Salix* are represented in every county.

Several species are cultivated for their ornamental value. The somewhat weak wood of many species is used as lumber, plywood, pulpwood, paper pulp, boxes, crates, food containers, matchsticks, matchboxes, and furniture stock (Tesky, 1992; Dirr, 1998; Little, 1998; Taylor, 2001). Members of the family commonly provide critical habitat for many wildlife and livestock species (Uchytil, 1989b; Tesky, 1992; Little, 1998; Taylor, 2001). They provide nesting habitat and cover for some nongame wetland bird species, forage for deer and livestock, and wood and shelter for many game birds and small mammals.

The objective of the work summarized in this chapter was to develop an understanding of the morphological circumscription of each species, clarify the nomenclatural history of each taxon, and write morphological descriptions and keys for identification to be incorporated in the *Flora of Oklahoma*. 
METHODOLOGY: PREPARATION OF THE TREATMENT

Preparation of the family treatment began with an extensive literature review. Principal publications examined included those by Stephens (1973), Dorn (1976, 1994, and 1998), Eckenwalder (1977), Correll and Johnston (1979), Argus (1986, 1997), Great Plains Flora Association (1986), Newsholme (1992), Dirr (1998), Little (1998), and Diggs, Lipscomb, and O’Kennon (1999). Loans of specimens from state herbaria were requested (Table 1.1). These specimens were identified using available keys of Gleason and Cronquist (1963), Waterfall (1969), Correll and Johnston (1979), Great Plains Flora Association (1986), and Diggs, Lipscomb, and O’Kennon (1999). All specimens were annotated as a result of this work.

The morphological description of each species was written using DELTA (DEscriptive Language for TAxonomy), a computer program developed by Dallwitz and Paine (1986) that provides a standardized format for taxonomic descriptions. As the borrowed herbarium specimens were examined, a list of characters (each with appropriate states) was compiled in the DELTA format for CHARs (Table 1.2). A corresponding SPECS file was created, in which each character was defined as to type – unordered multistate (UM), ordered multistate (OM), integer numeric (IN), real numeric (RN), and text (TE) (Table 1.3).

The characters and their states of the herbarium specimens of each species were observed or measured, recorded on character data sheets, and subsequently coded in the DELTA format for ITEMS (Table 1.4). As ITEMS was
compiled, CHARS was revised as necessary. A TONAT file (Table 1.5) was used to generate natural language descriptions. These descriptions were subsequently edited in Microsoft Word into the format adopted by the editorial committee; they are presented in the following text. Abbreviation of author names is according to Brummitt and Powell (1992). The paragraphs of informational notes are lengthy for the purposes of this dissertation, but will be condensed by the editorial committee.
Table 1.1 Herbaria from which specimens were borrowed and number of sheets of each taxon examined.

<table>
<thead>
<tr>
<th></th>
<th>P. alba</th>
<th>P. deltiodes</th>
<th>S. amygdaloides</th>
<th>S. caroliniana</th>
<th>S. exigua</th>
<th>S. humulis</th>
<th>S. nigra</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>OKLA</td>
<td>0</td>
<td>54</td>
<td>12</td>
<td>40</td>
<td>42</td>
<td>12</td>
<td>97</td>
<td>257</td>
</tr>
<tr>
<td>OKL</td>
<td>0</td>
<td>167</td>
<td>26</td>
<td>68</td>
<td>91</td>
<td>6</td>
<td>245</td>
<td>603</td>
</tr>
<tr>
<td>CAMU</td>
<td>9</td>
<td>19</td>
<td>0</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>11</td>
<td>49</td>
</tr>
<tr>
<td>NWOSU</td>
<td>0</td>
<td>9</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>7</td>
<td>22</td>
</tr>
<tr>
<td>OCLA</td>
<td>2</td>
<td>27</td>
<td>1</td>
<td>7</td>
<td>19</td>
<td>3</td>
<td>47</td>
<td>106</td>
</tr>
<tr>
<td>DUR</td>
<td>10</td>
<td>41</td>
<td>1</td>
<td>9</td>
<td>15</td>
<td>4</td>
<td>46</td>
<td>126</td>
</tr>
<tr>
<td>NOSU</td>
<td>0</td>
<td>7</td>
<td>1</td>
<td>8</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>22</td>
</tr>
<tr>
<td>CSU</td>
<td>2</td>
<td>13</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>14</td>
<td>38</td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>337</td>
<td>44</td>
<td>142</td>
<td>183</td>
<td>25</td>
<td>469</td>
<td>1223</td>
</tr>
</tbody>
</table>

Zero indicates lack of Oklahoma specimens in loan.

Herbaria acronyms follow Holmgren and Holmgren (2003). OKLA = Oklahoma State University Herbarium in Stillwater, OK; OKL = Robert Bebb Herbarium at the University of Oklahoma in Norman, OK; CAMU = Cameron University Herbarium in Lawton, OK; NWOSU = Northwestern State University Herbarium in Alva, OK; OCLA = University of Science and Arts of Oklahoma Herbarium in Chickasha, OK; DUR = Southeastern Oklahoma State University Herbarium in Durant, OK; NOSU = Northeastern State University Herbarium in Tahlequah, OK; CSU = University of Central Oklahoma Herbarium in Edmond, OK.
Table 1.2 CHARS: a list of characters and their states used in DELTA program to generate taxon descriptions.

*SHOW: Salicaceae DELTA Character List.

*CHARACTER LIST

#1. plants <habit> <MANDATORY>/
  1. trees/
  2. small trees/
  3. shrubs/

#2. plants <vegetative reproduction>/
  1. solitary <implicit>/
  2. colonial by rhizomes/
  3. colonial by layering/

#3. plants <height of trees>/
  m tall/

#4. bark <texture>/
  1. smooth/
  2. rough/
  3. fissured <finely, etc.>/
  4. furrowed <deeply, irregularly, etc.>/

#5. bark <specific color or colors that serve to distinguish the taxon>/

#6. stems <habit>/
  1. erect/
  2. decumbent/

#7. twigs <specific color or colors that serve to distinguish the taxon>/

#8. twigs <presence of indumentum>/
  1. glabrous/
  2. scabrous <rough to the touch with short, hard, rigid trichomes>/
  3. scaberulous <minutely scabrous>/
  4. pubescent <soft, short, dense trichomes>/
  5. puberulent <minutely pubescent>/
  6. velutinous <soft, short, dense, straight trichomes; velvety>/
  7. tomentose <soft, short, dense, matted trichomes>/
  8. villous <soft, long, dense, curly, ascending trichomes>/
  9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
 10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
 11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
 12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
 13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
 14. hispid <stiff, long, tapered, dense or sparse, erect or
ascending, straight trichomes; bristly/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#9. terminal buds <presence of terminal buds>/
1. present/
2. absent/

#10. terminal buds <shape> <Populus only>/
1. oblong/
2. conical/
3. ovoid/
4. lanceolate/
5. irregular/

#11. terminal buds <bud scales; specific color or colors that distinguish the taxon> <Populus only>/

#12. terminal buds <bud scales; presence of indumentum> <Populus only>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/
#13. terminal buds <length> <Populus only>/
   mm long/

#14. lateral buds <shape>/
   1. oblong/
   2. conical/
   3. triangular/
   4. narrowly triangular/
   5. ovoid/
   6. lancelate/
   7. irregular/

#15. lateral buds <bud scales; specific color or color that serves to distinguish the taxon>/

#16. lateral buds <bud scales; presence of indumentum>/
   1. glabrous/
   2. scabrous <rough to the touch with short, hard, rigid trichomes>/
   3. scaberulous <minutely scabrous>/
   4. pubescent <soft, short, dense trichomes>/
   5. puberulent <minutely pubescent>/
   6. velutinous <soft, short, dense, straight trichomes; velvety>/
   7. tomentose <soft, short, dense, matted trichomes>/
   8. villous <soft, long, dense, curly, ascending trichomes>/
   9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
  10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
   11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
   12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
   13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
   14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
   15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
   16. surfaces with glandular trichomes/
   17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
   18. surfaces with barbed trichomes/
   19. strigulose <diminutive of strigose>/
   20. hispidulous <diminutive of hispid>/
   21. hirsutellous <diminutive of hirsute>/

#17. lateral buds <apices>/
   1. apices caudate/
   2. apices acuminate/
   3. apices acute/
   4. apices rounded/

#18. lateral buds <length>/
   mm long/

#19. blades <shape>/
   1. linear/
2. lanceolate/
3. oblanceolate/
4. ovate/
5. obovate/
6. oblong/
7. deltoid/

#20. blades <width>/
    mm wide/

#21. blades <length>/
    mm long/

#22. blade <apices>/
    1. apices acute/
    2. apices acuminate/
    3. apices caudate/
    4. apices obtuse/

#23. blade <margins>/
    1. margins entire/
    2. margins serrate/
    3. margins dentate/
    4. margins revolute/
    5. margins sinuate/
    6. margins crenate/

#24. blade <margins> <number of teeth per cm> <Salix only>/
    teeth per cm/

#25. blade <of simple leaves; bases>/
    1. bases rounded/
    2. bases cuneate/
    3. bases acute/
    4. bases acuminate/
    5. bases cordate/

#26. adaxial surfaces <color or colors that characterize the abaxial surface of blades>/

#27. adaxial surfaces <indumentum of abaxial surfaces of blades>/
    1. glabrous/
    2. scabrous <rough to the touch with short, hard, rigid trichomes>/
    3. scaberulous <minutely scabrous>/
    4. pubescent <soft, short, dense trichomes>/
    5. puberulent <minutely pubescent>/
    6. velutinous <soft, short, dense, straight trichomes; velvety>/
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    8. villous <soft, long, dense, curly, ascending trichomes>/
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   10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
   11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
   12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/

1-10
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes/>
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#28. abaxial surfaces <color or colors that characterize the adaxial surface of blades>/

#29. abaxial surfaces <indumentum of adaxial surfaces of blades>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
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9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#30. basilaminar glands <presence of basilaminar glands>/
1. present <implicit>/
2. absent/

#31. basilaminar glands <number>/

#32. petioles <specific color or colors that serve to distinguish the taxon <Salix only>/

#33. petioles <shape>/
1. terete/
2. flattened perpendicular to blade/

#34. petioles <length>/
m m long/

#35. petioles <presence of indumentum>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#36. stipules <if present, distinctive, general descriptors that serve to characterize the taxon>/

#37. stipules <shape>/
1. linear/
2. lanceolate/
3. oblanceolate/
4. ovate/
5. obovate/
6. elliptic/
7. oblong/
8. reniform/
9. oval/

#38. stipules <length>/
m m long/

#39. stipules <indumentum>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minute/y scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minute/y pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. glandular/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#40. stipules <apices>/
1. apices caudate/
2. apices acuminate/
3. apices acute/
4. apices attenuate/
5. apices rounded/
6. apices obtuse/

#41. stipules <margins>/
1. margins entire/
2. margins serrate/
3. margins serrulate/
4. margins dentate/
5. margins glandular/

#42. catkins <flowering time and leaf development relationship>/
1. flowering before leaves/
2. flowering simultaneous with leaves/
3. flowering after leaves/

#43. catkins <density> <Populus only>/
1. densely flowered <rachis not or partially visible>/
2. moderately flowered <rachis partially visible>/
3. loosely flowered <rachis clearly visible>/

#44. catkins <length of catkins> <Populus only>/
m/m long/
#45. catkins <presence of indumentum on rachis>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#46. catkin bracts <specific color or colors that serve to distinguish the taxon> <Salix only>/

#47. catkin bracts <shape>/
1. ovate/
2. obovate/
3. oblong/
4. oval/
5. flabellate/

#48. catkin bracts <length>/
mm long/

#49. catkin bracts <indumentum>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes/>
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#50. catkin bracts <apices> <Salix only>/
   1. apices caudate/
   2. apices acuminate/
   3. apices acute/
   4. apices attenuate/
   5. apices rounded/
   6. apices inequalateral/

#51. catkin bracts <margins>/
   1. margins entire/
   2. margins erose/
   3. margins ciliate/
   4. margins toothed/
   5. margins fimbriate/

#52. catkin bracts <persistence> <Salix only>/
   1. persistent/
   2. deciduous after flowering/

#53. staminate catkins <catkin and stem relationship> <Salix only>/
   1. sessile on main branches/
   2. borne on leafy lateral branchlets/

#54. staminate catkins <catkin and stem relationship> <length of leafy branchlets> <Salix only>/
   mm long/

#55. staminate catkins <catkin density> <Salix only>/
   1. densely flowered <rachis not or partially visible>/
   2. moderately flowered <rachis partially visible>/
   3. loosely flowered <rachis clearly visible>/

#56. staminate catkins <length> <Salix only>/
   mm long/

#57. pedicels <length of pedicels> <Populus only>/
   mm long/

#58. floral disks <presence of floral disks>/
1. present <implicit>
2. absent

#59. floral disks <width>
   mm wide

#60. stamens <number>

#61. anthers <color of anthers>

#62. anthers <straightness of anthers after dehiscence> <Salix>
   1. straight/
   2. recurved <slightly or strongly>/

#63. anthers <length of anthers> <Salix>
   mm long

#64. filaments <filament indumentum> <Salix>
   1. glabrous/
   2. scabrous <rough to the touch with short, hard, rigid trichomes>/
   3. scaberulous <minutely scabrous>/
   4. pubescent <soft, short, dense trichomes>/
   5. puberulent <minutely pubescent>/
   6. velutinous <soft, short, dense, straight trichomes; velvety>/
   7. tomentose <soft, short, dense, matted trichomes>/
   8. villous <soft, long, dense, curly, ascending trichomes>/
   9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
  10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
  11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
  12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
  13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
  14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
  15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
  16. surfaces with glandular trichomes/
  17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
  18. surfaces with barbed trichomes/
  19. strigulose <diminutive of strigose>/
  20. hispidulous <diminutive of hispid>/
  21. hirsutellous <diminutive of hirsute>/

#65. nectaries on adaxial surfaces <staminate catkins> <whether present on adaxial surface> <Salix only>
   1. present/
   2. absent/

#66. nectaries on adaxial surfaces < staminate catkins> <number on adaxial surface> <if present in 66> <Salix only>
   1. 1/
2. 2/
3. 3/
4. 4/
5. 5/
6. several/

#67. nectaries on abaxial surfaces < staminate catkins> <whether present on abaxial surface> <Salix only>/
   1. present/
   2. absent/

#68. nectaries on abaxial surfaces < staminate catkins> <number on abaxial surface> <if present in 67> <Salix only>/
   1. 1/
   2. 2/
   3. 3/
   4. 4/
   5. 5/
   6. several/

#69. pistillate catkins <catkin and stem relationship> <Salix only>/
   1. sessile on main branches/
   2. borne on leafy lateral branchlets/

#70. pistillate catkins <catkin and stem relationship> <length of leafy branchlets if present> <Salix only>/
   mm long/

#71. pistillate catkins <catkin density> <Salix only>/
   1. densely flowered <rachis not or partially visible>/
   2. moderately flowered <rachis partially visible>/
   3. loosely flowered <rachis clearly visible>/

#72. pistillate catkins <length> <Salix only>/
   mm long/

#73. stipes <length of stipes> <Salix only>/
   mm long/

#74. stigmas <appearance of stigma> <Populus only>/
   1. filiform/
   2. flabellate with fimbriate margin/

#75. stigmas <lobe number per stigma>/
   1. 2-lobed/
   2. 3-lobed/
   3. 4-lobed/

#76. stigmas <persistence>/
   1. persistent after flowering/
   2. deciduous after flowering/

#77. styles <length> <Salix>/
   mm long/

#78. ovaries <shape in longitudinal section>/
1. hemispherical/
2. elliptical/
3. cylindrical/
4. ovoid/
5. obovoid/
6. clavate/
7. pyriform/

