FOOD HABITS AND NIGHTLY EMERGENCE ACTIVITY IN A FAMILY OF BEAVERS (*Castor canadensis*) IN THE TAIGA OF SOUTHEASTERN MANITOBA

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
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FACULTY OF GRADUATE STUDIES
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ABSTRACT

The yearly food habits and nightly emergence activity of a family of beavers (Castor canadensis) were studied from the spring of 1992 to the fall of 1993 in the taiga of Manitoba. In 1992 the adult female, the two yearling males and the yearling female of the beaver family were equipped with radio transmitters. In 1993 the adult female, one of the two-year old males and the two-year old female were re-equipped with radio transmitters. Detailed daily observations were made on the food selection, feeding site selection and time of nightly emergence for each of these beaver.

The beaver family was observed to feed on nine main plant species including; Alnus rugosa, Populus tremuloides, Betula papyrifera, Cornus stolonifera, Pinus banksiana, Amelanchier alnifolia, Salix spp., Nuphar variegatum and Zizania aquatica. Preferences for certain species and plant parts varied over the years and seasons suggesting that beaver may be opportunistic herbivores when the food supply is diverse. Pinus banksiana buds and bark were consumed primarily in the spring during the growing leaf stage, and, when available, leaves were selected for over bark. The two aquatic

species (Nuphar variegatum and Zizania aquatica) were also observed to be utilized when available.

No significant differences in food choice between the male and female beavers was found in this study. The beaver in this study also did not appear to be constrained by nutrient availability in the food they consumed.

Feeding site selection did not appear to be influenced by tree density or the diameter of trees at a height of 20 cm from the ground.

I found no correlation in this study between beaver emergence time from the lodge and weather conditions including air temperature, wind speed, wind direction, percent cloud cover and precipitation. A relationship was revealed between emergence time and time of sunset. As well, observed differences in nightly emergence time by the beaver family members was not found to be statistically significant.

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TABLE OF CONTENTS

PAGE

ABSTRACT ii

ACKNOWLEDGMENTS iv

TABLE OF CONTENTS v

LIST OF TABLES ix

LIST OF FIGURES x

CHAPTER 1. INTRODUCTION, LITERATURE REVIEW AND STUDY AREA

INTRODUCTION 1

LITERATURE REVIEW 6

Food Habits 6

Nocturnal Habits 7

STUDY AREA 9

LITERATURE CITED 13

CHAPTER 2. FOOD SELECTION BY BEAVER AND NUTRIENT ANALYSIS OF SELECTED FOODS

ABSTRACT 18

INTRODUCTION 19

METHODS 22

Tracking 22

Food Habits 24

RESULTS 27

Nutrient Analysis 27

Yearly Variations in Food Selection 73

Seasonal Variations in Food Selection 80

Differences in Food Choice Between Beavers 81

DISCUSSION 83

Nutrient Analysis 83

Yearly Variations in Food Selection 88

Seasonal Variations in Food Selection 90

CONCLUSIONS 96

LITERATURE CITED 98

CHAPTER 3. FEEDING SITE SELECTION BY BEAVER

ABSTRACT 101

INTRODUCTION 102

METHODS 104

RESULTS 106

Tree Density as a Function of Feeding

Site Selection 106

Diameter Lower Height (DLH) as a Function of

Feeding Site Selection 111

Distance Traveled for Food Harvesting as Measured by

Stump Density 115

DISCUSSION 117

Tree Density as a Function of Feeding

Site Selection 117

Diameter Lower Height (DLH) as a Function of

Feeding Site Selection 117

Distance Traveled for Food Harvesting as Measured by

Stump Density 118

CONCLUSIONS 120

LITERATURE CITED 121

CHAPTER 4. EMERGENCE TIME FROM THE LODGE

ABSTRACT 122

INTRODUCTION 123

METHODS 124

Emergence Time From the Lodge 124

Weather Data 124

RESULTS 126

Weather and Emergence Time 126

Sunset and Emergence Time 126

DISCUSSION 131

Sunset and Emergence Time 131

Weather and Emergence Time 132

CONCLUSIONS 133

LITERATURE CITED 134

MANAGEMENT RECOMMENDATIONS 135

LITERATURE CITED 136

APPENDICES 141

APPENDIX I: SUNSET TIMES FOR 1992 AND 1993 141

LIST OF TABLES

TABLE **PAGE**

CHAPTER 3

1 Stump density of control and experimental sites at 0-10, 11-20 and 21-30 m. 116

LIST OF FIGURES

FIGURE **PAGE**

CHAPTER 1

1 Location of study area in Manitoba. 11

2 Universal Transverse Mercator (UTM) grid map depicting the study area along the North shore of Wallace Lake. 12

CHAPTER 2

1 Crude protein levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 29

2 Calcium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 30

3 Magnesium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 31

4 Phosphorus levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 32

5 Potassium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 33

6 Sodium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 34

7 Sulphur levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 35

8 Zinc levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 37

9 Manganese levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 38

10 Iron levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 39

FIGURE **PAGE**

CHAPTER 2

11 Copper levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 40

12 Potassium : sodium ratios (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) 1993. 41

13 Crude protein levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 43

14 Calcium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 44

15 Magnesium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 45

16 Phosphorus levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 46

17 Potassium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 47

18 Sodium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 48

19 Sulphur levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 49

20 Zinc levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 52

21 Manganese levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 53

22 Iron levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 54

23 Copper levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 55

FIGURE PAGE

CHAPTER 2

24 Potassium : sodium ratios (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) 1993. 56

25 Crude protein levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 59

26 Calcium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 60

27 Magnesium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 61

28 Phosphorus levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 62

29 Potassium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 63

30 Sodium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 64

31 Sulphur levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 65

32 Zinc levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 68

33 Manganese levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 69

FIGURE **PAGE**

CHAPTER 2

34 Iron levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 70

35 Copper levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) 1993. 71

36 Potassium : sodium ratios (%) for the plant species and plant sampled during the senescence leaf stage (September - October) 1993. 72

37 Frequency distribution of the plant parts consumed by the beaver family during the growing leaf stage (May - June) of 1992. 74

38 Frequency distribution of the plant parts consumed by the beaver family during the mature leaf stage (July - August) of 1992. 75

39 Frequency distribution of the plant parts consumed by the beaver family during the senescence leaf stage (September - October) of 1992. 76

40 Frequency distribution of the plant parts consumed by the beaver family during the growing leaf stage (May - June) of 1993. 77

41 Frequency distribution of the plant parts consumed by the beaver family during the mature leaf stage (July - August) of 1993. 78

42 Frequency distribution of the plant parts consumed by the beaver family during the senescence leaf stage (September - October) of 1993. 79

CHAPTER 3

1 Tree density in control and experimental sites at a distance of 0 - 10 m from the lake's edge. 108

FIGURE **PAGE**

CHAPTER 3

2 Tree density in control and experimental sites at a distance of 11 - 20 m from the lake's edge. 109

3 Tree density in control and experimental sites at a distance of 21 - 30 m from the lake's edge. 110

4 Diameter lower height in control and experimental sites at a distance of 0 - 10 m from the lake's edge. 112

5 Diameter lower height in control and experimental sites at a distance of 11 - 20 m from the lake's edge. 113

6 Diameter lower height in control and experimental sites at a distance of 21 - 30 m from the lake's edge. 114

CHAPTER 4

1 Comparisons of observed emergence times from the lodge for the yearling males, yearling female and adult female of the family in 1992. 128

2 Comparisons of observed emergence times from the lodge for the two-year old male, two-year old female and adult female of the family in 1993. 129

CHAPTER 1: INTRODUCTION, LITERATURE REVIEW AND STUDY AREA

INTRODUCTION

The North American beaver (Castor canadensis) is a semi-aquatic, mainly nocturnal mammal and is strictly herbivorous (Seton 1909). Beaver families or colonies typically consist of a mated adult pair, yearlings and the kits which are the young of the year (Seton 1909, Anonymous 1950, Anonymous 1978).

The beaver is mainly a monogamist, however this may not always be so. The mating season is in February to March with a gestation period of three months. On average three to four kits are born in late May or early June (Seton 1909, Anonymous 1950, Anonymous 1978). At the age of one month kits begin to eat solid food which is brought into the lodge by other family members. At six weeks of age the kits are weaned but they stay with their family usually up until their second summer at which time they often disperse to establish new colonies (Seton 1909, Anonymous 1950, Anonymous 1978).

Beavers may inhabit lodges or bank burrows. They spend their time in caring for the kits, foraging for food, lodge and/or dam construction and maintenance, and in play. Their life span may be as long as 12-15 years (Seton 1909, Anonymous 1950, Anonymous 1978).