#79. ovaries <ovary indumentum>/
1. glabrous/
2. scabrous <rough to the touch with short, hard, rigid trichomes>/
3. scaberulous <minutely scabrous>/
4. pubescent <soft, short, dense trichomes>/
5. puberulent <minutely pubescent>/
6. velutinous <soft, short, dense, straight trichomes; velvety>/
7. tomentose <soft, short, dense, matted trichomes>/
8. villous <soft, long, dense, curly, ascending trichomes>/
9. sericeous <soft, long, dense or sparse, appressed, straight trichomes; silky>/
10. lanate <soft, long, dense, matted, ascending, curly trichomes; woolly>/
11. pilose <soft, long, sparse, ascending, curly or straight trichomes>/
12. arachnoid <soft, very long, dense, thin, loosely entangled trichomes; cobwebby>/
13. hirsute <stiff, long, dense or sparse, erect or ascending, straight trichomes>/
14. hispid <stiff, long, tapered, dense or sparse, erect or ascending, straight trichomes; bristly>/
15. strigose <stiff, long, sharp, bulbous base, dense or sparse, appressed, straight or curved trichomes>/
16. surfaces with glandular trichomes/
17. stellate <trichomes with branches radiating from base or separate hairs aggregated into star-like clusters>/
18. surfaces with barbed trichomes/
19. strigulose <diminutive of strigose>/
20. hispidulous <diminutive of hispid>/
21. hirsutellous <diminutive of hirsute>/

#80. capsules <length>/
mm long/

#81. seeds <per carpel> <when applicable>/
1. 1/
2. 2/
3. 3/
4. 4/
5. 5/
6. 6/
7. 7/
8. 8/
9. 9/
10. 10/
11. 11/
12. numerous/
#82. nectaries on adaxial surfaces <pistillate catkins> <whether present on adaxial surface> 
<Salix only>/
  1. present/
  2. absent/

#83. nectaries on adaxial surfaces <pistillate catkins> <number on adaxial surface> <if present in 83> <Salix only>/
  1. 1/
  2. 2/
  3. 3/
  4. 4/
  5. 5/
  6. several/

#84. nectaries on abaxial surfaces <pistillate catkins> <whether present on abaxial surface> 
<Salix only>/
  1. present/
  2. absent/

#85. nectaries on abaxial surfaces <pistillate catkins> <number on abaxial surface> <if present in 85> <Salix only>/
  1. 1/
  2. 2/
  3. 3/
  4. 4/
  5. 5/
  6. several/

#86. Taxonomy and nomenclature/

#87. Distribution/

#88. Ecology/

#89. Economic and wildlife significance/
Table 1.3 SPECS: characters defined as to type and used in DELTA program to generate taxon descriptions. Um=unordered multistate, OM=ordered multistate, IN=integer numeric, RN=real numeric, TE=text.

*SHOW: Salicaceae DELTA Specifications.

NUMBER OF CHARACTERS 89
MAXIMUM NUMBER OF STATES 21
MAXIMUM NUMBER OF ITEMS 9

CHARACTER TYPES 1-2, OM 3, RN 5, TE 7, TE 10, OM 11, TE 13, RN 14, OM 15, TE 17, OM 18, RN 20-21, RN 24, RN 26, TE 27, OM 28, TE 29, OM 31, IN 32, TE 34, RN 36, TE 38, RN 39, OM 44, RN 46, TE 48, RN 49-50, OM 54, RN 55, OM 56-57, RN 59, RN 60, IN 61, TE 63, RN 66, OM 68, OM 70, RN 71, OM 72-73, RN 75, OM 77, RN 80, RN 81, OM 83, OM 85, OM 86-89, TE

NUMBERS OF STATES 1, 3, 2, 3, 4, 4, 8, 21, 10, 5, 12, 21, 14, 7, 16, 21, 17, 4, 19, 7, 22, 4, 23, 6, 25, 5, 27, 21, 29, 21, 35, 21, 37, 9, 39, 21, 40, 6, 41, 5, 42, 3, 43, 3, 45, 21, 47, 5, 49, 21, 50, 6, 51, 5, 55, 3, 64, 21, 66, 6, 68, 6, 71, 3, 75, 3, 78, 7, 79, 21, 81, 12, 83, 6, 85, 6

IMPLICIT VALUES 2, 1, 30, 1, 58, 1

DEPENDENT CHARACTERS

MANDATORY CHARACTERS
Table 1.4 ITEMS, measurements and observations of specimens coded using CHARs in DELTA program to generate taxon descriptions.

*SHOW: Salicaceae DELTA Items.

*ITEM DESCRIPTIONS

<table>
<thead>
<tr>
<th>Populus &lt;L. Cottonwood&gt;</th>
</tr>
</thead>
</table>
| 1,1 3,5-20 4,1/4<deeply> 5<grayish-white or gray to light brown> 7<orange-brown to olive-brown> 8,7<densely white>/1 9,1 10,1/4 11<reddish-brown or tan to greenish-brown and resinous> 12,8-7<densely white>/1 13,5-15 14,1/6 15<reddish-brown or tan to greenish-brown and resinous> 16,8-7<densely white>/1 18,6-25 19,4/4-7 20,30-100 21,30-95 22,4-1/2-4<sometimes> 23,5/6 25,1-5 26<green to dark green or grayish-green> 27,1 28<white to silver or green to grayish-green> 29,7<densely white>/1 30,1 31,2<often> 33,1/2 34,15-100 35,7<white>/1 42,1 43,1/2 44,20-150 45,8-7/1 47,1-2/5 48,1 3 49,8/1 51,3&4<shallowly>/5 57,0,5-5 58,1 59,0,5-4 60,6-80 74,1/2 75,2/3 78,4<or narrowly ovoid> 79,7/1 80,1,5-18 81,4-12 86<Typically a northern temperate genus of about 35 species, Populus occurs throughout Europe, Asia, tropical Africa, Central America, and North America, of which 11 species are recognized. In Oklahoma, only 2 species are found. Populus is the Latin word for “tree of the people.” Common names of the genus include Aspen, Poplar, and Cottonwood.> 87<In Oklahoma, Populus is represented in every county.> 88<Members of this genus occupy a variety of habitats throughout their distribution in North America. These quick growing trees are often prized for their ornamental value and are easily propagated primarily by using stem cuttings. Many members of the genus are easily susceptible to damage by storms and strong winds, often diminishing their ornamental value. Members of this wind and insect pollinated genus typically flower in early spring.> 89<Populus provides critical habitat for many wildlife species that take advantage of cover and herbage. Many species of Populus are cultivated as ornamental trees and shrubs. The wood is used as lumber, veneer, plywood, fiberboard, pulpwood, paper pulp, boxes, crates, food containers, cutting boards, interior furniture parts, and agricultural implements.> 90,1-21

<table>
<thead>
<tr>
<th>Populus alba &lt;L. White or Silver Poplar/&gt;</th>
</tr>
</thead>
</table>
| 1,1 2,1-2 3,5-20 4,1<cracking or furrowing basally> 5<grayish-white> 7<orange brown to olive brown> 8,7<dense white> 10,3 11<reddish-brown> 12,8-7<dense white> 13,5-8 14,5 15<reddish-brown> 16,8-7<dense white> 18,6-10 19,4 20,35-75 21,40-80 22,4-1 23,5<often 3-5 palmately lobed> 25,1-5<narrowly> 26<green to dark green> 27,1 28<white to silver> 29,7<dense white> 31,2<often> 33,1 34,15-60 35,7<white> 42,1 43,1 44,20-60 45,7-8 47,1-2 48,1-3 49,8 51,3&4<shallowly> 57,0,5-1 59,0,5-1.5 60,6-14 74,1 75,3 78,4<narrowly> 79,7 80,1,5-8 81,4-6 86<P. alba is a morphologically and biologically distinct species whose classification has not been changed since its description by Linnaeus. The common name "abele" is sometimes used in reference to this taxon.> 87>The white poplar is indigenous to central and southern Europe, western Siberia, and central Asia. European immigrants introduced the tree to North America in 1748. The tree has since become naturalized in many parts of the continent including many areas of Oklahoma.> 88<It is an aggressive tree species that can take over portions of natural areas by shading out native vegetation. The species outcompetes many native tree and shrub species because it can grow in a variety of soils, produces large seed crops, and can resprout easily thus forming dense groves that are hard to eradicate. The trees grow best in full sunlight in areas such as fields, forest edges, and the margins of wetlands. Local spread of white poplar is by vegetative means, through root sprouts.> 89>The wood of many Prolars has significant commercial value. It is widely used as a source of pulpwood and for the manufacture of matchsticks, matchboxes, and fruit and flower baskets. Introduced originally as shade and ornamental tree, it now has very little ornamental value due to its susceptibility to a wide variety of pest, insects, and diseases.>
# Populus deltoides <Bartr. ex Marsh. Cottonwood>/
1, 1 3,20-30 4,4<deeply>/5<tan to yellow green when younger, gray to light brown when older>
7<olive-brown to orange-tan> 8,1 10,4 11<tan to greenish-brown, resinous>/12,1 13-15 14,6
15<tan to greenish-brown, resinous> 16,1 18,10-25 19,7 20,30-100 21,30-95 23,6 25,1-5
26<green to grayish green> 27,1 28<green to grayish green> 29,1 31,2<often>/32,3 34,30-100
35,1 42,1 43,3 44,35-150 45,1 47,5 49,1 51,5 57,1-8 59,1-4 60,20-80 61<reddish-brown>/74,2
75,2-3 78,4 80,6-18 81,12 86:<Morophologically variable, the species is divided by some
15<tan to greenish-brown, resinous>/taxonomist into three subspecies on the basis of pedicel length, appearance of leaf apex, and
presence of basilaminar glands. Some taxonomic and nomenclatural confusion has been caused
due to its ability to hybridize with other members of the genus. The binomial synonym P.
sargentii is encountered in historic literature. The common name "Cottonwood" relates to the
11<tan to greenish-brown, resinous>/cottony appearance exhibited by the seeds.>
87:<One of eight species of Populus native to North America, P. deltoides is distributed
throughout the eastern half of the continent with its westernmost expansion reaching the foothills
of the Rocky Mountains. P. deltoides occurs in every county in Oklahoma.> 88:<Germination and
14<1/2>/seed establishment require barren soils. Such requirements have led to the dominance
of floodplains and bottomland hardwood forest. It is not restricted to this habitat and has often been
found in upland habitats as well.> 89:<The wood is used as a source for paper pulp, pallets,
1/2<variously>/crates, and food containers. The inner bark has long been used medicinally for treatment of
1/8<narrowly>/headaches, fevers, and inflammations. The active component is the natural glycoside salicin, a
1/2<variously>/precursor of salicylic acid; which is used in making aspirin. Cottonwoods provide critical habitat
1/11<along midrib>/for many wildlife and livestock species.>

# Salix <L. Willow>/
1,1-3 2,1-2-3 3,1-5-20 4,1/3<finely>/4<irregularly>/5<reddish-brown or gray or light
gray or dark brown to blackish>/6,1/2 7<yellowish-brown to dark brown or light yellow to reddish-
gray or grayish brown or gray>/8,4<gray>/7-8<becoming glabrous>/1 9,2 14,1/2 15<reddish-
brown or yellowish-brown or tan> 16,5/8/1 17,3/4 18,1-4 19,1/2-1< lanceolate>/3-6-5
<narrowly>/20,5-50 21,20-170 22,1/2-3 23,1/2<variously>/24,2-15 25,2/1-3/4 30,2 32<tan or
yellow or yellowish to reddish-brown>/26<shiny dark green or yellow-green or green>
27,1/11<along midrib>/28<glaucous or yellowish to pale green or green>/29,4<densely
short>/1/4<along midrib>/34,1-20 35,7/8/11/1 36<absent or present, in which they are
1/10<narrowly>/persistent on vigorous twigs or minute or caducous>/37,8/4-2 38,1-12 39,4/16/1 40,3/6 41,2/5
42,1/2 45,8<variously>/1<at time of abscission>/46<glaucous or yellow to purple>/47,4-3/1/2
48,1-3.5 49,4/8/11 50,5/3-5 51,1/2 52,1/2 53,1/2 54,2-25 55,1/2 56,10-95 60,2/3-7 61<yellow or
purple>/62,1/2<slightly or strongly>/63,0-4<0.7 64,8/11/1 66,1/2 68,1-6 69,1/2 70,2-40 71,1/3
72,10-100 73,0-5<2.5 75,1/3 76,1/2 77,0-1<0.8 78,7/4<narrowly>/79,4/1 80,3-8 81,10-12 83,1 84,2
86:<Salix is the ancient common name of the willows. Comprising some 400 species of cold and
temperate areas of the northern hemisphere, with few in the southern hemisphere, the genus is
represented by about 90 species in North America and by only six species in Oklahoma.> 87-In
Oklahoma, Salix is represented in every county.> 88<With the exception of S. humilis, members
of the genus most commonly occur in bottomland habitats and wet areas in upland sites. Salix
species require barren soils for germination and seedling establishment. Although willows are
difficult to propagate in quantity by seed, rootstocks of young branches sprout prolifically, making
this the usual method of artificial regeneration.> 89<A variety of wildlife take advantage of cover
and herbage provided by members of the genus. Many species of Salix are cultivated as
ornamental trees and shrubs. The only North American species of any commercial importance is
S. nigra, which is used for furniture stock, boxes, crates, doors, and pulp. Used medicinally for
temperatures as an effective painkiller and treatment for inflammation, the natural glycoside salicin,
the precursor of salicylic acid, was isolated in 1829 from the inner bark of Salix. Today it is the
basic ingredient of aspirin, although the synthesized acetylsalicylic acid is used rather than the
natural form.>

# Salix amygdaloides <Anderss. Peachleaf Willow>/
1,1 3,4-20 4,4<irregularly>/5<dark brown>/6,1 7<gray to light yellow>/8,1 14,2
15<yellowish brown>/16,1 17,3 18,2-5 19,2-4<lanceolate>/20,10-50 21,20-100

1-22
22,2-3 23,2<finely> 24,6-15 26<yellowish-green> 27, 1 28<pale yellow to thickly white glaucous>
29, 1 32<yellowish> 25,2-1 34,5-20 35, 1-?<sparsely, adaxially> 36<, if present, minute and
caducous or sometimes persistent on vigorous twigs> 37,8 38,3-12 70,4-70 73,1-2.5
75,1/3 76,1 77,0.4-0.6 78,7 79,1 80,4-12 81,9 83,1 84,2 86.<The synonyms S. wrightii, S. nigra
var. wrightii, and S. nigra var. amygdaloides are encountered in historical literature.> 87<A native
species, S. amygdaloides is distributed across the continent with the exception of the SE ¼ of the
United States. In Oklahoma, populations are restricted to the western panhandle.> 88<A prolific
seed producer, S. amygdaloides requires barren soils for germination and seed establishment.
Germination is rapid, usually within 12 to 24 hours after dispersal if a moist seedbed is reached.
Adapted to a variety of soil types, S. amygdaloides is characteristically encountered in the moist,
fertile sandy or alluvium soils of riparian areas such as banks of streams and rivers. S.
amygdaloides is characteristic of early stages of succession. The trees are shade intolerant
therefore they persist only along a river's edge where repeated flooding prevents other species
from being established. Because of the soil-binding properties, the species helps stabilize
streambank and protect them from erosion. Flowering occurs in April and May and fruiting
follows in late May and early June.> 89<Like many members of the species, S. amygdaloides
contains the glycoside salicin, a precursor of salicylic acid (aspirin), which has been used
medically for millennia as an effective painkiller and treatment of inflammation. It belongs to a
structurally complex riparian vegetation community that provides an array of habitats and
supports many different species of animals.