Beavers have been observed to feed on a wide variety of plant species including deciduous species such as Maple (Acer spp.) (Brenner 1962, Jenkins 1979), Dogwood (Cornus stolonifera) (Belovsky 1984), Birch (Betula spp.) (Ingle-Sidorowicz 1982, Belovsky 1984), Alder (Alnus spp.) (Belovsky 1984) and coniferous species such as pines (Pinus spp.) (Chabreck 1958, Wheatley 1994).

As well, beavers will consume aquatic plant species such as Yellow water lily (Nuphar variegatum) and Wild rice (Zizania aquatica) (Aleksiuk 1970, Pils 1983). However, most observers list Trembling aspen (Populus tremuloides) and Willow (Salix spp.) as the preferred choices of food by beavers (Seton 1909, Green 1936, Anonymous 1950, Hall 1960, Brenner 1962, Aleksiuk 1970, Ingle-Sidorowicz 1982, Pils 1983, Beier and Barrett 1987, and Masslich et al 1988).

In areas of continuous ice cover over winter, beavers will construct food caches near the lodge. During winter months beaver movement is restricted under the ice generally to trips to the food cache (Seton 1909, Anonymous 1950, Anonymous 1978).

Historically, beavers have played important economic, cultural and ecological roles in North America and continue to do so to date. Beavers have been commercially harvested for their pelts for over four centuries (Anonymous 1950, Naiman et al 1988). The expansion of European settlement in North America was largely driven by the pursuit for beaver pelts (Bergstrom 1985). Today, beaver trapping still provides income for a large number of northern peoples.

Beavers also played significant roles in the cultures of many aboriginal peoples. Some North American tribes had strong aversions to the hunting of beaver as they recognized the important ecological roles beaver play in maintaining aquatic ecosystems (Morgan 1991).

Ecologically, beavers play key roles in regulating ecosystems (Ermer 1984, Bergstrom 1985, Naiman et al 1988). Beaver dams slow water, sediment and organic matter movement in watersheds. This in turn acts to increase groundwater recharge rates, increases plant community composition and diversity, affects nutrient cycling and decomposition rates and provides invaluable wildlife habitat to a diverse number of waterfowl, mammals, birds, reptiles, amphibians and fish (Hodgdon and Hunt 1953, Stegeman 1954, Ermer 1984, Bergstrom 1985, Naiman et al 1988). As well, beavers also create important recreational and aesthetic sites (Naiman et al 1988).

In the past beavers have not only been exploited by fur traders, but they have also been utilized by forest and wildlife managers. In the 1930's and 1940's beaver were utilized in the western United States to build dams to control stream flow and soil erosion. In the late 1970's beavers were used in Idaho, Montana and Wyoming to improve riparian habitat for cattle grazing and for fish and wildlife needs (Bergstrom 1985).

Beaver populations of pre-European arrival in North America were estimated to be between 60-400 million individuals with a geographic range of about 5 million km^2. By 1900 the beaver population was almost extinct in North America due to over-trapping and habitat loss (Bergstrom 1985, Naiman et al 1988).

Today, due to the reduction of predators, regulated trapping and plentiful habitat, beaver populations have increased to a level between 6-12 million individuals, to a point where beaver-human conflicts are on the rise (Naiman et al 1988). As a result, improved management techniques are required to deal with "nuisance" beavers. Therefore, the more information we have on beaver habitat requirements and behaviour, the better we can make appropriate management decisions not only for the beaver but also for the watersheds, wildlife and vegetation associated with beaver activity.

In Canada however, research on this important furbearing mammal is limited, especially in the boreal forest region. Studies in Canada have been conducted by such researchers as Green (1936) on the general ecology of beaver, Miller (1964) on the use of colored ear tags, Bovet and Oertli (1974) and Potvin and Bovet (1975) on circadian rhythms in beavers, Aleksiuk (1968, 1970, 1977) on scent communication and territory and food regimes, Aleksiuk and Cowan (1969 a, b) on winter energy expenditure in beaver, Bergerud and Miller (1977) on population dynamics in beaver, Novak (1977) on the size and composition of beaver families, Slough (1978) on food cache structure, Ingle-Sidorowicz (1982) on population dynamics and food selection, Payne (1982) on colony structure, Wheatley (1989 and 1994) on behaviour, ecology and habitat use, Dyck (1991) on thermal energetics, Fryxell and Doucet (1991) on central-place foraging and Fryxell (1992) on habitat use. As well, general information pamphlets on beavers have been published by governmental agencies such as the Canadian Wildlife Service (1978). However, further information into habitat use and requirements as well as general behaviour of beavers is required for the implementation of proper management programs.

This study was undertaken to obtain information on beaver food habitats and evening emergence behaviour in the southeastern boreal forest of Manitoba;

and factors influencing feeding site selections and nightly emergence from the lodge.

LITERATURE REVIEW

FOOD HABITS

Most of the papers published in the literature on beaver have a section devoted to food choice in terms of species and plant parts selected by beaver (Seton 1909, Green 1936, Bradt 1938, Anonymous 1950, Haseltine 1950, Hodgdon and Hunt 1953, Chabreck 1958, Hall 1960, Brenner 1962, Aleksiuk 1970 and 1977, Slough 1978, Hall 1972, Jenkins 1979, Jenkins 1981, Ingle-Sidorowicz 1982, Pils 1983, Belovsky 1984, Beier and Barrett 1987, Masslich et al 1988, and Wheatley 1994).

More recent studies have looked at the foraging behaviour of beaver in terms of species present, diameter and distance from the water's edge but only for feeding sites (Jenkins 1975, 1979 and 1980, Busher et al 1983, Belovsky 1984, McGinely and Whitman 1985, Fryxell and Doucet 1991, and Fryxell 1992). Studies looking at why beaver choose certain feeding sites over others is essentially lacking with only one study conducted by Masslich et al (1988) on differences between sites used by beaver for feeding and control sites in terms of aspen age class, stump density and diameter.

Other areas involving food habits have included studies on how beaver affect the environment in terms of beaver impacts on vegetation and watersheds (Ingle-Sidorowicz 1982, Bergstrom 1985, Beier and Barrett 1987, and Naiman et al 1988), habitat use along streams (Beier and Barrett 1987) and bogs (Rebertus 1986), winter food cache structure (Novakowski 1967, Aleksiuk 1970, and

Slough 1978), and differences in food selection between beaver colonies (Jenkins 1975).

Studies on the nutritional value of foods eaten by beaver has been limited to a few studies by Masslich et al (1988) and Wheatley (1994). As well, while researchers such as Brenner (1962) and Jenkins (1980) have discussed the fact that beaver may select certain species at particular sites based on nutritional values no studies have been conducted to prove or disprove this idea. Doucet and Ball (1994) have studied the digestibility of foods eaten by beaver. Studies have also been conducted on food selection by beavers of tree species which produce chemical defensive compounds (Basey et al 1990, and Muller-Schwarze et al 1994).

One study was also conducted by Stegeman (1954) on the growth rates of aspen and use by beaver. He also looked at food availability per tree for aspens of varying diameter at breast height (dbh) classes.

NOCTURNAL HABITS

Studies on nightly emergence times from the lodge are essentially lacking in the literature. Seton (1909) was one of the first naturalists to write that beavers were mainly nocturnal in habit. Other authors who have also reported this fact include (Green 1936, Schramm 1968, and the Canadian Wildlife Service 1978).

Studies have been conducted by Schramm (1968) and Brady and Svendsen (1981) on the order of family member emergence from the lodge. Wheatley (1989) looked at live trapping success in relation to moon phase.

STUDY AREA

This study was conducted from the Taiga Biological Station (TBS) about 1.5 km north of Wallace Lake at 51°02'40" N latitude, 95°20'40" W longitude in southeastern Manitoba, 250 km northeast of Winnipeg in the southwestern part of the Canadian Shield (Figure 1). The lake is bordered by granite ridges and numerous bogs and beaver ponds. The main study area was along the northwestern shore of Wallace Lake including the Twin Bays, Cave Lodge Bay, Gatlan Bay, and Woden Island areas of the lake (Figure 2).

The vegetation in the region is typical of the Boreal Forest and has been subjected to several forest fires in the past 25 years. Burnt areas support a regrowth of Jackpine (Pinus banksiana), some Trembling Aspen (Populus tremuloides), with an understory of lichens, various mosses and vascular plants including Blueberry (Vaccinium spp.), Bear Berry (Arctostaphylos uva-ursi), Wild Lily of the Valley, (Maianthemum canadense) and Bunchberry (Cornus canadensis) along dry, upland areas (Zoladeski et al 1995). Bogs are dominated by Black Spruce (Picea mariana) and an understory of Labrador Tea (Ledum groenlandicum), Bog Laurel (Kalmia polifolia), Bog Rosemary (Andromeda polifolia) and Sphagnum mosses (Zoladeski et al 1995). Trembling Aspen (Populus tremuloides), Alder (Alnus crispa), Paper Birch (Betula papyrifera) and Willow (Salix spp.) predominate along the lake shore.

Climatically, Wallace Lake is within the mid-continental boreal forest zone (Pruitt 1978). The temperatures in the area range from a summer high of +35 °C to -40 ^{0}C in the winter with a yearly mean temperature of +1.3 ^{0}C (Environment Canada 1990). Average precipitation for the area is 564.9 mm; 145.2 mm as snowfall and 428.8 mm as rainfall. Snowfall may occur as early as October with a continuous cover lasting until mid April to mid May. Ice cover is continuous in the winter with freeze-up beginning in late October or early November, and spring thaw occurring in late April or early May (Environment Canada 1990).

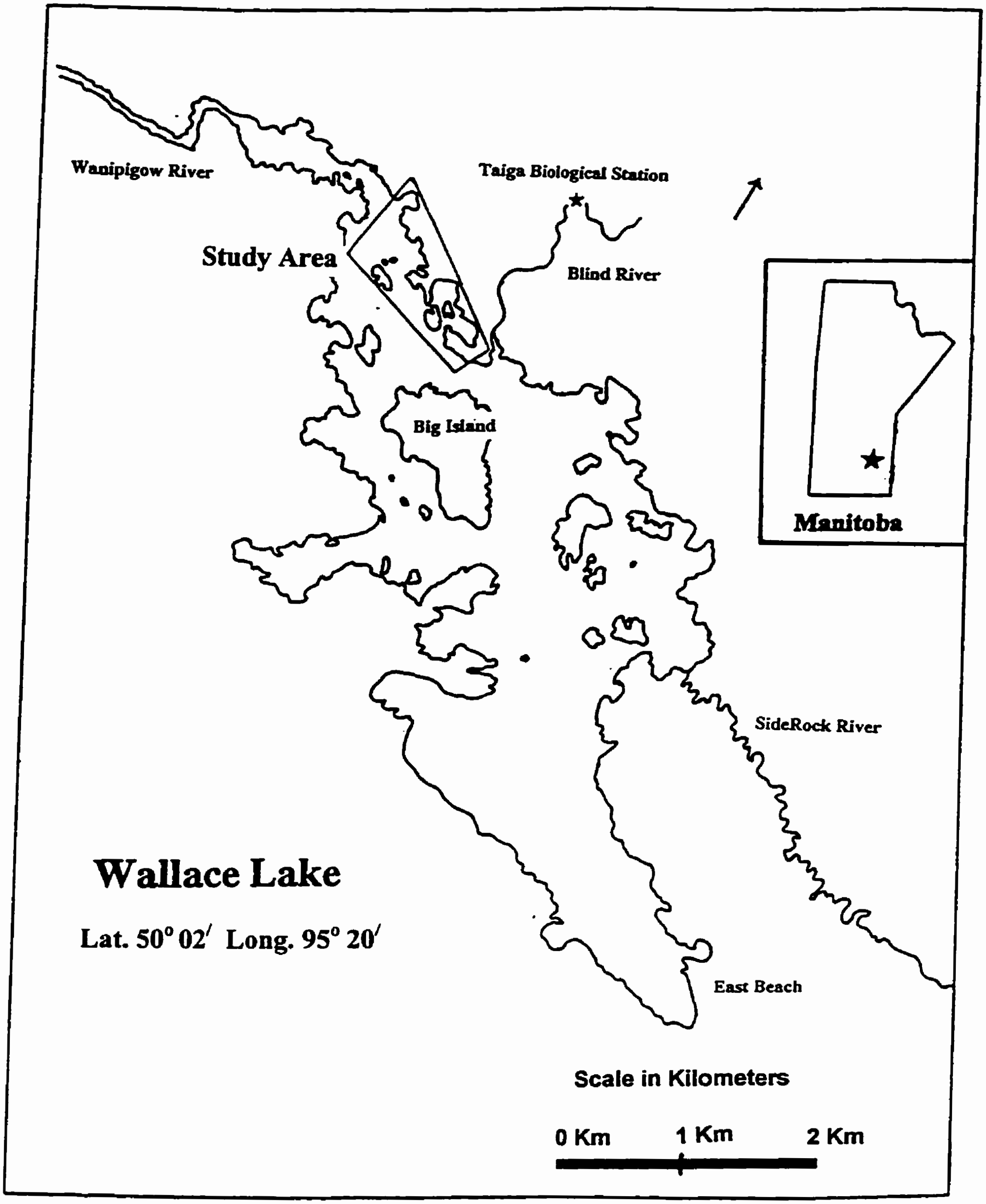

Figure 1: Location of study area in Manitoba.

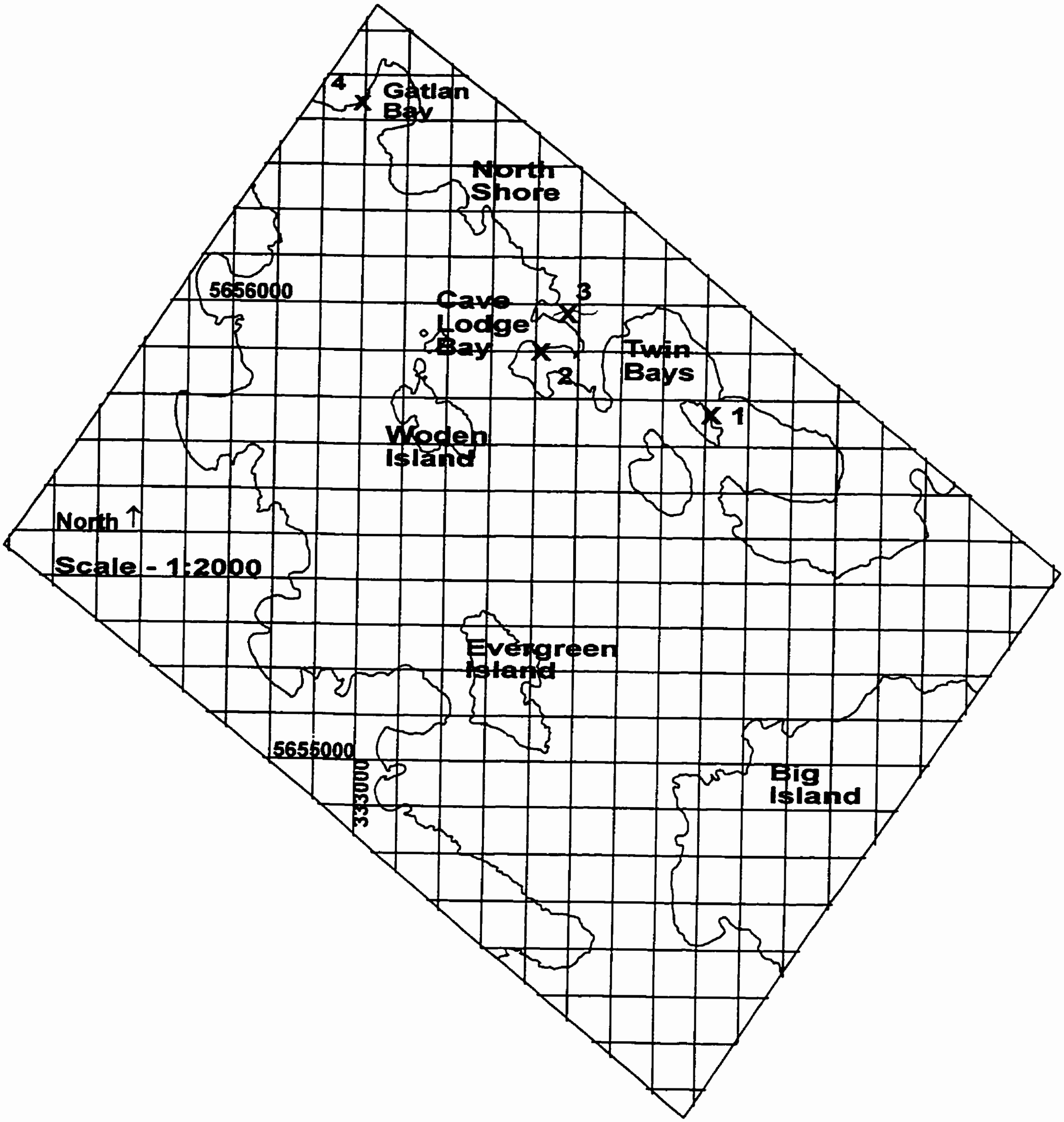

Figure 2: Universal Transverse Mercator (UTM) grid map depicting the study area along the North shore of Wallace Lake.