# Salix caroliniana <Michx. Carolina Willow>/
1,1 3,1,5-10 4,3<finely> 5<light gray> 6,1 <reddish to grayish-brown> 8,1-4<gray> 14,2
15<reddish-brown> 16,9<sparsely> 17,3 18,1,5-4 19,2 20,7-20 21,50-170 22,2 23,2 24,6-12
25,2-1 26<shiny dark green> 27,1-11<along midrib> 28<thickly, white glaucous> 29,1/4<along
veins> 32<yellowish to reddish-brown> 34,3-8 35,7-11<sparsely, adaxially> 36<persistent on
vigorous twigs> 37,8 38,2-7 39,16<usually, adaxially> 40,6-3 41,2 42,2 45,8-1<at time of
abscission> 46<yellowish> 47,2-1<broadly> 48,1-2 49,8 50,3-5 51,2 52,2 53,2 54,4-25 55,2
56,35-95 60,6<rarely 4 or 5> 61<yellow> 62,1-2<strongly> 63,0.4-0.6 64,11 66,1-2 68,1-2 69,2
70,6-40 71,3 72,45-100 73,1-2 75,1 76,1 77,0.3-0.8 78,7 79,1 80,3-6 81,10-12 83,1 84,2 86.<The
synonyms S. longipes, S. nigra var. longipes, S. wardii, and S. occidentalis are encountered in
historical literature. Closely related to the black willow, S. caroliniana has been known to
hybridize with S. nigra when ranges intersect> 87<A native species, S. caroliniana is found from
south Pennsylvania to south Florida, west to central Texas and north to southeast Nebraska. In
Oklahoma, populations occur in northeast and southeast as well as isolated populations in south­
central and southwest part of the state.> 88<Classified as an obligate wetland species, S.
caroliniana occurs in wet soils of rocky stream banks and other wet areas. Flowering occurs in
late March and April and fruiting typically follows in May.> 89<S. caroliniana provides cover for
birds and small mammals. The wood of this tree is used in making toys, charcoal, and furniture.

# Salix exigua <Nutt. var. interior (Rowlee) Cronq. Sandbar Willow, Coyote Willow>/
1,3 2,2 3,4-6 4,1-3<slightly> 5<gray> 6,1 7<light yellow to reddish-brown> 8,7/8<becoming
glabrous> 14,1 15<reddish-brown> 16,9<becoming glabrous> 17,4 18,1,4 19,1 20,3-10 21,45-
100 22,1 23,<remotely or irregularly> 24,2-5 25,4 26<yellowish-green> 27,1-9<sparsely>
28<yellowish to pale-green> 29,1-9<sparsely> 32<yellowish-brown> 34,1-5 35,1 36<absent>
42,2 45,8<sparsely to densely> 46<yellowish> 47,3-2 48,1,5-3 49,11 50,3-5 51,2 52,2 53,2
54,2-25<1st catkins, 40-180 mm long on later catkins> 55,1 56,20-50 60,2 61<reddish becoming
yellow> 62,2<strongly to slightly> 63,0.4-0.7 64,8 66,2 68,2 71,3 72,35-70 73,0.4-1.5 75,3 76,2
77,0.1-0.2 78,7-4<narrowly> 79,1/9<light silky when mature> 80,5-8 81,12 83,1 84,2 86.<S.
exigua is divided by some taxonomists into a number of varieties on the basis of indumentum
type, leaf shape, and the number of teeth on blade margins. One such variety is S. exigua var.
interior. Although some classifications treat S. exigua and S. interior as separate species, the
classification presented here follows that of Cronquist (1964), Argus (1986) and Dorn (1998) in
which *S. interior* is treated as a variety. Variety *interior*, considered the eastern phase of the *Salix exigua* complex by Argus (1986), differs from variety *exigua*, the western phase, in having leaves that are less densely sericeous, more distinctly toothed, and more conspicuously veined. In addition the catkins are more loosely flowered and capsules longer. The specific epithet, *exigua*, is the Latin term meaning small or short, referring to the usually small size of the plant.> 87<A native species, *S. exigua* is distributed across the western two thirds of the continent. In Oklahoma, populations occur across the state.> 88<*S. exigua* requires barren soils for germination and seed establishment. Unlike the other members of the genus in Oklahoma, *S. exigua* can reproduce vegetatively by sprouting from underground shoot buds in a process called suckering. Characteristic of early seral communities, *S. exigua* is commonly found in association with other members of the family, namely *Populus deltoides* and *Salix nigra*. *S. exigua* is characteristically encountered in the moist, fertile sandy or alluvium soils of riparian areas such as banks of streams and rivers but can occasionally be found in periodically wet areas in upland sites. Flowering can typically occur twice during a growing season, the first in April and May, then again during mid to later times during the summer.> 89<Like many members of the species, *S. exigua* contains the glycoside salicin, a precursor of salicylic acid (aspirin), which has been used medicinally for millennia as an effective pain killer and treatment of inflammation. *S. exigua* is used for erosion control along streambanks, lakeshore, and riparian area development and restoration. A common forage species for deer, *S. exigua* also provides wood and shelter for many game birds.>

# *Salix humilis* **<Marsh. Prairie Willow>/**

1,3 2,3 3,1-3 5<rreddish-brown> 6,2 7<yellowish brown to dark brown> 8,4<gray> 14,1 15<rreddish-brown> 16,5 17,4 18,2-1 19,3-5-6<narrowly> 20,5-20 21,30-85 22,1 23,1-4-2<remotely or irregularly> 24,7-13 25,2 26<shiny dark green> 27,1 28<glaucous> 29,4<densely short> 32<tan> 34,8 35,7/11/8 36<foliaceous on vigorous twigs, minute rudiments, or absent on older twigs> 37,2-3 38,3-7 39,4 40,3 41,2<sparsely> 42,1 45,6<sparsely> 43<dark brown to purple> 47,3-4 48,1-2 49,8 50,5 51,1 52,1 53,1<with 2 or 3 leafy bracts> 55,1 56,10-40 60,2 61<purple> 62,1 63,0-4-0.6 64,1-11<sparsely> 66,1 68,2 71,1 72,10-60 73,0.5-2 75,1/3 76,1 77,0.2-0.4 78,7-4<narrowly> 79,4 80,4-7 81,12 83,1 84,2 86<Some taxonomists recognize two varieties of *S. humilis*, based on leaf shape and abaxial leaf appearance.> 87<A native species, *S. humilis* occurs in southeastern Canada and distributed through the eastern part of the Great Plains, south to Texas. In Oklahoma, populations occur in the southeastern part of the state.> 88<As its common name, "prairie willow" suggests, *S. humilis* is found in upland prairies and savannas, especially in sandy soils.> 89<The species provides cover for small and medium sized mammals and deer and livestock occasionally eat the herbage.>

# *Salix nigra* **<Marsh. Black Willow>/**

1,1 3,2-20 4,<deeply> 5<dark brown to blackish> 6,1 7<r light reddish-brown to dark grayish-brown> 8,1-4 14,2 15<tan> 16,1 17,3 18,1.5-2.5 19,2-1<lanceolate> 20,7-20 21,40-150 22,2 23,2 24,7-13 25,3-2-1 26<green> 27,11-11<sparsely along midrib> 28<green> 29,1-11<sparsely along midrib> 32<yellowish-brown> 34,3-10 35,11<sparsely adaxially> 36<caducous or sometimes persistent on vigorous twigs> 37,4-2 38,1-6 40,3 41,5 42,2 45,6-1<at time of abscission> 46<yellowish> 47,2 48,1-3 49,4 50,3-5 51,1 52,2 53,2 54,4-15 55,2 56,15-70 60,6<rarely 4 or 5> 61<yellow> 62,1-2<strongly> 63,0.4-0.6 64,1 66,1 68,2-3 69,2 70,5-35 71,1 72,30-100 73,0.5-2 75,3 76,1 77,0.2-0.4 78,7 79,1 80,3-5 81,10-12 83,1 84,2 86<Some taxonomists recognize numerous varieties of *S. nigra*, based on petiole length, blade shape, and blade width. *S. nigra* has been known to hybridize with *S. amygdaloides* (*Salix x glattererii* Schneidner) when ranges intersect in other states, although this has not been encountered in collections of Oklahoma.> 87<A native species, *S. nigra* is distributed across the eastern half of the continent. In Oklahoma, populations occur across the state, except for the panhandle.> 88<Along with *Populus deltoides*, *S. nigra* occurs as a codominant in many early seral floodplain communities where it often forms gallery forest with distinct cohorts of different heights. *S. nigra* requires barren soils for germination and seed establishment. Due to the distance that can be traveled by the largely wind dispersed cottony diaspore, it is not restricted to bottomland habitat and has often been found in upland habitats, such as ditches, drainages, and other period wet
areas, where conditions for germination and seedling establishment are favorable. *Salix nigra* is very intolerant of shade. Very susceptible to fire damage, *S. nigra* has the ability to sprout from the base following fire. Flowering occurs in late March and April and fruiting typically follows in May.

Like many members of the species, *S. nigra* contains the glycoside salicin, a precursor of salicylic acid (aspirin), which has been used medicinally for millennia as an effective pain killer and treatment of inflammation. *S. nigra* is the largest and only commercially important willow of about 90 species native to North America. Once used extensively for artificial limbs because of its light weight, the wood holds its shape well and does not splinter. The most common uses of the wood today is for furniture stock, boxes, crates, doors, and pulp. Rated fair in nutritional value, *S. nigra* is a food source for birds, deer, small mammals, and some livestock. *S. nigra*, along with associated species *Populus deltoides*, are commonly used as nesting habitat and cover by some non-game wetland bird species. Honeybees are common spring visitors, obtaining substantial amounts of pollen from flowers.
Table 1.5 TONAT: instructions to generate word descriptions of taxa from CHARS in DELTA program.

*SHOW: Translate into natural language
*HEADING: Salicaceae DELTA
*LISTING FILE TONAT.LST *PRINT FILE TONAT.PRT
*DATA BUFFER SIZE 6000
*INPUT FILE SPECS.TXT
*SPECIAL STORAGE
*TRANSLATE INTO NATURAL LANGUAGE
*OMIT TYPSETTING MARKS
*REPLACE ANGLE BRACKETS
*OMIT CHARACTER NUMBERS
*OMIT INAPPLICABLES

*ITEM SUBHEADINGS

*LINK CHARACTERS 1-3 4-5 7-8 9-13 14-18
19-21 22-25 26-27 28-29 30-31 32-35 36-41
69-72 74-76 78-79 82-83 84-85

*INPUT FILE CHARS.TXT

*PRINT HEADING
*INPUT FILE ITEMS.TXT
TAXONOMIC TREATMENT OF THE SALICACEAE

SALICACEAE C.F.B. de Mirabel Willow Family

Plants trees or shrubs; dioecious. Leaves simple; alternate; venation pinnate; stipules present, persistent or caducous. Inflorescences catkins; axillary; bracts present, small or scale like, often deciduous. Flowers produced before or simultaneously with leaves; imperfect, staminate and pistillate similar; perianths absent or in 1-series. Sepals absent or modified into cup-like disk or 1 or 2 glands. Petals absent. Androecia bilaterally symmetrical. Stamens 1 or 2 to numerous; free or fused by filaments. Pistils 1; compound, carpels 2 or 4; sessile or short stipitate; stigmas 2 or 4, 2-lobed or not lobed; styles short or absent; ovaries superior; locules 1; placentation parietal or rarely basal.

Nectaries absent or present. Fruits capsules. Seeds numerous; comose.

The family is represented in Oklahoma by 2 genera and 7 species. Its distribution is almost cosmopolitan with greatest diversity in north temperate and arctic regions. Ours are typically found in wet or moist habitats. The inner bark of both genera contains the precursor of aspirin and acetametaphin which has been used medicinally for headaches, fevers, and as an anti-inflammatory for thousands of years (Tyrl et al., 2003).

1. Leaves deltoid or ovate. Terminal buds present. Axillary bud scales 3-7. Bract margins fimbriate or laciniate. .......................................................... Populus

1. Leaves lanceolate or falcate or elliptic or linear or oblanceolate. Terminal buds absent. Axillary bud scales 1. Bract margins entire. ................. Salix
Populus C. Linnaeus  Cottonwood

Plants trees; 5-20 m tall. Bark smooth or deeply furrowed; grayish-white or gray to light brown. Twigs orange-brown to olive-brown; densely white tomentose or glabrous. Terminal buds present; oblong or lanceolate; reddish-brown or tan to greenish-brown and resinous; villous to densely white tomentose or glabrous; 5-15 mm long. Lateral buds oblong or lanceolate; reddish-brown or tan to greenish-brown and resinous; villous to densely white tomentose or glabrous; 6-25 mm long. Blades ovate or ovate to deltoid; 30-100 mm wide; 30-95 mm long; apices obtuse to acute or acuminate; margins sinuate or crenate; bases rounded to cordate; adaxial surfaces green to dark green or grayish-green; glabrous; abaxial surfaces white to silver or green to grayish-green; densely white tomentose or glabrous. Basilaminar glands present or absent. Petioles terete or flattened perpendicular to blades; 15-100 mm long; white tomentose or glabrous. Catkins flowering before leaves; densely or moderately flowered; 20-150 mm long; villous to tomentose or glabrous; bracts ovate to obovate or flabellate; 1-3 mm long; villous or glabrous; margins ciliate and shallowly toothed or fimbriate. Pedicels 0.5-8 mm long. Floral disks present; 0.5-4 mm wide. Stamens 6-80. Stigmas filiform or flabellate with fimbriate margins; 3-lobed or 4-lobed. Ovaries ovoid or narrowly ovoid; tomentose or glabrous. Capsules 1.5-18 mm long. Seeds 4 to numerous.

Populus is a Latin word meaning “of the people.” Other common names of the genus are aspen and poplar. Principally a northern temperate genus of about 35 species, Populus occurs throughout Europe, Asia, tropical Africa,
Central America, and North America (Dirr, 1998), where 11 species are recognized (Schreiner, 1974; USDA, 2003). In Oklahoma, only two species occur, but the genus is present in every county (Figure 1.1a-b). Rapid growing, trees are often prized for their ornamental value and are easily propagated, primarily via stem cuttings. They are, however, susceptible to damage by storms and strong winds, which diminishes their ornamental value (Taylor, 2001). Their wood is used for lumber, veneer, plywood, fiberboard, pulpwood, paper pulp, boxes, crates, food containers, cutting boards, interior furniture parts, and agricultural implements (Young and Young, 1992; Dirr, 1998; Taylor, 2001).

*Populus* provides critical habitat for many wildlife species that take advantage of cover provided or consume the herbage (Little, 1998; Taylor, 2001; Tyrl et al., 2002). Members of this wind pollinated genus typically flower in early spring with fruiting and seed dispersal soon following.

1. Leaves ovate; abaxial surfaces white tomentose. Petioles terete. Catkin rachises tomentose. Capsules 3-5 mm long......................... *P. alba*

1. Leaves deltoid; abaxial surfaces glabrous. Petioles flattened. Catkin rachises glabrous. Capsules 15-20 mm long............. *P. deltiodes*

*Populus alba* L. White Poplar, Silver Poplar. Plants trees; solitary to colonial by rhizomes; 5-20 m tall. Bark smooth cracking or furrowing basally; grayish-white. Twigs orange brown to olive brown; densely white tomentose. Terminal buds ovoid; reddish-brown; villous to densely white tomentose; 5-8 mm long. Lateral buds ovoid; reddish-brown; villous to densely white tomentose; 6-10 mm long. Blades ovate; 35-75 mm wide; 40-80 mm long; apices obtuse to acute;
margins sinuate often 3-5 palmately lobed; bases rounded to narrowly cordate; adaxial surfaces green to dark green; glabrous; abaxial surfaces white to silver; densely white tomentose. **Basilaminar glands** 2. **Petioles** terete; 15-60 mm long; white tomentose. **Catkins** flowering before leaves; densely flowered; 20-60 mm long; tomentose to villous; bracts ovate to obovate; 1-3 mm long; villous; margins ciliate and shallowly toothed. **Pedicels** 0.5-1 mm long. **Floral disks** 0.5-1.5 mm wide. **Stamens** 6-14. **Stigmas** filiform; 4-lobed. **Ovaries** narrowly ovoid; tomentose. **Capsules** 1.5-4 mm long. **Seeds** 4 to 6.