Note: Each grid square = 100 x 100 m

X denotes the location of lodges used by the beaver in this study:

X 1 - Twin Bays Lodge **X 3** - Bog Lodge

X 2 - Cave Lodge **X 4** - Gatlan Lodge

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CHAPTER 2: FOOD SELECTION BY BEAVER AND NUTRIENT ANALYSIS OF SELECTED FOODS

ABSTRACT

The beaver family was observed to feed on nine main plant species including; Alnus rugosa, Populus tremuloides, Betula papyrifera, Cornus stolonifera, Pinus banksiana, Amelanchier alnifolia, Salix spp., Nuphar variegatum and Zizania aquatica during 1992 and 1993. Preferences for certain species and plant parts varied over the years and seasons, suggesting that beaver may be opportunistic herbivores when the food supply is diverse, choosing those species which meet their energy and nutritional requirements at a particular time. Pinus banksiana buds and bark were consumed primarily in the spring during the growing leaf stage, and when available leaves were selected for over bark. The two aquatic species (Nuphar variegatum and Zizania aquatica) were also observed to be utilized when available. Nutrient levels were found to be a probable factor influencing food selection by beaver.

No significant differences in food choice between the male and female beavers was found in this study.

The beaver in this study also did not appear to be constrained by nutrient availability in the food they consumed.

INTRODUCTION

Beavers (Castor canadensis) are strictly herbivorous in food habit and have been described as being "choosy generalists" (Harper 1969, in Jenkins 1981) and "opportunistic herbivores" (Jenkins 1981), "capable of subsisting on practically every species imaginable "(Hall 1972). Diet preferences by the beaver vary both seasonally and yearly in terms of plant species and vegetative part (Seton 1909, Green 1936, Bradt 1938, Anonymous 1950, Haseltine 1950, Hodgdon and Hunt 1953, Chabreck 1958, Hall 1960, Brenner 1962, Aleksiuk 1970 & 1977, Slough 1978, Hall 1972, Jenkins 1979, Jenkins 1981, Ingle-Sidorowicz 1982, Pils 1983, Belovsky 1984, Beier and Barrett 1987, Masslich et al 1988, Wheatley 1994).

In northern climates once spring thaw is completed, beaver feed upon the bark and developing buds of deciduous and some coniferous tree species (Green 1936, Hall 1960, Aleksiuk 1970 & 1977, Jenkins 1981, Wheatley 1994). Later, during the summer months their food preferences favor growing shoot tips and leaves of trees as well as the leaves and roots of some herbaceous and aquatic species (Seton 1909, Green 1936, Hodgdon and Hunt 1953, Chabreck 1958, Hall 1972, Brenner 1962, Jenkins 1979, Ingle-Sidorowicz 1982, Pils 1983, Belovsky 1984, Wheatley 1994). In the fall, beaver switch back to bark as leaves are shed from trees. Beaver also begin to store a winter food cache consisting of a raft of branches near their lodge for use once ice cover on ponds, lakes and streams is continuous throughout the winter season (Green 1936, Anonymous 1950, Aleksiuk 1970, Slough 1978, Jenkins 1979, Pils 1983).

Plant species utilized by beaver are widely cited in the literature and include a broad variety of both deciduous and coniferous species. Beaver have been reported to consume such species as Lobolly pine (Pinus taeda), Sweetgum (Liquidambar styraciflua) (Chabreck 1958), Ironwood (Carpinus caroliniana), Ash (Fraxinus americana) (Jenkins 1979), Maple (Acer spp..) (Brenner 1962, Jenkins 1979), Poplar (Populus spp.) (Aleksiuk 1970, Pils 1983), Jackpine (Pinus banksiana) (Wheatley 1994), Alder (Alnus rugosa), Dogwood (Cornus stolonifera) (Belovsky 1984), Birch (Betula spp.) (Ingle-Sidorowicz 1982, Belovsky, 1984) as well as herbaceous and aquatic species including Sawgrass (Cladium jamaicense) (Chabreck 1958), Sedges (Carex spp.) (Pils 1983), Blueberry (Vaccinium spp.) (Jenkins 1979), and Water lilies (Castilia odorata and Nuphar variegatum) (Aleksiuk 1970, Pils 1983). However, by far the most frequently cited plant species utilized by beaver are Trembling aspen (Populus tremuloides) and Willow (Salix spp.) (Seton 1909, Green 1936, Anonymous 1950, Hall 1960, Brenner 1962, Aleksiuk 1970, Ingle-Sidorowicz 1982, Pils 1983, Beier and Barrett 1987, Masslich et al 1988, Wheatley 1994).

Jenkins (1975) suggested that food selectivity may be related to differing nutritional and chemical values between sites. However, studies on the effects of nutrient concentrations in plant species as a factor influencing food selection by beaver are limited. Aleksiuk (1970), Jenkins (1975) and Masslich et al (1988) have conducted some research on this topic. More recently Wheatley (1994) examined the nutrient content of plants utilized by boreal beavers but her examination only covered three plant species.

This study was conducted to provide further insight into some of the factors that define beaver food habits in the boreal forest including plant species and vegetative part selection, nutritional values of plants utilized by beavers, and yearly and seasonal changes in food choice.

METHODS

TRACKING

The beaver family inhabiting lodges in the Twin Bays and Cave Lodge Bay areas of Wallace Lake were tracked daily from May 1992 to October 1993 as they moved throughout the study area. Beavers were located during their evening activity periods through the use of radio telemetry equipment and visual observations. Observations on food choices and location of feeding sites were made for each family member of the beaver colony.

When I began my field work in May 1992 the beaver family was inhabiting a lodge in Twin Bays and was already equipped with radio transmitters implanted intraperitoneally during Michelle Wheatley's study (Wheatley 1994). Each transmitter had a specific frequency and a life span of up to two years. The family group at this time consisted of five members; an adult male, an adult female, two yearling males, and a yearling female.

Signals from the beavers' radio transmitters were received using an H - shaped Yagi antenna and a 24 channel radio receiver box (Wildlife Materials Inc.). Each beaver was also equipped with uniquely numbered metal ear tags (Monel, number 3) to which colored pieces of polyvinyl plastic were attached (Miller, 1964) to enable me to identify each beaver visually as well. Both the colored ear tags and the radio transmitters had limited life spans, after which beavers could only be identified by live trapping them and reading the numbered metal ear tags. This necessitated the re-trapping and re-equipping of the beaver with more than one radio transmitter.

Beavers were monitored from 16:00 to 07:00 hours with most of the nightly observations recorded between the hours of 16:00 and 23:00 hours. Beavers were tracked throughout the study area from a 16 foot freighter canoe. I followed the beaver around as they moved throughout the study area, anchored the canoe approximately 30-40 m away from the beaver, and with the use of binoculars, visual observations of the beavers' activities (i.e.: patrolling, feeding, lodge maintenance, etc.) were recorded. One minute of observation was considered to be one observation. I attempted to locate each colony member at least once during each monitoring period. A particular beaver would be monitored from 1 minute up to 30 minutes at a time. I attempted to remain as inconspicuous as possible during each monitoring period to ensure that the beavers' activities were not influenced by my presence.

Each beaver's location was recorded for an observation point on a 1:25,000 scale air photo that was enlarged to a 100 x 70 cm map size. Superimposed on this map was a Universal Transverse Mercator (UTM) grid with a 10 m accuracy. Beaver activity was also recorded at that moment in a field notebook. The data from the UTM map were subsequently transcribed to paper to determine the locations of feeding sites utilized by the beaver family. The same procedure was followed throughout both field seasons.

FOOD HABITS

Food Selection

During daily observations of the beaver colony in 1992 and 1993, visual observations by binoculars were made of what the beaver were feeding on during daylight periods. When darkness set in I would wait until the beaver had finished feeding at a site and then approach the site and pick up the left-over branches to determine what the beaver had consumed. I recorded what plant species the beavers were feeding on, as well as what part of the plant they consumed including bark, leaves, or leaves and petioles for trees and shrubs, and stems, stems/leaves or roots for aquatic species. This provided me with a baseline of food selection by the beavers from spring through to the fall. I determined from observations of food selection that the following nine main plant species made up the bulk of these beavers' diets on Wallace Lake: Alder (Alnus rugosa), Trembling Aspen (Populus tremuloides), Paper Birch (Betula papyrifera), Red-osier Dogwood (Cornus stolonifera), Jackpine (Pinus banksiana), Saskatoon (Amelanchier alnifolia), Willow (Salix spp.), Wild Rice (Zizania aquatica), and Yellow Water Lily (Nuphar variegatum).

Note that the generic names of these plant species will be used throughout the remainder of this thesis.

Nutrient Analysis

In 1993 vegetation samples of these species were collected to determine whether nutrient content influences food selection by the beaver colony.

Samples were collected every 3-5 weeks to ensure that plants were sampled at each developmental stage including growing leaf (unfurling and small leaf), mature growth and senescence (Kenkel 1992). Sampling began on May 4 with subsequent sampling taking place on May 13, June 5, July 2, July 13, August 14, September 14, and ending on October 2. A half pound of bark, leaves, and leaves plus petioles were collected during each sampling period for Alnus, Populus, Betula, Cornus, Amelanchier and Salix. Pinus bark and needles were also collected at most of the sampling times and buds were collected during the May 4 - July 2 sampling dates. Nuphar and Zizania stems and leaves were also collected during the July 2 - October 2 dates. All collections were dependent upon plant growth.

Sample sites for plant collection were chosen based on feeding sites used by the beaver family. The beavers typically fed on plant species at specific sites around the lake. Five to ten saplings or small trees and two to three aquatic plants were collected from each site during one sampling period. Trees which were at a similar stage of leaf growth were sampled. A sub-sample of each of the vegetative parts (bark, leaves etc.) were collected from each sapling/tree or aquatic plant. Sub-samples were then combined to create one composite sample for each vegetative part for each species, and then placed in a plastic bag and kept frozen until it was analyzed for nutrient content.

The vegetative samples were analyzed for various macro and trace nutrients by Nor-West Labs Inc., Agricultural Service Complex on the University of Manitoba campus. Firstly, the dry matter was determined as a percentage of the fresh, frozen material. The concentrations of the following minerals were then determined as either percent (%) or parts per million (ppm) per 100 g of dry matter from each sample: crude protein (%), sulphur (%), zinc (ppm), phosphorous (%), manganese (ppm), iron (ppm), magnesium (%), calcium (%), copper (ppm), sodium (%) and potassium (%). To standardize all of the minerals to a common measure, minerals that were reported in ppm were converted to percent where 10,000 ppm = 1%.

RESULTS

NUTRIENT ANALYSIS

Descriptions of the nutrient analysis are based upon the nine main plant species consumed by the beaver family in 1992 and 1993 including Alnus, Populus, Betula, Cornus , Pinus, Amelanchier, Salix., Zizania and Nuphar.

Initial results of nutrient levels in leaves and leaves plus petioles were very similar, therefore the nutrient values for these two plant parts were averaged and are listed under the heading of "leaves".

Nutrient Content During the Growing Leaf Stage (May - June)

Crude Protein

Crude protein levels were much lower (68-82%) in the bark than in the leaves for all of the tree species (Figure 1). As well, crude protein levels in Pinus buds were lower than levels observed for the leaves of the deciduous species but higher than levels observed in the bark.

Crude protein levels were fairly similar in all of the species for both bark and leaves with Amelanchier having slightly lower levels in the leaves.

Macro Elements

Calcium and sodium levels were found to be higher in the bark compared to the leaves of the 7 tree species sampled with the exception of Cornus and Populus species respectively (Figures 2, 6). Magnesium, phosphorus, potassium and sulphur (except Alnus) levels were found to be lower in the bark compared to the leaves while sodium levels were similar in both bark and leaves in all 7 tree species (Figures 3, 4, 5, 7).

Pinus buds were found to have low levels of magnesium and sulphur, similar to levels of these nutrients observed in the bark (Figures 3, 7). In addition, Pinus buds were observed to have very low levels of calcium (Figure 2). Moderate levels of phosphorus and potassium were found in Pinus buds whereas the levels of these two nutrients were lower than those levels observed in the leaves but higher than those levels observed in the bark of the tree species (Figures 4, 5). As well, Pinus buds were observed to have very high sodium levels (Figure 6).

Bark macro element levels between species were found to be similar for magnesium, phosphorus, potassium, sodium and sulphur, however, levels were variable between species for calcium (Figures 2, 3, 4, 5, 6, 7). Macro element levels in the leaves were similar between species for magnesium, phosphorus, potassium and sulphur while calcium and sodium levels in the leaves were variable between species (Figures 2, 3, 4, 5, 6, 7).