*P. alba* is a morphologically and biologically distinct species whose classification has not been changed since its description by Linnaeus. The common name “abele” is sometimes used in reference to this taxon. Indigenous to central and southern Europe, western Siberia, and central Asia, *P. alba* was introduced in North America in 1748 by European immigrants (Dirr, 1998). The taxon has since naturalized in many regions of the continent, including areas of Oklahoma (Figure 1.1a). Because of its ability to grow in a variety of soils, produce large seed crops, and form dense groves via root sprouts, it is an aggressive species that can take over portions of natural areas by outcompeting many native tree and shrub species. When shoots are cut or damaged it resprouts easily, thus making established colonies difficult to eradicate (Glass, 1990; Little, 1998). The trees grow best in full sunlight in fields, at forest edges, and at the margins of wetlands. The wood of *P. alba* has significant commercial value. It is widely used as a source of pulpwood and for the manufacturing of matchsticks, matchboxes, and fruit and flower baskets. Introduced originally as a
shade and ornamental tree, it now has little ornamental value due to its susceptibility to a wide variety of pest, insects, and diseases (Dirr, 1998).

Flowering occurs in March and April, with fruiting and seed dispersal following in late April and May.

*Populus deltoides* Bartr. ex Marsh. Cottonwood, Eastern Cottonwood. Plants trees; 20-30 m tall. Bark deeply furrowed; tan to yellow green when younger gray to light brown when older. Twigs olive-brown to orange-tan; glabrous. Terminal buds lanceolate; tan to greenish-brown resinous; glabrous; 6-15 mm long. Lateral buds lanceolate; tan to greenish-brown resinous; glabrous; 10-25 mm long. Blades deltoid; 30-100 mm wide; 30-95 mm long; apices acuminate to obtuse; margins crenate; bases rounded to cordate; adaxial surfaces green to grayish green; glabrous; abaxial surfaces green to grayish green; glabrous. Basilaminar glands 0-2. Petioles flattened perpendicular to blade; 30-100 mm long; glabrous. Catkins flowering before leaves; loosely flowered; 35-150 mm long; glabrous; bracts flabellate; glabrous; margins fimbriate. Pedicels 1-8 mm long. Floral disks 1-4 mm wide. Stamens 20-80; anthers reddish-brown. Stigmas flabellate with fimbriate margins; 3 to 4-lobed. Ovaries ovoid. Capsules 6-18 mm long. Seeds numerous.

Morphologically variable, the species is divided by some taxonomists into three subspecies on the basis of pedicel length, appearance of leaf apex, and presence of basilaminar glands (Eckenwalder, 1977; Cooper and Van Haverbeke, 1990). Some taxonomic and nomenclatural confusion exists due to its ability to hybridize with other members of the genus (Great Plains Flora
Association, 1986; Dirr, 1998). The synonym *P. sargentii* is encountered in the older literature (Gleason and Cronguist, 1963). The common name “cottonwood” reflects the cottony appearance exhibited by the masses of comose seeds. One of eight species of *Populus* native to North America, *P. deltoides* is distributed primarily throughout the eastern half of the continent, but extends into the southwestern part of the United States (Eckenwalder, 1977; Little, 1979). *Populus deltoides* occurs in every county in Oklahoma (Figure 1.1b). Often forming gallery forests of distinct cohorts of differing heights, *P. deltoides* requires barren soils for germination and seed establishment (Schreiner, 1974). Such requirements result in its codominance with *Salix nigra* in floodplains and bottomland hardwood forests (Cooper and Van Haverbeke, 1990; Tyril et al, 2002). Due to the distance that the wind dispersed seeds can travel, it is not restricted to bottomland habitats and is often found in upland habitats, such as ditches, drainages, and other periodically wet areas, where conditions for germination and seedling establishment are favorable (Taylor, 2001). Although difficult to propagate in quantity by seed, rootstocks of young branches sprout prolifically, making this the usual method of artificial regeneration (Dirr, 1998). Cottonwoods provide important habitat for many wildlife and livestock species. The wood is used for pallets, crates, food containers, and paper pulp (Taylor, 2001). The pulp produces a very high-grade gloss paper (Cooper and Van Haverbeke, 1990). The inner bark has long been used medicinally for treatment of headaches, fevers, and inflammations. The active component is the natural glycoside salicin, a precursor of salicylic acid, which is used in making aspirin.
(2002; Duke 1983). An important component of windbreak plantings in the Great Plains, *P. deltiodes* is frequently used as an ornamental to provide quick, yet rather temporary, esthetic and protective effects (Cooper and Van Haverbeke, 1990). Flowering occurs from early March through April, with fruiting and seed dispersal soon following in mid May through July.

**Salix C. Linnaeus  Willow**

**Plants** shrubs to trees; solitary to colonial by rhizomes or by layering; 1.5-20 m tall. **Bark** smooth or finely deeply or irregularly furrowed; reddish-brown or gray or light gray or dark brown to blackish. **Stems** erect or decumbent. **Twigs** yellowish-brown to dark brown or light yellow to reddish-brown to grayish-brown or gray; gray pubescent or tomentose to villous becoming glabrous or glabrous. **Terminal buds** absent. **Lateral buds** oblong or conical; reddish-brown or yellowish-brown or tan; puberulent or sericeous or glabrous; apices acute or rounded; 1-4 mm long. **Blades** linear or lanceolate to linear-lanceolate or ovate to ovate-lanceolate or oblanceolate to oblong to narrowly obovate; 5-50 mm wide; 20-170 mm long; apices acute or acuminate to caudate; margins entire or variously serrate; 2-15 teeth per cm; bases cuneate or rounded to acute or acuminate; adaxial surfaces shiny dark green or yellow-green or green; glabrous or pilose along midribs; abaxial surfaces glaucous or yellowish to pale green or green; densely short pubescent or glabrous or pubescent or glabrous along midribs. **Basilaminar glands** absent. **Petioles** tan or yellow or yellowish to reddish-brown; 1-20 mm long; tomentose or villous or pilose or glabrous. **Stipules** absent or present, when present persistent on vigorous twigs or minute
or caducous; reniform or ovate to lanceolate; 1-12 mm long; pubescent or glandular or glabrous; apices acute or obtuse; margins serrate or glandular.

**Catkins** flowering before or simultaneous with leaves; variously villous or glabrous at time of abscission; bracts yellowish or dark brown to purple; oval to oblong or ovate or obovate; 1-3.5 mm long; pubescent or villous or pilose; apices rounded or acute to rounded; margins entire or erose; persistent or deciduous after flowering. **Staminate catkins** sessile on main branches or borne on leafy lateral branchlets 2-25 mm long; densely or moderately flowered; 10-95 mm long.

**Stamens** 2 or 3-7; anthers yellow or purple; straight or slightly or strongly recurved; 0.4-0.7 mm long; filaments villous or pilose or glabrous. **Nectaries** on adaxial surfaces 1 to 2; on abaxial surfaces 1 to several. **Pistillate catkins** sessile on main branches or borne on leafy lateral branchlets 2-40 mm long; densely or loosely flowered; 10-100 mm long. **Stipes** 0.5-2.5 mm long. **Stigmas** 2 or 4-lobed; persistent or deciduous after flowering. **Styles** 0.1-0.8 mm long.

**Ovaries** pyriform or narrowly ovoid; pubescent or glabrous. **Capsules** 3-8 mm long. **Seeds** 10 to numerous. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent.

*Salix* is derived from the Celtic word *sallis*, the ancient common name for willows, which is derived from 'sal' meaning 'near', and 'lis' meaning 'water' (Warren-Wren, 1973). A taxonomically confusing genus due to a high degree of morphological variability, *Salix* comprises some 400 species in cold and temperate areas of the northern hemisphere, with only few species in the southern hemisphere (Dorn, 1976; Burnsfeld et al., 1992; Argus, 1997). The
The genus is represented in North America by about 90 species (USDA, 2003) and in Oklahoma by six species, where it is present in every county (Figure 1.1c-g). With the exception of *S. humilis*, members of the genus most commonly occur in bottomland habitats or wet areas in upland sites (Stephens, 1973). Plants require barren soils for germination and seedling establishment (Brinkman, 1974; Pitcher and McKnight, 1990). Although willows are difficult to propagate in quantity by seed, rootstocks of young branches sprout prolifically, making this the usual method of artificial regeneration (Tesky, 1992). A variety of wildlife species take advantage of cover and herbage provided by members of the genus (Uchytil, 1989b; Tesky, 1992; Little, 1998). Many species of *Salix* are cultivated as ornamental trees and shrubs. The only North American species of any commercial importance is *S. nigra*, which is used for furniture stock, boxes, crates, doors, and pulp (Pitcher and McKnight, 1990; Tesky, 1992). Used medicinally for millennia as an effective painkiller and treatment for inflammation, the natural glycoside salicin, the precursor of salicylic acid, was isolated in 1829 from the inner bark of *Salix*. Today it is the basic ingredient of aspirin, although synthesized acetylsalicylic acid is used rather than the natural form (Pitcher and McKnight, 1990; Newsholme, 1992). Members of this wind and insect pollinated genus typically flower in early spring.

1. Plants producing catkins before leaves. Stems decumbent. Staminate and pistillate catkins borne on main stems. Leaves obovate or oblanceolate. .................................................................**S. humilis**

1. Plants producing catkins simultaneously with leaves or after leaves are formed. Stems erect. Staminate and pistillate catkins borne on leafy lateral twigs. Leaves linear or lanceolate or ovate.
2. Leaf surfaces similar, both green; abaxial surfaces not glaucous.

3. Plants trees; not rhizomatous. Leaves lanceolate to linear-lanceolate; margins with 7-13 teeth per cm. Stamens 4-6 ...................... S. nigra

3. Plants shrubs; rhizomatous. Leaves linear; margins with 2-6 teeth per cm. Stamens 2........ S. exigua var. interior

2. Leaf surfaces different; adaxial surfaces green or yellowish green; abaxial surfaces white or whitish green glaucous.


Salix amygdaloides Anderss. Peachleaf Willow. Plants trees; 4-20 m tall.
Bark irregularly furrowed; dark brown. Stems erect. Twigs gray to light yellow; glabrous. Lateral buds conical; yellowish-brown; glabrous; apices acute; 2.5-4 mm long. Blades lanceolate to ovate-lanceolate; 10-50 mm wide; 20-100 mm long; apices acuminate to caudate; margins finely serrate; 6-15 teeth per cm; bases cuneate to rounded; adaxial surfaces yellowish-green; glabrous; abaxial surfaces pale yellow to thickly white glaucous; glabrous. Petioles yellowish; 5-20 mm long; glabrous to sparsely tomentose adaxially. Stipules if present minute and caducous or sometimes persistent on vigorous twigs; reniform; 3-12 mm long; margins serrate. Catkins flowering simultaneous with leaves; densely villous; bracts pale yellow; obovate to oblong; 1.5-3 mm long; villous; apices slightly inequalateral; margins entire; deciduous after flowering. Staminate catkins borne on leafy lateral branchlets 10-20 mm long; moderately flowered; 25-60 mm long. Stamens 3-7; anthers yellow; slightly recurved; 0.5-0.6 mm long;
filaments pilose. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent. **Pistillate catkins** borne on leafy lateral branchlets 4-40 mm long; loosely flowered; 25-70 mm long. **Stipes** 1-2.5 mm long. **Stigmas** 2 or 4-lobed; persistent after flowering. **Styles** 0.4-0.6 mm long. **Ovaries** pyriform; glabrous. **Capsules** 4-12 mm long. **Seeds** 9. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent.

**S. amygdaloides** is sometimes referred to as the almondleaf willow, which more appropriately recognizes the origin of the specific epithet which stems from **Amygdalus**, the genus for almond (Warren-Wren, 1973). The synonyms **S. wrightii**, **S. nigra** var. **wrightii**, and **S. nigra** var. **amygdaloides** are encountered in the older literature. **S. amygdaloides** hybridizes with **S. nigra** (*Salix x glatfferteri* Schnedider) where their distributions overlap (Stephens, 1973; Tesky, 1992); this phenomenon, however, has not been reported in Oklahoma populations. A native species, **S. amygdaloides** is distributed across the continent with the exception of the southeast quarter of the United States (Little, 1971; USDA, 2003). In Oklahoma, populations are restricted to the western end of the Panhandle (Figure 1.1c). A prolific seed producer, germination is rapid, usually 12 to 24 hours after dispersal if a moist seedbed is reached (Brinkman, 1974). Adapted to a variety of soil types, **S. amygdaloides** is characteristically encountered in the moist, fertile sandy or alluvial soils of riparian areas (Froiland, 1962; Dorn, 1977). The tree willow of the Panhandle, it is characteristic of early stages of succession and is usually associated with **Populus deltoides**. Trees are shade intolerant, persisting only along a river’s edge where repeated flooding
prevents other species from being established. Because of its soil-binding properties, the species helps stabilize streambanks and protect from erosion (Uchytil, 1998a). It contributes to the structural complexity of riparian communities and thus provides an array of habitats that support many different species of animals (Stevens and Dozier, 2001). Flowering occurs in April and May and fruiting follows in late May and early June.

**Salix caroliniana** Michx. Carolina Willow. **Plants** trees; 1.5-10 m tall. **Bark** finely fissured; light gray. **Stems** erect. **Twigs** reddish to grayish-brown; glabrous to gray pubescent. **Lateral buds** conical; reddish-brown; sparsely sericeous; apices acute; 1.5-4 mm long. **Blades** lanceolate; 7-20 mm wide; 50-170 mm long; apices acuminate; margins serrate; 6-12 teeth per cm; bases cuneate to rounded; adaxial surfaces shiny dark green; glabrous to pilose along midribs; abaxial surfaces thickly white glaucous; glabrous or pubescent along veins. **Petioles** yellowish to reddish-brown; 3-8 mm long; tomentose to sparsely pilose adaxially. **Stipules** persistent on vigorous twigs; reniform; 2-7 mm long; usually glandular adaxially; apices obtuse to acute; margins serrate. **Catkins** flowering simultaneous with leaves; villous to glabrous at time of abscission; bracts yellowish; obovate to broadly ovate; 1-2 mm long; villous; apices acute to rounded; margins erose; deciduous after flowering. **Staminate catkins** borne on leafy lateral branchlets 4-25 mm long; moderately flowered; 35-95 mm long. **Stamens** 6 rarely 4 or 5; anthers yellow; straight to strongly recurved; 0.4-0.6 mm long; filaments pilose. **Nectaries** on adaxial surfaces 1 to 2; on abaxial surfaces 1 to 2. **Pistillate catkins** borne on leafy lateral branchlets 6-40 mm long.
long; loosely flowered; 45-100 mm long. **Stipes** 1-2 mm long. **Stigmas** 2-lobed; persistent after flowering. **Styles** 0.3-0.8 mm long. **Ovaries** pyriform; glabrous. **Capsules** 3-6 mm long. **Seeds** 10 to numerous. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent.

The synonyms *S. longipes*, *S. nigra* var. *longipes*, *S. wardii*, and *S. occidentalis* are encountered in the older literature (Argus, 1986; USDA, 2003). Closely related to *S. nigra*, *S. caroliniana* has been known to hybridize with it where their ranges intersect in the Gulf Coastal Plains region (Diggs et al., 1999). This phenomenon, however, apparently is not seen in populations of the Ozarks (Argus, 1986). A native species, *S. caroliniana* is found from southern Pennsylvania to southern Florida, west to central Texas, and north to southeastern Nebraska (Little, 1971; Argus, 1986). Populations occur primarily in eastern Oklahoma, with isolated populations in the Arbuckle and Wichita mountains (Figure 1.1d). Classified as an facultative wetland species (Reed, 1988), *S. caroliniana* occurs in wet soils of rocky stream banks and other wet areas. Flowering occurs in late March and April and fruiting typically follows in May.

**Salix exigua** Nutt. var. *interior* (Rowlee) Cronq. Sandbar Willow, Coyote Willow. **Plants** shrubs; colonial by rhizomes; 4-6 m tall. **Bark** smooth to slightly fissured; gray. **Stems** erect. **Twigs** light yellow to reddish-brown; tomentose or villous becoming glabrous. **Lateral buds** oblong; reddish-brown; sericeous becoming glabrous; apices rounded; 1-4 mm long. **Blades** linear; 3-10 mm wide; 45-100 mm long; apices acute; margins remotely or irregularly dentate; 2-6 teeth
per cm; bases acuminate; adaxial surfaces yellowish-green; sparsely sericeous to glabrous; abaxial surfaces yellowish to pale-green; sparsely sericeous to glabrous. **Petioles** yellowish-brown; 1-5 mm long; glabrous. **Stipules** absent. **Catkins** flowering simultaneous with leaves; sparsely to densely villous; bracts yellowish; oblong to obovate; 1.5-3.5 mm long; pilose; apices acute to rounded; margins erose; deciduous after flowering. **Staminate catkins** borne on leafy lateral branchlets 2-25 mm long on 1st catkins and 40-180 mm long on later catkins; densely flowered; 20-50 mm long. **Stamens** 2; anthers reddish becoming yellow; strongly to slightly recurved; 0.4-0.7 mm long; filaments villous. **Nectaries** on adaxial surfaces 2; on abaxial surfaces 2. **Pistillate catkins** loosely flowered; 35-70 mm long. **Stipes** 0.4-1.5 mm long. **Stigmas** 4-lobed; deciduous after flowering. **Styles** 0.1-0.2 mm long. **Ovaries** pyriform to narrowly ovoid; glabrous or long silky sericeous when mature. **Capsules** 5-8 mm long. **Seeds** numerous. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent.

*S. exigua* is divided by some taxonomists into a number of varieties on the basis of indumentum type, leaf shape, and the number of teeth on blade margins. One such variety is *S. exigua* var. *interior*. Although some classifications treat *S. exigua* and *S. interior* as separate species (Burnseld et al., 1992; USDA, 2003), the classification presented here follows that of Cronquist (1964), Argus (1986) and Dorn (1998) in which *S. interior* is treated as a variety. **Variety interior**, considered the eastern phase of the *Salix exigua* complex by Argus (1986), differs from variety *exigua*, the western phase, in having leaves that are less
densely sericeous, more distinctly toothed, and more conspicuously veined. In addition the catkins are more loosely flowered and capsules longer.

The specific epithet *exigua* means small or short, referring to the usually small size of the plants. A native species, *S. exigua* is distributed across the western two-thirds of the continent (Brinkman, 1974; Little, 1971). In Oklahoma, populations occur across the western two-thirds of the state, as well as isolated populations in eastern Oklahoma (Figure 1.1e). Unlike other members of the genus in Oklahoma, the species can reproduce vegetatively by sprouting from underground shoot buds in a process called suckering (Uchytil, 1989b).

Characteristic of early seral communities, *S. exigua* is commonly associated with other members of the family, namely *Populus deltoides* and *Salix nigra*. The species is characteristically encountered in the moist, fertile, sandy or alluvial soils of riparian areas such as banks of streams and rivers, but can occasionally be found in periodically wet areas in upland sites. It is used for erosion control along streambanks, lakeshores, and for development and restoration of riparian areas. A common forage species for deer, *S. exigua* also provides shelter for many game birds (Stevens et al., 2000). Flowering typically occurs twice during the growing season, first in April and May and again mid to late summer.

*Salix humilis* Marsh. Prairie Willow. Plants shrubs; colonial by layering; 1-3 m tall. Bark reddish-brown. Stems decumbent. Twigs yellowish-brown to dark brown; gray pubescent. Lateral buds oblong; reddish-brown; puberulent; apices rounded; 2-5 mm long. Blades oblanceolate to obovate to narrowly oblong; 5-20 mm wide; 30-85 mm long; apices acute; margins entire to revolute to remotely or
irregularly serrate; 7-13 teeth per cm; bases cuneate; adaxial surfaces shiny dark green; glabrous; abaxial surfaces glaucous; densely short pubescent. Petioles tan; 2-8 mm long; tomentose or pilose or villous. Stipules foliaceous on vigorous twigs minute rudiments or absent on older twigs; lanceolate to ovate; 3-7 mm long; pubescent; apices acute; margins sparsely serrate. Catkins flowering before leaves; sparsely villous; bracts dark brown to purple; oblong to oval; 1-2 mm long; villous; apices rounded; margins entire; persistent. Staminate catkins sessile on main branches with 2 or 3 leafy bracts; densely flowered; 10-40 mm long. Stamens 2; anthers purple; straight; 0.4-0.6 mm long; filaments glabrous to sparsely pilose. Nectaries on adaxial surfaces 1; on abaxial surfaces 2.

Pistillate catkins densely flowered; 10-60 mm long. Stipes 0.5-2 mm long.

Stigmas 2 or 4-lobed; persistent after flowering. Styles 0.2-0.4 mm long.

Ovaries pyriform to narrowly ovoid; pubescent. Capsules 4-7 mm long. Seeds numerous. Nectaries on adaxial surfaces 1; on abaxial surfaces absent.

Some taxonomists recognize two varieties of S. humilis, based on leaf shape and abaxial leaf appearance. A native species, it occurs throughout the eastern part of the Great Plains, from southeastern Canada south to Texas (Stevens and Dozier, 2000). In Oklahoma, populations occur in the southeastern part of the state (Figure 1.1f). As its common name “prairie willow” suggests, S. humilis is found in upland prairies and savannas, especially in sandy soils (Stephens, 1973). The species provides cover for birds and small and medium-sized mammals and deer and livestock occasionally eat the herbage (Stevens and Dozier, 2000). Flowering occurs in April and May.
**Salix nigra** Marsh. Black Willow. **Plants** trees; 2-20 m tall. **Bark** deeply furrowed; dark brown to blackish. **Stems** erect. **Twigs** light reddish-brown to darker grayish-brown; glabrous to pubescent. **Lateral buds** conical; tan; glabrous; apices acute; 1.5-2.5 mm long. **Blades** lanceolate to linear-lanceolate; 7-20 mm wide; 40-150 mm long; apices acuminate; margins serrate; 7-13 teeth per cm; bases acute to cuneate to rounded; adaxial surfaces green; glabrous to sparsely pilose along midribs; abaxial surfaces green; glabrous to sparsely pilose along midribs. **Petioles** yellowish-brown; 3-10 mm long; sparsely pilose adaxially. **Stipules** caducous or sometimes persistent on vigorous twigs; ovate to lanceolate; 1-8 mm long; apices acute; margins glandular. **Catkins** flowering simultaneous with leaves; villous to glabrous at time of abscission; bracts yellowish; obovate; 1-3 mm long; pubescent; apices acute to rounded; margins entire; deciduous after flowering. **Staminate catkins** borne on leafy lateral branchlets 4-15 mm long; moderately flowered; 15-70 mm long. **Stamens** 6 rarely 4 or 5; anthers yellow; straight to strongly recurved; 0.4-0.6 mm long; filaments pilose. **Nectaries** on adaxial surfaces 1; on abaxial surfaces 2 to 3. **Pistillate catkins** borne on leafy lateral branchlets 5-35 mm long; densely flowered; 30-100 mm long. **Stipes** 0.5-2 mm long. **Stigmas** 4-lobed; persistent after flowering. **Styles** 0.2-0.4 mm long. **Ovaries** pyriform; glabrous. **Capsules** 3-5 mm long. **Seeds** 10 to numerous. **Nectaries** on adaxial surfaces 1; on abaxial surfaces absent.
Some taxonomists recognize numerous varieties of *S. nigra*, based on petiole length, blade shape, and blade width. *S. nigra* hybridizes both with the closely related *S. amygdaloides* (*Salix x glatfereri* Schnedider) and *S. caroliniana* where their ranges intersect (Argus, 1986). *S. nigra* is the largest and most widespread tree species of the genus. A native species, it is distributed across the eastern half of the continent (Little, 1971; Duncan and Duncan, 1988). In Oklahoma, populations occur across the state, except for the western Panhandle (Figure 1.1g). *Salix nigra* occurs with *Populus deltoides* as a codominant in many early seral floodplain communities where it often forms gallery forests with distinct cohorts of differing heights. Due to the distances that the wind dispersed comose seeds travel, it is not restricted to bottomland habitats and is often found in upland sites such as ditches, drainages, and other periodically wet areas, where conditions for germination and seedling establishment are favorable (Argus, 1986). Very susceptible to fire damage, *S. nigra* has the ability to sprout from the shoot base following fire (Adams et al., 1982). It is the only commercially important willow of the 90 species native to North America (Pitcher and McKnight, 1990). Once used extensively for artificial limbs because of its light weight, the wood holds its shape well and does not splinter. The most common uses of the wood today are for furniture stock, boxes, crates, doors, and pulp (Pitcher and McKnight, 1990; Tesky, 1992). Rated fair in nutritional value, *S. nigra* is a food source for birds, deer, small mammals, and some livestock. Plants are commonly used as nesting habitat and cover by some nongame wetland bird species. Honeybees are common
spring visitors and obtain substantial amounts of pollen from the staminate flowers (Tesky, 1992). Flowering occurs in late March and April with fruiting and seed dispersal following in May.
Figure 1.1 County distribution maps of Salicaceae in Oklahoma based on herbaria collections. a) *Populus alba*, b) *P. deltiodes*, c) *Salix amygdaloides*, d) *S. caroliniana*, e) *S. exigua*, f) *S. humilis*, g) *S. nigra*. 

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CHAPTER 2

MOLECULAR SYSTEMATIC INVESTIGATIONS OF ECHINACEA
(ASTERACEAE: HELIANTHEAE) BASED ON NUCLEAR RIBOSOMAL
ITS AND ETS SEQUENCES

INTRODUCTION

Described by Conrad Moench in 1794 Echinacea is a North American
genus comprising 4–9 species. It is distributed primarily in the Midwest (Figure
2.1). Taxonomists differ in their opinions as to its position in the Asteraceae
(Snyder, 1991; Baskin et al., 1993). Using only morphological characters, Cox
and Urbatsch (1990) and Bremer (1994) classify the genus in the subtribe
Rudbeckiinae. Related genera of the tribe include Rudbeckia, Ratibida, and
Dracopsis. In contrast, Urbatsch and coworkers (2000) using chloroplast DNA
restriction site data, suggested Echinacea to belong in the Zinniinae. Related
genera of this tribe are Heliopsis, Sanvitalia, and Zinnia.

Likewise, there are differences of opinion as to the number of species. In
the last 40 years, taxonomists have followed the classification scheme of Ronald
L. McGregor (1968) or Arthur Cronquist (1955, 1980); both of whom based their
systems on morphological characters. McGregor recognized nine species and
four varieties, whereas Cronquist circumscribed only four species and four
varieties (Table 2.1). Binns and coworkers (2002a) recently proposed a revision
of the genus based on a morphometric analysis. The results of their work agree
with the scheme of Cronquist except for their recognition of E. pallida var.
tennesseensis as a distinct variety rather than an eastern outlier of E. pallida var. angustifolia as proposed by Cronquist (Table 2.1).

Advances in molecular biology, especially in the techniques of sequencing DNA, now permit from a molecular perspective an examination of the taxonomic position of Echinacea in the family and the relationship of its species. Thus the objective of this study was to construct a phylogeny of the genus using nucleotide sequence data from the internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of nuclear ribosomal DNA (nrDNA) to examine the monophyly and circumscription of Echinacea and its species, and possibly provide evidence in support of the classification proposed by McGregor (1968), Cronquist (1955, 1980), or Binns and coworkers (2002a). I present here an analysis of DNA sequences from the nine species recognized by McGregor (1968) and from six related genera in the Asteraceae.
Figure 2.1. Distribution of *Echinacea* Moench in North America (McGregor, 1968; Binns et al., 2002)
Table 2.1. Taxonomic treatments of *Echinacea* Moench. Synonyms are indented and placed in brackets.

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<td><em>E. pallida</em> (Nutt.) Nutt.</td>
<td><em>E. pallida</em> (Nutt.) Nutt. var. <em>pallida</em></td>
<td><em>E. pallida</em> (Nutt.) Nutt. var. <em>pallida</em></td>
</tr>
<tr>
<td><em>E. sanguinea</em> Nutt.</td>
<td>[E. <em>sanguinea</em> Nutt.]a</td>
<td><em>E. pallida</em> var. <em>sanguinea</em> (Nutt.) K.N.Gandhi &amp; R.D.Thomas</td>
</tr>
<tr>
<td><em>E. angustifolia</em> DC. var. <em>angustifolia</em></td>
<td></td>
<td><em>E. pallida</em> (Nutt.) Nutt. var. <em>angustifolia</em> (DC.) Cronquist</td>
</tr>
<tr>
<td><em>E. atrorubens</em> Nutt.</td>
<td><em>E. atrorubens</em> Nutt. var. <em>atorubens</em></td>
<td><em>E. atrorubens</em> Nutt. var. <em>atorubens</em></td>
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<tr>
<td><em>E. laevigata</em> S.F. Blake</td>
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<td><em>E. purpurea</em> (L.) Moench</td>
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*a* Suggested that plants might be formally recognized as a variety, but was not doing so at this time.

*b* Suggested that plants formerly recognized as *E. tennesseensis* are merely eastern outliers.
METHODS AND MATERIALS

The ITS and ETS regions are part of the 18S-26S nrDNA multigene family which includes the 18S, 5.8S, and 26S subunits. This multigene family is highly repeated in the plant nuclear genome, allowing for a high level of detection, amplification, cloning, and sequencing of nrDNA (Baldwin et al., 1995).

ITS is one of the most widely used sources of characters for phylogenetic studies of closely related plant taxa. Many of the present-day phylogenies, at least at the family and genus level, use nuclear sequences based on ITS (Savard et al., 1993; Sang et al., 1995a; Bayer et al., 1996; Bena et al., 1998; Prather and Jansen, 1998). Illustrative of this are recent publications presenting data attempting to resolve the phylogeny of many members of the Asteraceae (Baldwin et al., 1995; Sang et al., 1995b; Urbatsch and Jansen, 1995; Urbatsch et al., 2000).

The popularity of the ITS and ETS regions can be attributed to the relatively high rate of nucleotide substitution resulting in rapid sequence evolution. This allows for systematic comparison of relatively recently diverged taxa (Liston et al., 1996; Moritz and Hillis, 1996). Using these gene regions offers increased phylogenetic precision over that of restriction site mapping techniques typical of studies incorporating chloroplast DNA (Baldwin et al., 1995).

The ITS comprises two regions, ITS-1 and ITS-2, located on either side of the 5.8S subunit, which exhibits very low levels of sequence variation (Figure 2-5).
2.2). An appealing aspect of using ITS is that this region can be readily polymerase chain reaction (PCR) amplified and sequenced using universal primers. A limiting factor in using ITS to examine angiosperm phylogeny is that it provides a small amount of sequence data. Baldwin and coworkers (1995) report ITS region as varying from 565-700 base pairs (bp) in length, although I have encountered sequences as long as 900 bp. Excluding the 5.8S nrDNA region (163-165 bp), about 400-700 bp of ITS-1 and ITS-2 are phylogenetically informative.

Until recently, most of the nrDNA data used in phylogenetic studies involved only ITS, and the phylogenetic utility of ETS was relatively unexplored, with the exception of few plant groups (Andreasen and Baldwin, 2001). ETS is part of the larger intergenic spacer (IGS), which also includes the nontranscribed spacer (NTS) (Figure 2.2). ETS is longer than ITS-1 and ITS-2 combined, with products varying between 800 and 1,900 bp in length for members of the Asteraceae (Linder et al., 2000). Its also appears to have the similar rapid evolution characteristic of the ITS region. Comparisons of ITS and ETS sequence data in the Calycadenia/Osmadenia complex by Baldwin and Markos (1998) suggested the evolutionary rate in ETS is 1.3 to 2.4 times faster than that of ITS. They concluded that ETS fulfills the need for additional nucleotide characters to augment the small number of sites present in ITS and predicted that ETS will prove useful in increasing resolution and support for nrDNA-based phylogenies. This has recently been the case in a number of phylogenetic studies involving members of the Asteraceae that incorporate sequence data
from the two gene regions, e.g., Clevinger and Panero (2000); Linder and coworkers (2000); Chan and coworkers (2002); Lee and coworkers (2002); and Markos and Baldwin (2002).