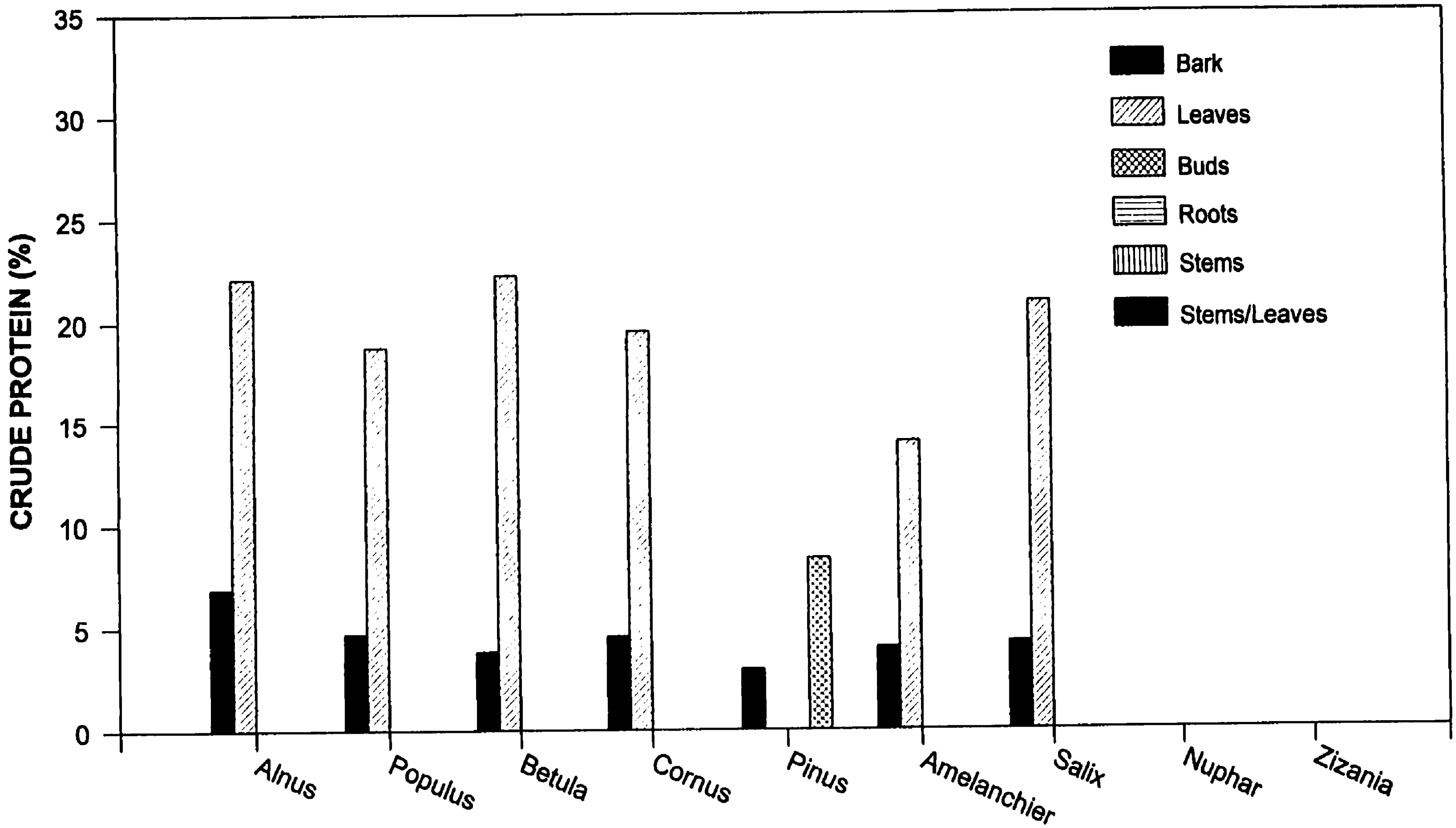

Figure 1: Crude protein levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

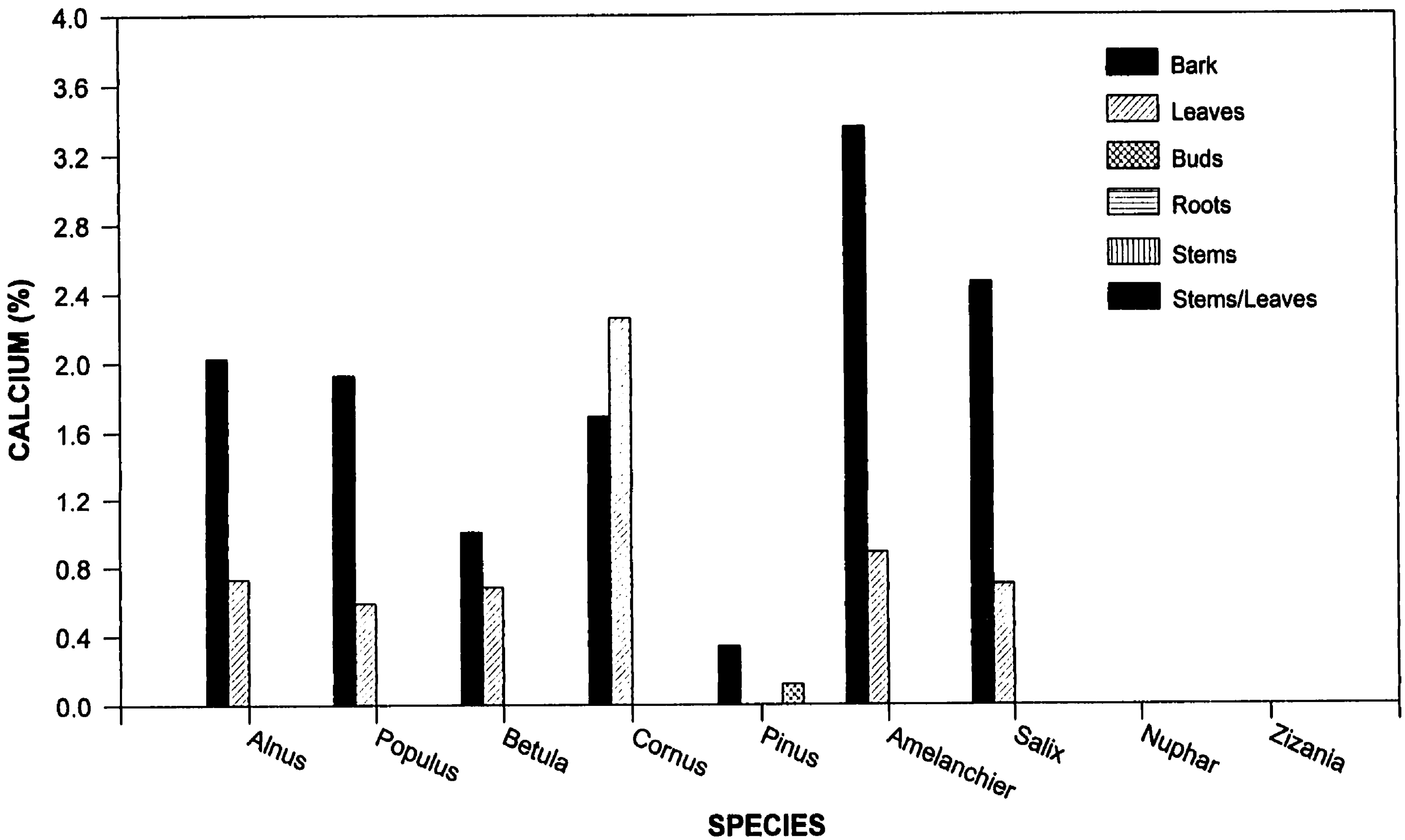

Figure 2: Calcium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

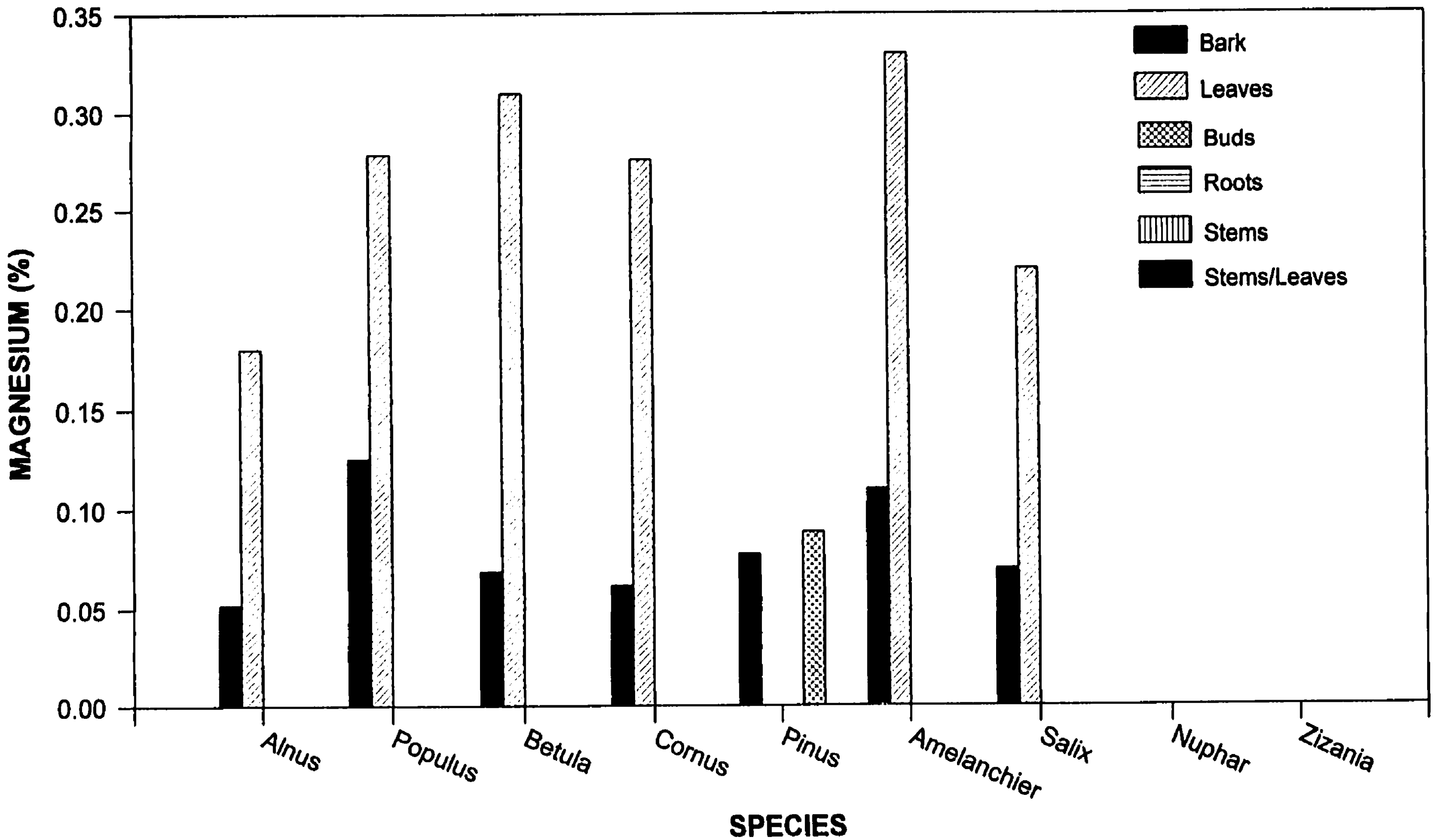

Figure 3: Magnesium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

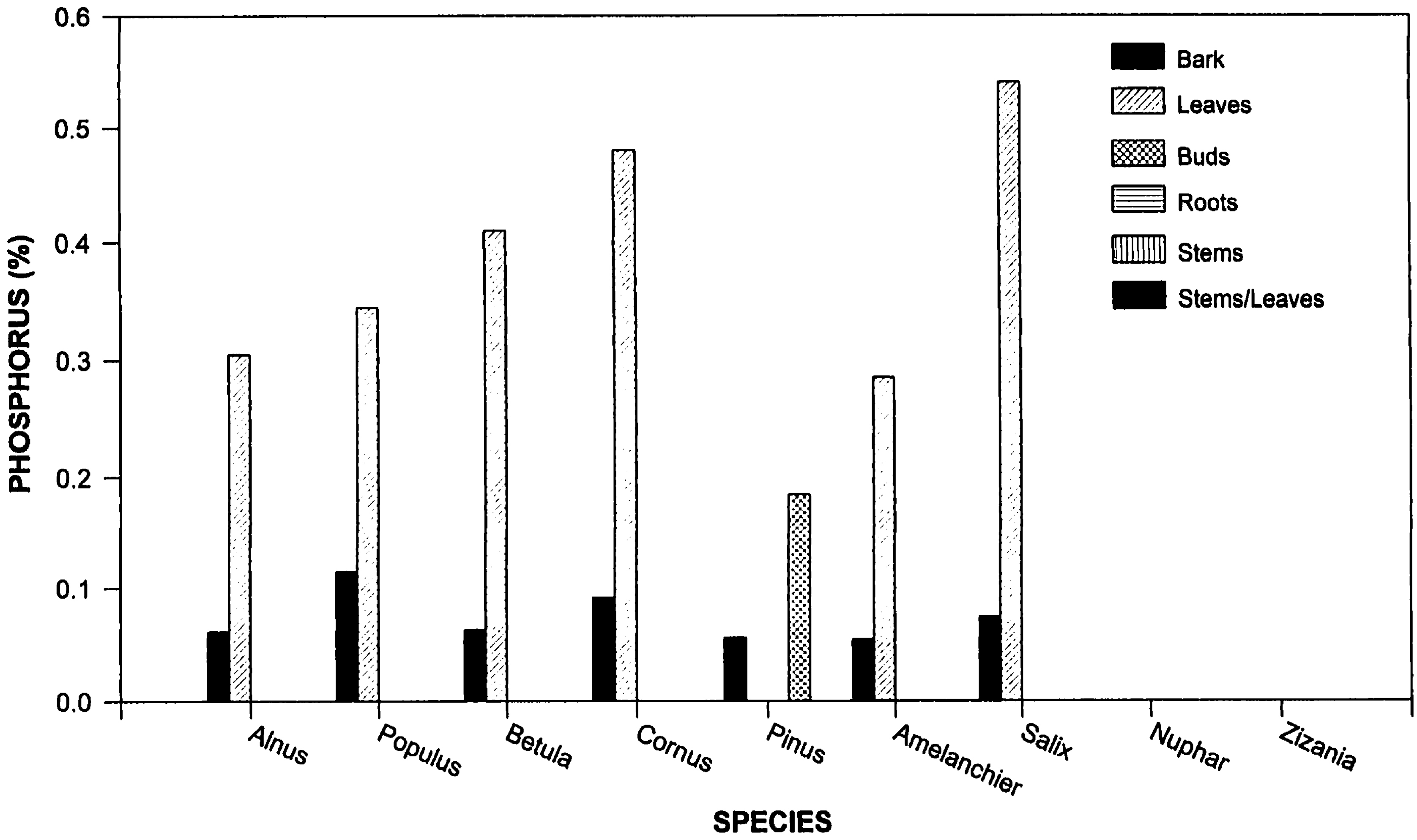

Figure 4: Phosphorus levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

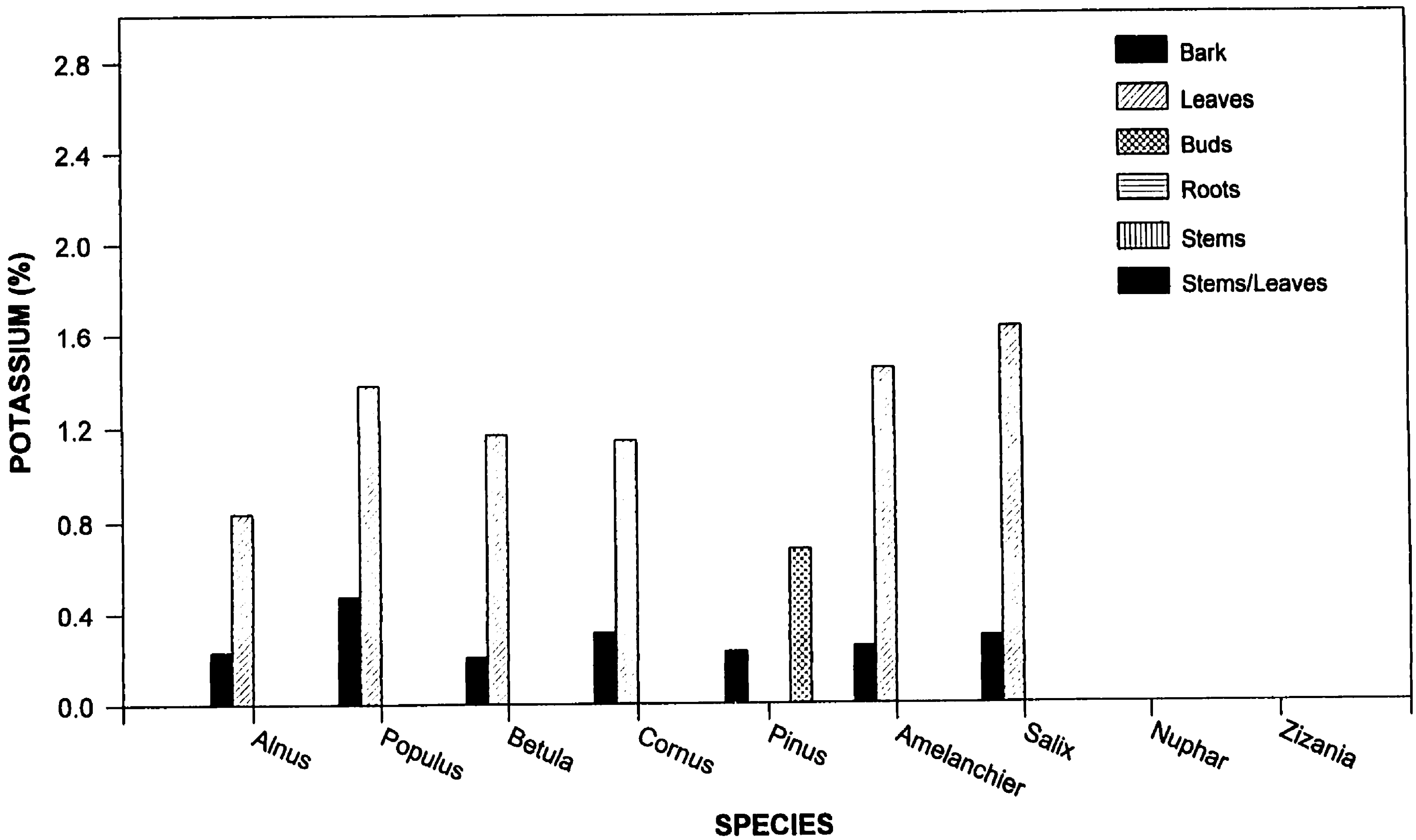

Figure 5: Potassium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

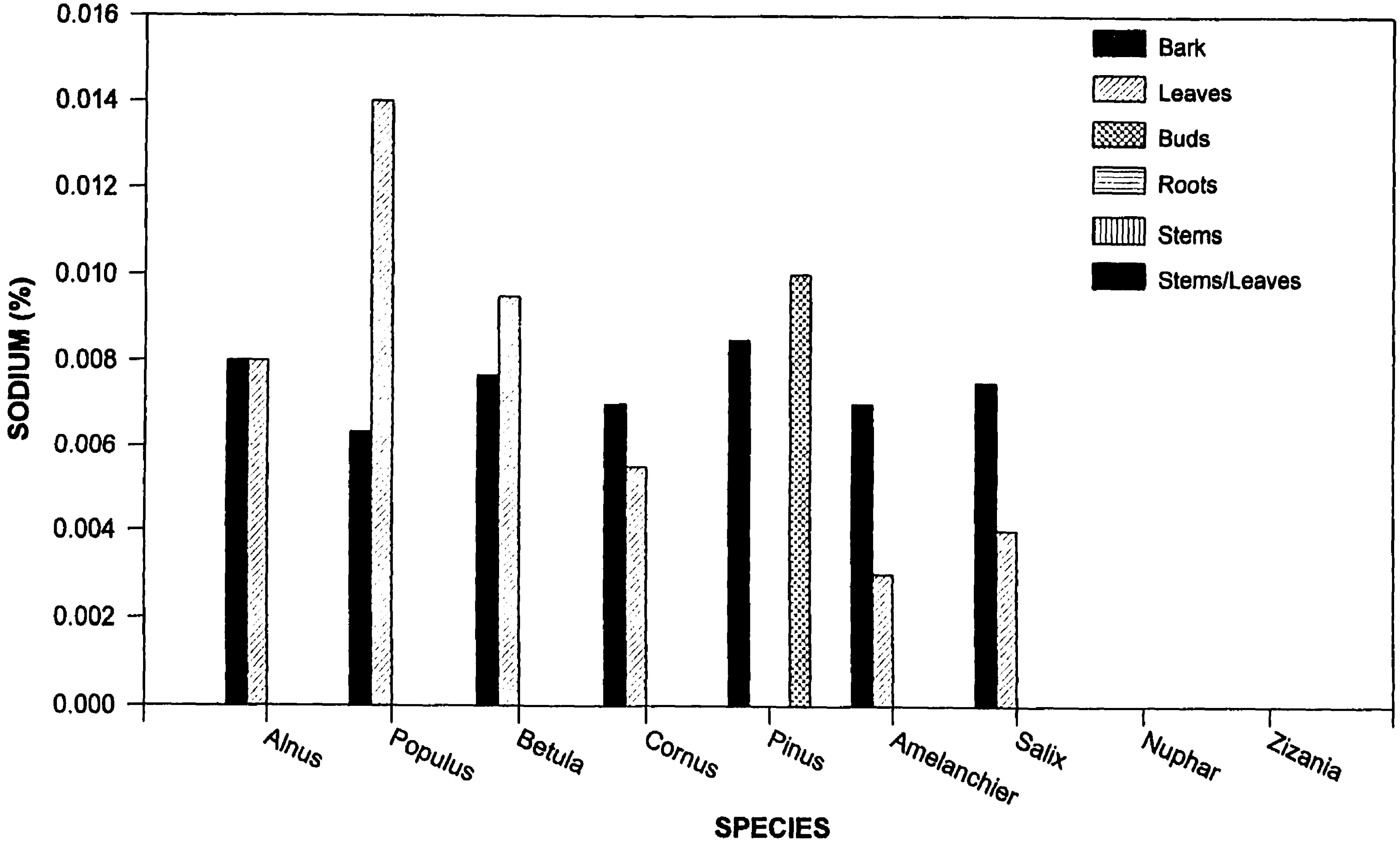

Figure 6: Sodium levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

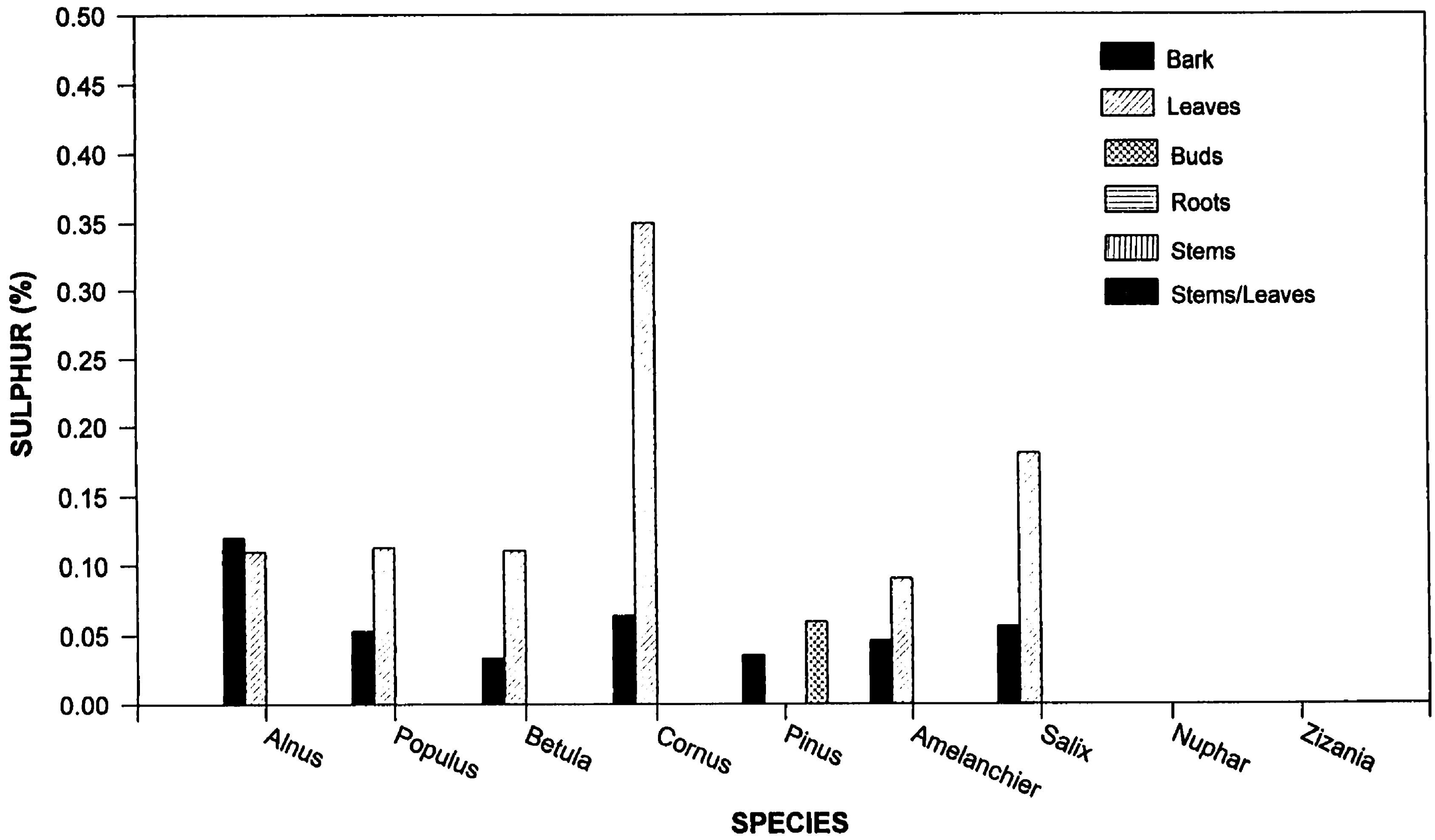

Figure 7: Sulphur levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