The major disadvantage of using ETS sequence data involves the amplification process. Exhaustive efforts to construct universal primers for ETS amplification by Baldwin and Markos (1998) and Linder and coworkers (2000) have yielded substantial primer possibilities for amplification of the ETS region over a wide range of taxa. Finding the best fitting primer for the taxa in question is a tedious process; one which this investigator was not spared.

**Taxa Sampled.** Seventeen taxa were examined in this study—the 11 taxa of *Echinacea* recognized by McGregor (1968), and 6 outgroup species (Table 2.2). Only one specimen of each taxon was used. The outgroup species are representative of the Rudbeckiinae and Zinniinae, the two subtribes in which *Echinacea* has been positioned (Cox and Urbatsch, 1990; Bremer, 1994; and Urbatsch et al., 2000). With the exception of *Sanvitalia fruticosa*, all of the outgroup taxa are native to North America north of Mexico and are typically found associated with species of *Echinacea*. *Sanvitalia fruticosa* is a Mexican and Central American genus of about seven species (Bremer, 1994).

**Genomic DNA Extraction.** Established molecular techniques were used to extract total genomic DNAs from the taxa (Table 2.2). Quality DNA was extracted from leaves of herbarium material (20–40 mg), silica gel dried leaf material (20–40 mg), and fresh material (approximately 100 mg). Many of the ITS regions of taxa were isolated using the 2X CTAB protocol of Doyle and Doyle.
(1987), whereas the ETS region of all taxa were isolated using plant DNA extraction kits—DNeasy Plant Mini Kit (Qiagen, Clarita, CA) and REDExtract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St. Louis, MO).

Sequences of ITS-1 and ITS-2 for *Zinnia grandiflora* (ZGU74397 and ZGU74446), *Heliopsis helianthoides* (HHU73154 and HHU74424), and *Sanvitalia fruticosa* (SFU74394 and SFU74443 were obtained from GenBank®.

**Polymerase Chain Reaction.** Total genomic DNA (template DNA), primers, and the ready-to-use solutions—*Taq* PCR Master Mix (Qiagen, Clarita, CA) and REDExtract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St. Louis, MO)—were used in the amplification of the ITS and ETS regions by the polymerase chain reaction (PCR). Appropriate primers were obtained from Integrated DNA Technologies (IDT, Coralville, IA). Primers ITS4 (5'-TCCTCCGCTTATTGATATGC-3') and ITS5 (5'-GGAAGTAAAAGTCGTAACAAGG-3') designed by White and coworkers (1990), were used in the amplification of the ITS region. PCR was conducted in a 9600 Perkin-Elmer thermal cycler using a modified protocol of Clevinger and Panero (2000). This protocol involved an initial denaturation of 95°C for 4 minutes followed by 33 cycles of 95°C for 45 seconds (denaturation), 48°C for 45 seconds (annealing of primers), and 72°C for 1 minute. The reaction was terminated with an 8-minute primer extension at 72°C and then held at 4°C.

Primers 18S-ETS (5'-ACTTACACATGCATGGCTIAATCT-3') and ETS-Hel-1 (5'-GCTCTTTGTCGTCGAACCACT-3') (Baldwin and Markos, 1998) were used for amplification of the ETS region. PCR was conducted in a PTC-0150 Mini Cycler (MJ Research Inc., Waltham, MA) using the protocol of Baldwin and
Markos, (1998). This protocol involved an initial denaturation of 97°C for 1 minute followed by 40 cycles of 97°C for 10 seconds (denaturation), 55°C for 30 seconds (annealing of primers), and 72°C for 20 seconds, and concluding with 72°C for 7 minutes (for completion of primer extension). The final product was held at 4°C.

**Sequencing and Sequence Alignment.** ITS nucleotide sequences of PCR products were determined using automated cycle-sequencing and an ABI Prism 377 DNA Sequencer (Perkin-Elmer Applied Biosystems, Foster City, CA) at the University of Oklahoma. The sequences were assembled and edited using Sequencer™ 4.0 (Gene Codes Corp., Ann Arbor, MI).

All sequences were aligned using the program Clustal X (Thompson et al., 1997) with default settings. Afterwards it was necessary to make some manual adjustments to the alignment.

Sequences from this study that are new to science were submitted to GenBank® using the protocols of the National Center for Biotechnology Information.

**Phylogenetic Analyses.** Sequences were imported into PAUP* 4.0 (Swofford, 2002), from which phylogenies were generated. Characters were equally weighted and their states were unordered. Parsimony analyses were carried out with gaps treated as missing data, and heuristic tree search options included RANDOM sequence addition for 500 replicates—each of which held 10 trees—, following tree bisection-reconstruction (TBR) branch swapping, MulTrees on, and steepest descent off.
Bootstrap analyses of 500 replicates were conducted to measure relative support for clades (Felsenstein, 1985); heuristic tree search options were simple sequence addition, TBR branch swapping, MulTrees on, and steepest decent off. In bootstrap analysis, multiple randomized matrices are constructed from the data by a random sampling of characters with replacement of the characters. From these matrices, most-parsimonious trees are constructed and used to form a consensus tree. The bootstrap values given indicate a 50% or higher representation of a branch in the parsimonious trees produced. Only those branches that receive a 50% or higher value are retained in the consensus tree, all others are collapsed (Judd et al., 2002).

To further evaluate the relative robustness of clades found in the most parsimonious trees, decay index values were determined. The decay value indicates how many extra steps are required to find a tree without a particular branch or clade. So the higher the decay value, the more robust a particular clade (Donoghue et al., 1992).

Robustness and topology of the trees were evaluated using the consistency index (Cl), the retention index (RI), and the rescaled consistency index (RC). The consistency index measures homoplasy by dividing the minimum amount of evolutionary steps by the actual tree length. Cl falls between 0 and 1. The lower the Cl value, the more characters contradict the evolutionary tree (Wiley et al., 1991). In other words, the closer to one the better the topology. The retention index differs in that it accounts for multiple independent origination events for derived characters. This index equals the
maximum tree length minus the actual tree length, divided by the maximum length minus the minimum length (Judd et al., 2002). Not all characters may be contributing to the tree topology (e.g. autapomorphies). In cases like this the CI may be an overestimate. This may be overcome by calculating a rescaled consistency index (RC), sometimes referred to in the literature as “CI excluding uninformative characters.” The RC is simply calculated by multiplying the CI and RI. All three of these indices are indicators of the validity of the tree produced.
Figure 2.2. Structure of 18S-26S nrDNA multigene family (not drawn to scale). Taken from Markos and Baldwin (2002).
Table 2.2. Taxa examined, sources of leaf material, preparation methods, and DNA extraction methods. Classification follows McGregor (1968). Herbaria acronyms follow Holmgren and Holmgren (2003)

<table>
<thead>
<tr>
<th>Taxa</th>
<th>ITS</th>
<th>Leaf Source / DNA Extraction Method</th>
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</thead>
<tbody>
<tr>
<td><em>Echinacea angustifolia</em> DC. var. <em>angustifolia</em></td>
<td>OKL / CTAB(^a)</td>
<td>Fresh / DNeasy</td>
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<tr>
<td><em>Echinacea angustifolia</em> DC. var. <em>strigosa</em> R.L. McGregor</td>
<td>SiGel / CTAB</td>
<td>Fresh / XNAPS</td>
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<td><em>Echinacea atrorubens</em> Nutt.</td>
<td>OKLA / CTAB</td>
<td>Fresh / XNAPS</td>
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<td><em>Echinacea laevigata</em> S.F. Blake</td>
<td>MO / CTAB</td>
<td>KANU / DNeasy</td>
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<td><em>Echinacea pallida</em> (Nutt.) Nutt.</td>
<td>MO / CTAB</td>
<td>KANU / DNeasy</td>
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<td><em>Echinacea paradoxa</em> (J.B.S. Norton) Britt. <em>paradoxa</em></td>
<td>OKL / CTAB</td>
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<td><em>Echinacea purpurea</em> (L.) Moench</td>
<td>MO / CTAB</td>
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<td><em>Echinacea sanguinea</em> Nutt.</td>
<td>MO / CTAB</td>
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<td><em>Echinacea simulata</em> McGregor</td>
<td>MO / CTAB</td>
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<td><em>Echinacea tennesseensis</em> (Beadle) Small</td>
<td>MO / CTAB</td>
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<td><em>Dracopis amplexicaulis</em> (Vahl) Cass.</td>
<td>SiGel / CTAB</td>
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<td><em>Heliopsis helianthoides</em> Sweet</td>
<td>GenBank(^\circ)</td>
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<td><em>Ratibida columnifera</em> (Nutt.) Wooton &amp; Standl.</td>
<td>SiGel / CTAB</td>
<td>Fresh / XNAPS</td>
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<td><em>Rudbeckia hirta</em> L.</td>
<td>SiGel / CTAB</td>
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<td><em>Sanvitalia fruticosa</em> Hemsl.</td>
<td>GenBank(^\circ)</td>
<td>KANU / DNeasy</td>
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<tr>
<td><em>Zinnia grandiflora</em> Nutt.</td>
<td>GenBank(^\circ)</td>
<td>KANU / DNeasy</td>
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</table>

\(^a\) DNA extracted without regard for variety represented.

OKL: Robert Bebb Herbarium, University of Oklahoma, Norman
OKLA: Oklahoma State University, Stillwater
MO: Missouri Botanical Garden, St. Louis
KA\(\text{\textdegree}\)NU: R.L. McGregor Herbarium, University of Kansas, Lawrence

GenBank\(^\circ\): sequences acquired from GenBank
SiGel: silica gel dried leaf material
Fresh: fresh leaf material
CTAB: 2X CTAB protocol of Doyle and Doyle (1987)
DNeasy: DNeasy Plant Mini Kit (Qiagen, Clarita, CA)
XNAPS: REDExtract-N-Amp\(^\text{TM}\) Plant PCR Kit (Sigma-Aldrich, St. Louis, MO)
RESULTS

ITS—Genomic DNA Extraction. High-quality DNA was extracted from the ITS region of all ingroup taxa and three of the six outgroup taxa (Dracopis amplexicaulis, Ratibida columnifera, and Rudbeckia hirta), in the spring of 2001. It should be noted that not all taxa recognized by McGregor (1968) were included as part of the ingroup taxa. DNA was extracted from Echinacea angustifolia without regard for the variety represented (i.e. var. angustifolia and strigosa). Also, DNA from E. laevigata was not obtained because of its limited availability due to its federally threatened status (U.S. Fish & Wildlife Service, 1999). Herbarium material of E. laevigata has since been acquired but difficulty in extracting quality DNA for PCR amplification has hindered the efforts of including the species in this molecular systematic study up to now.

ITS—PCR, Sequencing, and Sequence Alignment. Primers ITS4 and ITS5 provided quality PCR amplification of the ITS region. Amplification of the 18S-26S nrDNA ITS region (ITS-1, 5.8S, and ITS-2 combined) and subsequent alignment resulted in an average fragment length of 867 base pairs (ranging from 804 bp in Ratibida columnifera to 918 bp in E. tennesseensis) for all taxa studied (Table 3). This included 165 bp for the 5.8S subunit. Proper alignment of ITS-1 and ITS-2 sequences required the introduction of minimal gaps for most taxa, resulting in the total of 743 sites (414 for ITS-1, 329 for ITS-2).

ITS—Phylogenetic Analyses. Of the 918 characters, 647 were constant. The number of parsimony uninformative characters (autapomorphies) was 136, and the number of parsimony informative characters (synapomorphies) was 135.
The heuristic search of ITS sequences resulted in two most parsimonious trees requiring 416 evolutionary steps (a.k.a. tree length). The consensus tree, with a consistency index (CI) of 0.803, a retention index (RI) of 0.733, and a rescaled consistency index (RC) of 0.588, is presented in Figure 2.3. Support for the *Echinacea* clade—using bootstrap values—was very strong (100%) while infrageneric branches were very weakly supported (56, 61, 52%).

**ETS—Extraction.** Numerous unsuccessful attempts were made to amplify the ETS region of the 17 taxa. PCR product was obtained from only six: *E. atrorubens*, *E. paradoxa* var. *paradoxa* and var. *neglecta*, *S. fruticosa*, *Rudbeckia hirta*, and *Ratibida columnifera*. Because PCR product from the remaining taxa was not obtained, these six were not sequenced and included in the phylogenetic analysis. Inability to obtain amplified ETS product is most likely attributed to the existence of phenolics and polysaccharides in the 11 taxa. These compounds are known inhibitors in extraction techniques (Michael Berg, Gnanambal Naidoo, personal communication; Couch and Fritz, 1990; Rether et al., 1993; Savolainen, 1995, and Buldewo and Jaufeerally-Fakim, 2002.)
DISCUSSION

Phylogenetic analysis of the ITS region for *Echinacea* has generated a well-supported cladistic hypothesis for the placement of the genus in the Zinniinae as suggested by Urbatsch and coworkers (2000) (Figure 2.3). *Echinacea* is monophyletic with 100% bootstrap support. This is supported by studies of Urbatsch and Jansen (1995) and Urbatsch and coworkers (2000) who looked at the phylogenetic affinities among the coneflower genera of the Asteraceae based on chloroplast DNA and ITS sequences.

The relationships among species of the genus, however, are not well defined. In this thesis, I had hoped to elucidate the relationships and provide evidence in support of one of the previously published treatments. ITS data by themselves do not provide overwhelming support for any of the three classification schemes. Low levels of intrageneric ITS variation illustrated by very small branch lengths—some as low as zero—as well as decay values of one, preclude detailed phylogenetic inferences and any consideration of classification would be premature until better resolution can be provided by complementary data (such as ETS). A number of observations can be drawn from the topology produced using only ITS data. They are the following with the caveat that they lack the traditional strong support associated with such analyses.

1. Representing the most basal taxon in the *Echinacea* clade and noticeably distant from the other species of the genus, the federally threatened
Echinacea tennesseensis appears to be a distinct taxon as recognized by McGregor (1968) (Figure 2.3). It does not appear to be an eastern outlier of E. angustifolia as suggested by Cronquist (1980) or a variety of E. pallida as proposed by Binns and coworkers (2002a). Work by Baskauf and coworkers (1994) on the relative genetic variability of E. tennesseensis and E. angustifolia revealed that E. tennesseensis has substantially less genetic variability than its widespread prairie relative, at both the species and population levels. My results agree with their observations.

2. The taxon recognized as E. paradoxa var. paradoxa by McGregor and E. atrorubens var. paradoxa by Binns and coworkers (2002a) appears to be a distinct taxon not related to other members of either species (Figure 2.3). Baldwin (1993) noted that useful phylogenetic information can be derived at the intraspecific level using ITS sequences. If this is indeed the case, one would expect these two varieties to be in the same clade. My ITS data also are supported by ecological and morphological differences. Restricted to the prairies and open wooded hillsides of the Arbuckle Mountains of southern Oklahoma, Echinacea paradoxa var. neglecta has the rose-colored ray florets typical of other members of Echinacea. In contrast, var. paradoxa is endemic to the west-central and southern portions of the Ozark Plateau in Missouri and Arkansas is the only member of the genus with yellow ray florets. Work done by Urbatsch and Jansen (1995) has provided chloroplast DNA data that suggests that the yellow pigmented rays unique to var. paradoxa are autapomorphic rather than pleisomorphic.
3. Cronquist's and Binns and coworkers' recognition of *E. pallida* with four varieties is not supported by the topology generated in this study (Figure 2.3). Only var. *pallida* and var. *angustifolia* show a close relationship. Interestingly, they are sister taxa to the morphologically quite different *E. purpurea*.

4. Likewise, Cronquist's and Binns and coworkers' recognition of *E. atrorubens* with three varieties is not supported by the topology (Figure 2.3). As noted above variety *paradoxa* pairs with *E. pallida* var. *simulata* and is quite different from both *E. paradoxa* and *E. atrorubens*. Variety *atrorubens* pairs with *E. pallida* var. *sanguinea*; and var. *neglecta* pairs with *E. purpurea*, and *E. pallida* var. *pallida* and var. *angustifolia*.

5. My ITS data provide support for the hypothesis of Binns (2001) that the parents of tetraploid (2n = 44) *E. pallida* included one or more taxa from a complex that comprises *E. atrorubens*, *E. paradoxa* var. *paradoxa*, and var. *neglecta*. Sharp (1935), McGregor (1968) Binns (2001) believed *Echinacea pallida* to be the most recently derived taxon of the genus, albeit they differed in their opinions as to its origin. McGregor (1968) hypothesized that its origin was the result of stabilized introgression of an allopolyploid hybrid between *E. sanguinea* and *E. simulata*. Binns combined phytochemical, morphological, and geographical data in her hypothesis.

Future work will be an examination of the relationship among *E. purpurea*, *E. angustifolia*, and *E. pallida*, which have been touted for their putative medicinal benefits (Li, 1998; Sari et al., 1999). My ITS results suggest these three species are sister taxa (Figure 2.3). An interesting question is whether genetic material
from the 18S-26S nrDNA multigene family might code for the properties that have led the medicinal popularity of the genus. Numerous publications (Bauer and Wagner, 1985; Bauer et al., 1988; Bailey et al., 1999; Letchamo et al., 1999; Binns et al., 2000a; Binns et al., 2000b; Binns et al., 2000c) have cited phytochemicals such as phenolics, polysaccharides, and caffeic acid derivatives as the sources of Echinacea’s medicinal properties. The use of the germplasm of Echinacea species to predict quantitative phytochemical markers is being evaluated by Benard Baum and his colleagues at the Eastern Cereal & Oilseed Research Center in Ottawa, Ontario (Baum and Binns; 1999; Baum et al.; 2001). Future collaborations with this group may prove to be beneficial in achieving my goals.

I intend to continue my efforts to extract quality DNA and PCR product from the 11 taxa from which ETS sequences were not attained. I plan to employ the techniques of Couch and Fritz (1990), Rether and coworkers (1993), Savolainen (1995), and Buldewo and Jaufeerally-Fakim (2002). Once all ETS sequences are obtained and aligned, another phylogenetic analysis using both ETS and ITS data will be conducted. Results will hopefully elucidate relationships among the species and provide information on the relationship of Echinacea to other members of the family.
Table 2.3. Aligned matrix of DNA sequences (5' to 3') of ITS region of ingroup and outgroup taxa. ITS1, 1–414; 5.8S, 415–579; and ITS2, 580–918

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E. atrorubens  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAACACTAGTGGGC-TTT
E. pallida  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
E. paradoxa var. neglecta  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
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E. sanguinea  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
E. simulata  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
E. tennesseensis  ATCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
Dracopis amplexicaulis  ACCCTGCAAAGCAGAACGACTTGTGAACAAGTAAAAACAACTGGTC-TTT
Heliopsis helianthoides  -ACAACCCGTGAACATGTAAAA-CTATTGGCC-TTG
Ratibida columnifera  ACCCTGCATAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
Rudbeckia hirta  AACCTGCCTAGCAGAACGACCCGTGAACATGTAAAAACTACTGGCC-TTT
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E. atrorubens  CAGGGACCGAAGCA--TTTGTTTTCGAGCCTTGTGAGGCCTTGTT-GACGA
E. pallida  CAGGGACCGAAGCA--TTTGTTTTCGAGCCTTGTGAGGCCTTGTT-GACGA
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Sanvitalia fruticosa  CAGGGACCGAAGCA--TTTGTTTTCGAGCCTTGTGAGGCCTTGTT-GACGG
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E. pallida  GCATTCATGTCTTGGCTCTCT-CAGGGGACATCATGTGTGCTCTGTTGACAC
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E. purpurea  GCATTCATGTCTTGGCTCTCT-CAGGGGACATCATGTGTGCTCTGTTGACAC
E. sanguinea  GCATTCATGTCTTGGCTCTCT-CAGGGGACATCATGTGTGCTCTGTTGACAC
E. simulata  GCATTCATGTCTTGGCTCTCT-CAGGGGACATCATGTGTGCTCTGTTGACAC
E. tennesseensis  GCATTCATGTCTTGGCTCTCT-CAGGGGACATCATGTGTGCTCTGTTGACAC
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Heliopsis helianthoides  GTGTCATGTCTTGGCTCTCT-TGGACATCATGTGTGCTCTGTTGACAC
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Rudbeckia hirta  GTGTCATGTCTTGGCTCTCT-TGGACATCATGTGTGCTCTGTTGACAC
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Figure 2.3. Strict consensus tree of the *Echinacea* and closely related taxa based on ITS data. Bootstrap support (%) is shown above branches and decay index below. Upper name of pairs is that of McGregor (1968), lower name of pairs in parentheses is that of Cronquist (1955, 1980) and Binns and coworkers (2002a).
LITERATURE CITED


rare and a widespread species of *Echinacea* (Asteraceae). Evolution 48:180–188.


CHAPTER 3

POPULATION DYNAMICS OF *ECHINACEA PALLIDA* (ASTERACEAE) AT THE TALLGRASS PRAIRIE PRESERVE (OKLAHOMA)

INTRODUCTION

Commonly known as pale purple coneflower, *Echinacea pallida* is one of the more widespread species of the New World genus (Figure 3.1). It occurs from the Prairie Peninsula of Iowa and Illinois to the eastern one-third of the lower Great Plains, as well as the Ozark and Ouachita Mountains of Oklahoma, Missouri, and Arkansas and reaches its southern most distribution in southwestern Louisiana (McGregor, 1968; McKeown, 1999; Binns et al., 2002). Although small populations have been recorded in a number of eastern states—some as disjunct as northeastern Maine—these populations are probably adventive; their occurrence no doubt a result of cultivation because of the medicinal value of the taxon (McGregor, 1968).

The geographic distribution of *E. pallida* reflects its specific habitat requirements. Populations are restricted to rocky prairies, open wooded hillsides, and cedar glades, all of which must have calcareous, well-drained soils (McGregor, 1968). Many such sites exist throughout the Great Plains, most commonly in the area known as the tallgrass prairie.

*Echinacea pallida* differs from the other members of the genus in that it typically has light purple to pink or white, highly reflexed ray florets and dark
brown disk florets that are subtended by brown or darkly colored receptacular bracts. Stems are typically 30–90 cm tall, and the distinctly 3-nerved, hirsute leaves are 10–30 cm long and 1–4 cm wide. The most important distinguishing character for this species is pollen grain color. It is the only member of the genus with white pollen, and the specific epithet actually refers to the color of these pollen grains rather than the light colored ray florets.

Containing a variety of compounds such as alkaloids, polysaccharides, glycoproteins, caffeic acid derivates, flavonoids, and essential oils, *Echinacea* is an extremely popular medicinal taxon (Bauer et al. 1988; Bauer and Wagner, 1985, Small and Catlig, 1999). *Echinacea pallida* is one of three species in the genus being studied as a medicinal plant. Its economic and medicinal value is well documented (Bauer et al., 1988; Schulthess et al., 1991; Li, 1998; Small and Catlig, 1999).

The popularity of this medicinal genus has led to an increase in cultivation as well as a rapid decrease in the wild populations of its species because of indiscriminant extirpation of plants by collectors (Ladd and Oberle, 1995). Devastation of natural populations of *E. pallida* increases the need for a better understanding of its biology. Previous work on the genus has focused on *E. tennesseensis* and *E. laevigata*, designated as endangered by the U.S. Fish and Wildlife Service (1999). *Echinacea angustifolia* and *E. purpurea* also have been investigated in field studies by Leuszler (1996) and Hurlburt (1999). *Echinacea pallida* has not been studied, especially with respect to its population biology. Thus the purpose of this study was to provide information about the population
dynamics of *Echinacea pallida*. Using methods employed by population
dynamics, the following objectives were addressed:

1) To determine whether the population of *Echinacea pallida* at the
   Tallgrass Prairie Preserve (TGPP) is stable, increasing, or decreasing.

2) To determine the variables most likely contributing to the transformation
   of vegetative individuals into reproductive ones and vice-versa.

3) To determine the variables most likely contributing to the mortality of
   individuals at the TGPP.
Figure 3.1 Distribution map of *Echinacea*. The shaded portion indicates the distribution of the genus. Diagonal lines designate the distribution of *Echinacea pallida*. 
METHODS AND MATERIALS

Field Site Description

This study was conducted in the bison (*Bos bison*) grazing area of the Tallgrass Prairie Preserve in Osage County, Oklahoma (36.8481°N, 96.4219°W). This native tallgrass prairie of approximately 15,800 ha has been owned and managed by The Nature Conservancy since 1989. Approximately 90% of the site is grassland which contains a diverse assemblage of plant species (Palmer, 2003). Approximately 80% of the prairie vegetation is dominated by C₄ warm-season grasses including *Andropogon gerardii* (big bluestem), *Schizachyrium scoparium* (little bluestem), *Sorghastrum nutans* (Indian grass), *Sporobolus compositus* (composite dropseed), and *Panicum virgatum* (switch grass). Other common species include members of the Asteraceae—*Erigeron philadelphicus* (Philadelphia fleabane), *Coreopsis grandiflora* (largeflower tickseed), *Rudbeckia hirta* (Black-eyed Susan), and *Ratibida columnifera* (Mexican hat)—, Fabaceae—*Mimosa quadrivalvis* (sensitive briar), *Amorpha canescens* (lead plant), *Dalea candida* (white prairie clover), and *Dalea purpurea* (purple prairie clover)—, as well as other species such as *Eryngium yuccifolium* (rattlesnake master), *Linum sulcatum* (grooved flax), and *Asclepias tuberosa* (butterfly milkweed). Much of the remaining area of the TGPP is forested predominantly by *Quercus stellata* (post oak) and *Quercus marilandica* (blackjack oak) (Arévalo, 2002).

The TGPP is managed to restore a remnant of the tallgrass prairie landscape in Oklahoma (Hamilton, 1996). Many studies on the tallgrass prairie stress the importance of fire and bison grazing in determining species.
composition and structure (Collins, 1989; Collins, 1990; Fahnestock and Knapp, 1994). Prescribed burns are conducted throughout the year—dormant spring burns (March-April), late growing season burns (July-September), and dormant fall burns (October-November). Burn locations are randomly selected according to the fuel load of the vegetation (Hamilton, 1996).

We selected one population of *Echinacea pallida* located just north of the preserve's headquarters, in an area where bison grazing and fire have been restored (Figure 3.2). A 100 X 100 m area was established. Within this area, seven 10 x 10 m sites were randomly selected and permanently marked at their corners with rebar and aluminum caps. These sites were identified by a four digit number which symbolized the Cartesian coordinates with respect to the 100 X 100 m study area. The first two digits signified placement along the X axis and the last two along the Y axis (e.g., XXYY). Within each site, one hundred 1 x 1 m quadrats were established and used to map the location of each plant observed.

*Data Collection*

The population was studied each year from 1997 to 2000 from about the first of June to mid July, the peak flowering period for this prairie species. We monitored the population at the individual plant level. The location of each plant was marked by an aluminum tag driven into the ground beside it by a galvanized nail. The number of the plant and its Cartesian coordinates with respect to the 10 X 10 m sites were recorded and placed on each tag. The following characters were measured and recorded: number of leaves, length of each leaf, number of
flowering heads per plant (if present), and height of each flowering head (if present). These measurements were recorded using a handheld microcassette recorder, transcribed later onto field data sheets, and then entered into a Microsoft® Excel spreadsheet (Appendix A). Incidence of pathogens, fungal infection, and herbivory was not recorded for individuals of the population.

**Data Analysis**

Assuming that the population was closed, i.e., no immigration or emigration occurring, the following equation was used to determine its current status \( (N_t) \) with respect to its status one year earlier \( (N_{t-1}) \):

\[
N_t = N_{t-1} + B - D
\]  

(3.1)

\( B \) is the number of births—or new individuals—and \( D \), the number of deaths (Akcakaya et al., 1999).

We summarized the dynamics of the population by calculating the finite rate of increase or \( \lambda \) (lambda). Lambda was calculated by the equation:

\[
\lambda = \frac{N_t}{N_{t-1}}
\]  

(3.2)

A population is considered stable when \( \lambda = 1 \), increasing when \( \lambda > 1 \); and decreasing when \( \lambda < 1 \) (Silvertown and Doust, 1993).

The following variables were calculated for each plant: sum of leaf lengths, maximum leaf length, number of flowering heads (if present), sum of stem heights (if present), maximum stem heights (if present). The status of each plant was recorded each year as either vegetative (basal rosette of leaves), reproductive (having one or more flowering heads), or missing (dead or not
found). From this information it was possible to construct a database (Appendix B) that allowed us to describe the status of each plant from year to year.

In order to examine the variables most likely contributing to the transformation of vegetative individuals into reproductive ones and vice-versa, as well as those variables most likely contributing to the mortality of individuals at the site, we employed backward stepwise logistic regression using the LOGISTIC procedure in SAS 8.2 (SAS Institute, Cary, NC). Logistic regression, like most regression analyses, is a valuable tool in that it allows us to find the best fitting, yet biologically most reasonable model to describe the relationship between a response or dependent variable and a set of independent variables (Lemeshow and Hosmer, 1998). Unlike other regression models, such as linear regression, logistic regression requires that the response or dependent variables be recorded in a binary fashion. In a backward stepwise logistic regression, the analysis begins with a large model consisting of all independent variables and then eliminates the least significant ones until only the significant ($\alpha=.05$) remains (Menard, 1995).

The following equation is the model used to illustrate the relationship between a single dependent variable and the independent variables:

$$\Pr(Y = 1) = \frac{e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \ldots \beta_k x_k}}{1 + e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \ldots \beta_k x_k}}$$ \hspace{1cm} (3.3)

where $\Pr(Y = 1)$ is the probability that the dependent variable is equal to 1, $e$ is the natural log base (2.718), $\alpha$ is the intercept or constant, $\beta$ is the value of independent variable, and $X$ is the estimate of the independent variable (given in a SAS output).

3-8
The dependent variables used in the analyses were those of the stage of the life cycle (vegetative, reproductive, and missing) from one year to the next. The independent variables were the size characteristics cited above (number of leaves, sum of leaf lengths, maximum leaf length, number of flowering heads, sum of stem heights, maximum stem heights). The squared values of the size characteristics also were included in the analyses to allow for nonlinearity. Appendix C illustrates the input file used for the LOGISTIC procedure.
Figure 3.2 Aerial photograph of the Tallgrass Prairie Preserve headquarters and adjacent area. Inset is an outline of the study area containing the seven randomly selected sites.
RESULTS AND DISCUSSION

Population Status

During the four-year period, 8,038 recordings were made during the data collection process. A majority of the individuals studied (73%) were located at two sites—0351 (44%) and 0074 (29%). There were 2,813 new plants encountered at the seven randomly selected sites. Of these, 1,299 were mapped and tagged in 1997; 313 in 1998; 679 in 1999; and 504 in 2000. Appendix D illustrates the distribution of individuals present at each site over the four-year period.

The number of new individuals in the population was considerably higher than those that died in nearly all sites during all years (Table 3.1). An overall increase in the population size of *E. pallida* was seen—662 individuals (*N*<sub>2000</sub>—*N*<sub>1997</sub>)—from the time the study began until it ended, resulting in a λ value of 1.53. An increase in individuals at every site was seen in every growing season (1997–1998, 1998–1999, and 1999–2000) except at 0351 in 1999–2000 (λ = 0.74). At this site, a large number of individuals died. Because it encompasses the highest percentage (44%) of individuals in the entire population, it caused a slight decrease in the population during 1999–2000 (λ = 0.97).

These results agree with those of Arévalo and coworkers (2003a) who concluded the population is still in a state of change and has not yet reached a steady state.
Transition Analyses Using Logistic Regression

Although the study sites showed differences in numbers of individuals, all possessed similar size structure and flowering patterns in each study period. Considerable differences are seen in the ratio of vegetative to reproductive individuals observed during 1998 and 2000 versus 1997 and 1999 (Table 3.2). Throughout the four-year period, the total number of vegetative (V) individuals recorded were 5,559, reproductive (R) individuals 1,647, and those that died or were missing (M), 832. Logistic regression involving stage classes as dependent variables and plant size characters as independent variables provided the following results (Table 3.3).

The transition from a vegetative plant to a reproductive one the following year was best explained by maximum leaf lengths ($p<0.0001$), maximum leaf lengths squared ($p=0.0020$), and number of leaves ($p=0.0021$). As illustrated in Figure 3.3, the smaller the maximum leaf lengths, the less likely a vegetative plant was to be recruited to a reproductive stage the next year. As maximum leaf lengths increase, so too did the likelihood the plant to make the transition from a vegetative stage of its life cycle to a reproductive one. The same can be said for number of leaves. Individuals with fewer leaves were less likely than those with more leaves to make a transition to a reproductive stage the following year.

The transition from a reproductive plant to a vegetative one the following year was best explained by maximum leaf lengths ($p<0.0001$) and maximum leaf lengths squared ($p=0.0004$). The likelihood of a reversion is illustrated in Figure 3.4, a plot of the probability of individuals remaining reproductive as a function of
maximum leaf lengths. The data clearly suggest that the greater the maximum leaf lengths of a reproductive individual, the higher the probability of that individual to remain in a reproductive stage and not revert to a vegetative stage the following year.

Mortality is as an important part of the dynamics of a population as the establishment of viable offspring. Because of this, it is important to know what variables might suggest when individuals will reach the end of their life cycle. The transition of an individual from a reproductive plant to a dead (missing) plant the following year was best explained by maximum leaf lengths ($p=0.0097$). The probability of individuals remaining reproductive as a function of maximum leaf lengths is shown in Figure 3.5. The results suggest that as maximum leaf lengths of reproductive individuals increase, so too does the likelihood of these individuals to remain reproductive and not succumb to mortality before the next growing season.

The transition of an individual from a vegetative stage to a dead (missing) plant the following year was best explained by maximum leaf lengths ($p<0.0001$) and maximum leaf lengths squared ($p<0.0001$). The results suggest that vegetative plants with smaller maximum leaf lengths will most likely not return the next year. This result agrees with the trend found in the raw data. It appears that once a vegetative individual has reached a maximum leaf length of about 10 cm, its chances of remaining a part of the population increases.
Possible environmental variables affecting the population dynamics of *E. pallida* at the TGPP

One might hypothesize that a variety of environmental conditions could be affecting the population of *E. pallida* at the TGPP and contributing to the results of this study. Some of these environmental variables were examined by Arévalo and coworkers (2003a&b). They did not find a strong relationship between soil composition and chemistry and population features. Likewise, climatic parameters (mean monthly average temperature, total precipitation, and mean monthly soil temperature) also were considered. These parameters, acquired from a Mesonet station (Oklahoma Climatological Survey, 2002) located less than 500 m from the study site, were not clearly related with the differences among the transition probabilities during the study (Arévalo et al., 2003b).

Arévalo and coworkers (2003b) suggested that the difference in numbers of vegetative and reproductive plants in 1998 and 2000 from those in 1997 and 1999 are a result of the prescribed fire regime instituted at the TGPP. Their results suggest that *E. pallida* exhibits a dynamic response to fire, i.e., producing a large number of reproductive individuals in the growing season after fall fires (1997 and 1999) and smaller numbers of reproductive individuals when fire is absent (1998 and 2000). In years without fire, there was more competition for adequate solar radiation due to accumulation of litter and grass biomass from the previous growing season. This resulted in an increase in leaf biomass per plant, both in terms of surface area and number of leaves, as well as a decrease in the number of flowering heads. Although the effect of fire in reproductive dynamics
of prairie plants has been extensively reported (Dudley and Lajha, 1993; Hamilton, 1996; Hurlburt, 1999; Vickery, 2002), especially with respect to survivorship in different species (Maret and Wilson, 2000), reversion of the size during those years has not been documented as a common response. Arevalo and coworkers (2003b) considered a regular rate of fire an intrinsic factor of the population dynamic of *E. pallida* that facilitates the maintenance of the population.

It should clearly be determined what effect fire has on the population with demographic parameters. Altering the current method of fire management may result in a non sustainable population of *Echinacea pallida*. If current management practices on the preserve are maintained, populations of *E. pallida* will persist.
Table 3.1 Finite rate of increase $\lambda$ and summed values of individuals new to the population ($B$), those that died ($D$), and total number of individuals for each site in a given year ($N_t$).

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Table 3.2 Numbers of individuals in vegetative (V), reproductive (R), and dead/missing (M) stage classes for each site during each year.

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Table 3.3. Summary of backward stepwise logistic regression results as explained in text. Estimates and intercepts generated using SAS 8.2 (SAS Institute, Cary, NC).

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<th>Transition from vegetative to reproductive individual</th>
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Figure 3.3 Transition from vegetative stage previous year to reproductive stage the following year. Constructed from logistic model (Equation 3.3).
Figure 3.4 Transition from reproductive stage previous year to vegetative stage the following year. Constructed from logistic model (Equation 3.3).
Figure 3.5 Transition from reproductive stage previous year to dead (missing) plant the following year. Constructed from logistic model (Equation 3.3).
LITERATURE CITED


Appendix A. Representative database sheet used in organizing field data of *Echinacea pallida*. site = 0074, 0351, 1371, 1834, 4387, 5979, and 7065; year = 1997-2000; plant ID = 1-2236; x and y = Cartesian coordinates with respect to 10 X 10 m site; quad # = 1 X 1 m quadrat within each site (1-100); stage (life cycle stage at time of data collection) = R (reproductive/flowering), V (vegetative), M (missing/dead); fh # = number of heads; L1-L200 = leaf lengths; FH1-FH15 = stem heights.

| site  | year | plant ID | x   | y   | quad# | stage | fh# | L1 | L2 | L3 | L4 | L5 | L6 | L7 | FH1 | FH2 |
|-------|------|----------|-----|-----|-------|-------|-----|----|----|----|----|----|----|-----|-----|
| 1371  | 1997 | 1        | 36  | 588 | 6     | R     | 1   | 9  | 7  | 13 | 5  | 15 | 2  | 3   | 28  |
| 1371  | 1998 | 1        | 36  | 588 | 6     | V     | 0   | 16 | 12 | 4  | 3  | 25 | 12 | 12  |     |
| 1371  | 1999 | 1        | 36  | 588 | 6     | R     | 4   | 14 | 13 | 14 | 12 | 10 | 11 | 12  | 64  |
| 1371  | 2000 | 1        | 36  | 588 | 6     | V     | 16  | 17 | 15 | 13 | 14 | 13 | 13 |     |
| 1371  | 1997 | 2        | 182 | 219 | 13    | R     | 1   | 8  | 7  | 6  | 9  | 10 | 11 | 12  | 49  |
| 1371  | 1998 | 2        | 182 | 219 | 13    | V     | 6   | 6  | 12 | 7  | 6  | 8  | 13 |     |
| 1371  | 1999 | 2        | 182 | 219 | 13    | V     | 30  | 29 | 18 | 15 | 19 | 23 |     |
| 1371  | 2000 | 2        | 182 | 219 | 13    | V     | 16  | 25 | 27 | 36 | 33 | 35 | 35 |     |
| 7065  | 1997 | 3        | 41  | 511 | 6     | R     | 3   | 6  | 9  | 11 | 9  | 11 | 11 | 8   | 51  |
| 7065  | 1998 | 3        | 41  | 511 | 6     | V     | 0   | 7  | 8  | 10 | 17 | 18 | 11 | 15  |     |
| 7065  | 1999 | 3        | 41  | 511 | 6     | R     | 2   | 17 | 16 | 17 | 14 | 14 | 13 | 12  | 61  |
| 7065  | 2000 | 3        | 41  | 511 | 6     | V     | 6   | 21 | 13 | 26 | 21 | 21 | 24 |     |
| 7065  | 1997 | 4        | 41  | 311 | 6     | R     | 1   | 4  | 3  | 5  | 8  | 5  | 3  | 41  |     |
| 7065  | 1996 | 4        | 41  | 311 | 6     | V     | 0   | 10 | 10 | 4  |     |     |     |     |
| 7065  | 1999 | 4        | 41  | 311 | 6     | R     | 1   | 14 | 13 | 12 | 11 | 10 | 10 | 8   | 46  |
| 7065  | 2000 | 4        | 41  | 311 | 6     | V     | 10  | 14 | 5  | 5  | 2  | 15 | 8  |     |
| 7065  | 1997 | 5        | 9   | 590 | 7     | V     | 0   | 12 | 9  | 11 | 12 | 12 | 12 |     |
| 7065  | 1998 | 5        | 9   | 590 | 7     | V     | 0   | 7  | 12 | 10 | 8  | 12 | 12 | 6   |
| 7065  | 1999 | 5        | 9   | 590 | 7     | R     | 1   | 13 | 12 | 14 | 13 | 11 | 11 | 69  |     |
| 7065  | 2000 | 5        | 9   | 590 | 7     | V     | 9   |    |    |    |    |    |    | 6   |     |
| 7065  | 1997 | 6        | 6   | 662 | 7     | V     | 0   | 12 | 12 | 11 |     |     |     |     |
| 7065  | 1998 | 6        | 6   | 662 | 7     | V     | 0   | 5  | 13 | 12 |     |     |     |     |
| 7065  | 1999 | 6        | 6   | 662 | 7     | V     | 21  | 22 | 19 | 17 | 11 |     |     |     |
| 7065  | 2000 | 6        | 6   | 662 | 7     | V     |     |    |    |    |    |    |    |     |     |
| 7065  | 1997 | 7        | 15  | 756 | 8     | R     | 2   | 10 | 9  | 11 | 12 | 10 | 7  | 9   | 50  |
| 7065  | 1998 | 7        | 15  | 756 | 8     | V     | 0   | 4  | 3  | 8  | 8  | 6  | 6  | 7   |     |
| 7065  | 1999 | 7        | 15  | 756 | 8     | R     | 1   | 14 | 13 | 14 | 13 | 11 | 11 | 10  | 61  |
| 7065  | 2000 | 7        | 15  | 756 | 8     | V     | 8   | 12 | 26 | 8  | 16 | 23 | 29 |     |
| 7065  | 1997 | 8        | 38  | 770 | 8     | R     | 2   | 9  | 9  | 12 | 11 | 8  | 9  | 3   | 45  |
| 7065  | 1998 | 8        | 38  | 770 | 8     | V     | 0   | 11 | 17 | 6  | 16 | 8  | 5  |     |     |
| 7065  | 1999 | 8        | 38  | 770 | 8     | R     | 2   | 15 | 15 | 16 | 15 | 16 | 17 | 59  | 47  |
| 7065  | 2000 | 8        | 38  | 770 | 8     | M     |     |    |    |    |    |    |    |     |     |
| 7065  | 1997 | 9        | 45  | 752 | 8     | R     | 4   | 10 | 8  | 10 | 11 | 14 | 10 | 11  | 55  |
| 7065  | 1998 | 9        | 45  | 752 | 8     | V     | 0   | 11 | 18 | 18 | 18 | 9  | 11 | 16  |     |
| 7065  | 1999 | 9        | 45  | 752 | 8     | R     | 3   | 16 | 15 | 14 | 13 | 12 | 10 | 11  | 65  |
| 7065  | 2000 | 9        | 45  | 752 | 8     | V     | 8   | 13 | 25 | 15 | 12 | 32 | 27 |     |     |
| 7065  | 1997 | 10       | 67  | 799 | 8     | R     | 2   | 7  | 7  | 7  | 8  | 9  | 9  | 6   | 45  |
| 7065  | 1998 | 10       | 67  | 799 | 8     | V     | 0   | 5  | 7  |    |    |    |    |     |
| 7065  | 1999 | 10       | 67  | 799 | 8     | M     |     |    |    |    |    |    |    |     |     |
Appendix B. Representative database sheet summarizing recorded variables. site = 0074, 0351, 1371, 1834, 4387, 5979, and 7065; year = 1997-2000; plant ID = 1-2236; stage this year (life cycle stage at time of data collection) = R (reproductive/flowering), V (vegetative), M (missing/dead); stage previous year (life cycle stage year prior to data collection if applicable) = R (reproductive/flowering), V (vegetative), M (missing/dead).

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<th>number of leaves</th>
<th>sum stem heights (cm)</th>
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Appendix C. SAS input for logistic regression (LOGISTIC procedure).

DATA ONE;
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INPUT PLANTID YEAR SITE STAGETHIS$ STAGEFOLLOW$ SUMLEAFLEN MAXLEAFLEN NOLEAVES SUMSTEMHT MAXSTEMHT NOSTEMS;
SUMLEAFLEN2 = SUMLEAFLEN**2;
MAXLEAFLEN2 = MAXLEAFLEN**2;
NOLEAVES2 = NOLEAVES**2;
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DATA TWOVR;
SET TWO;
IF STAGEFOLLOW = 'V' OR STAGEFOLLOW = 'R';

PROC LOGISTIC;
TITLE 'PREVIOUS STAGE = V';
MODEL STAGEFOLLOW = SUMLEAFLEN SUMLEAFLEN2 MAXLEAFLEN MAXLEAFLEN2 NOLEAVES NOLEAVES2 SUMSTEMHT SUMSTEMHT2 MAXSTEMHT MAXSTEMHT2 NOSTEMS NOSTEMS2 /SELECTION = BACKWARD;

DATA TWOVD;
SET TWO;
IF STAGEFOLLOW = 'V' OR STAGEFOLLOW = 'D';

PROC LOGISTIC;
TITLE 'PREVIOUS STAGE = D';
MODEL STAGEFOLLOW = SUMLEAFLEN SUMLEAFLEN2 MAXLEAFLEN MAXLEAFLEN2 NOLEAVES NOLEAVES2 SUMSTEMHT SUMSTEMHT2 MAXSTEMHT MAXSTEMHT2 NOSTEMS NOSTEMS2 /SELECTION = BACKWARD;

DATA THREE;
SET ONE;
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SET THREE;
IF STAGEFOLLOW = 'R' OR STAGEFOLLOW = 'V';

PROC LOGISTIC;
TITLE 'PREVIOUS STAGE = V';
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RUN;
Appendix D. Distribution of individual plants in each 10 X 10 m site studied. Mapping is based on Cartesian coordinate system.
Appendix D Continued.
CURRICULUM VITAE
ADAM K. RYBURN
Candidate for the Degree of
Doctor of Philosophy

Thesis: Taxonomic Investigations of Oklahoma Flora
Major Field: Plant Sciences/Botany

EDUCATION

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1990-1993 Anadarko High School, Anadarko, OK

PROFESSIONAL EXPERIENCE

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Teaching Associate
1999 - Present Department of Botany / Oklahoma State University

Teaching Assistant
1999 - 2003 University of Oklahoma Biological Station, Lake Texoma, OK

Research Assistant
2002 Department of Botany / Oklahoma State University

Research Assistant
1999 - 2000 Department of Botany / Oklahoma State University

Teaching Assistant
1998 - 1999 Department of Biological Sciences / Southwestern Oklahoma State University (SWOSU)

AWARDS RECEIVED
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OSU Distinguished Graduate Student Fellowship, 2001-present
OSU Leadership Legacy Recipient, 2000
Outstanding Teaching Assistant, College of Arts and Sciences, 2000 (OSU)
Southwestern Oklahoma State University Outstanding Biology Student of the Year, 1997, 1998
Who's Who Among American College Students, 1997 (SWOSU)
Mary Miller Award for Outstanding Field Research Student, 1996 (SWOSU)