Trace Elements

Levels of trace elements including zinc, manganese, iron and copper were variable between bark and leaves. Zinc levels were lower in the bark than in the leaves for Alnus and Cornus while the rest of the species had higher zinc levels in the bark (Figure 8). Manganese and iron levels were higher in Salix bark compared to its leaves while the remaining species had manganese and iron levels that were lower than or similar to levels in the bark (Figures 9, 10). Copper levels were lower in the bark than in the leaves for all of the tree species with the exception of Amelanchier which had higher levels in the leaves (Figure 11).

Pinus buds had low levels of iron similar to levels observed in the bark of the deciduous tree species, and moderate levels of zinc, manganese and copper, whereby levels were higher than in the bark but lower than in the leaves of the deciduous tree species.

Levels of manganese and iron were variable in the bark between species while copper levels were similar between species (Figures 9, 10). Moreover, levels of manganese, iron and copper were variable in the leaves between species (Figures 9, 10, 11).

Potassium : Sodium Ratio

Overall, the bark of the tree species had much lower potassium:sodium ratios than did the leaves especially in the case of Amelanchier and Salix (Figure 12). Pinus buds had a lower ratio similar to that observed for the bark at 1:70. Ratios in the bark were fairly similar, ranging between 1:30 and 1:50 with

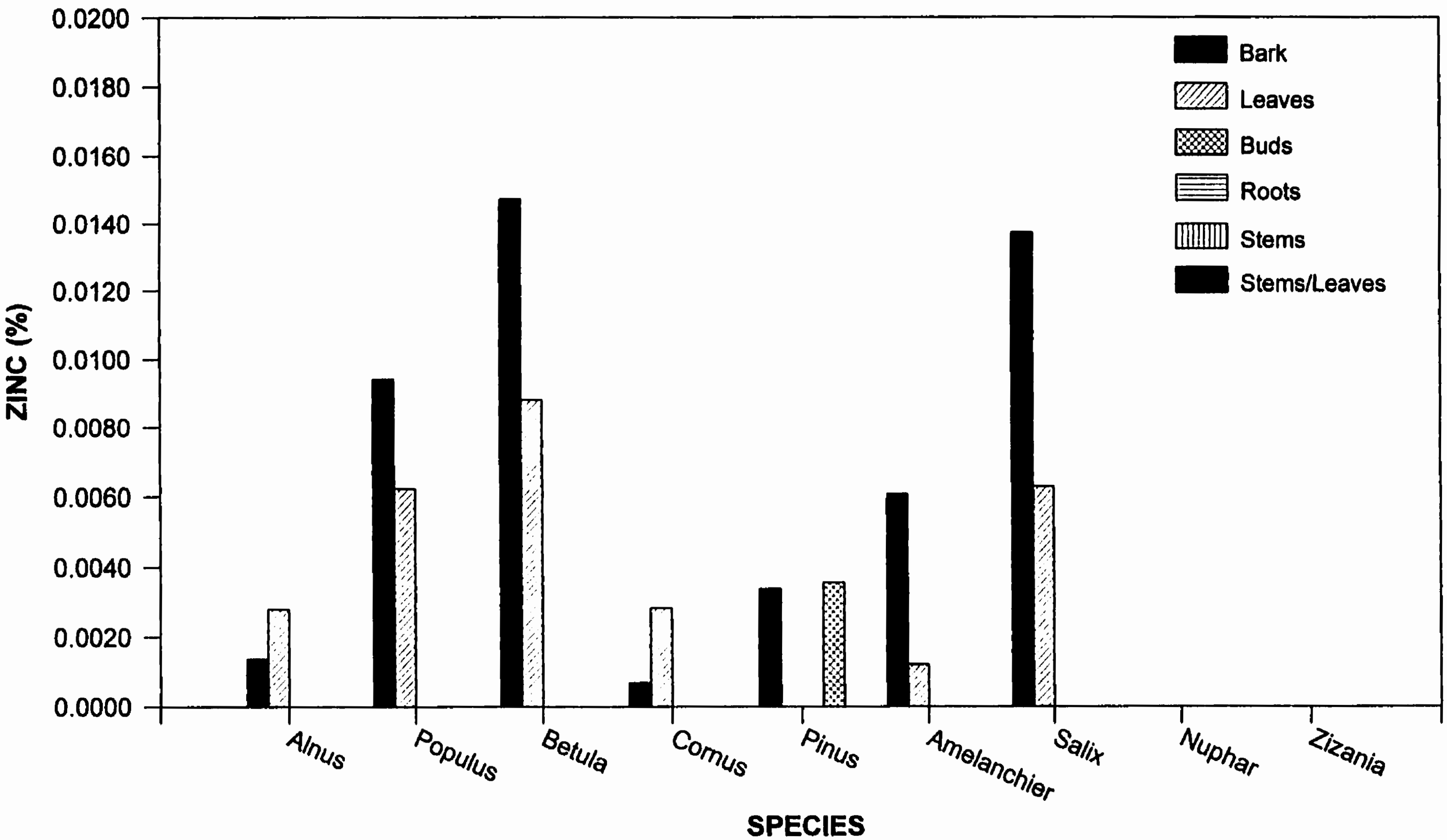

Figure 8: Zinc levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

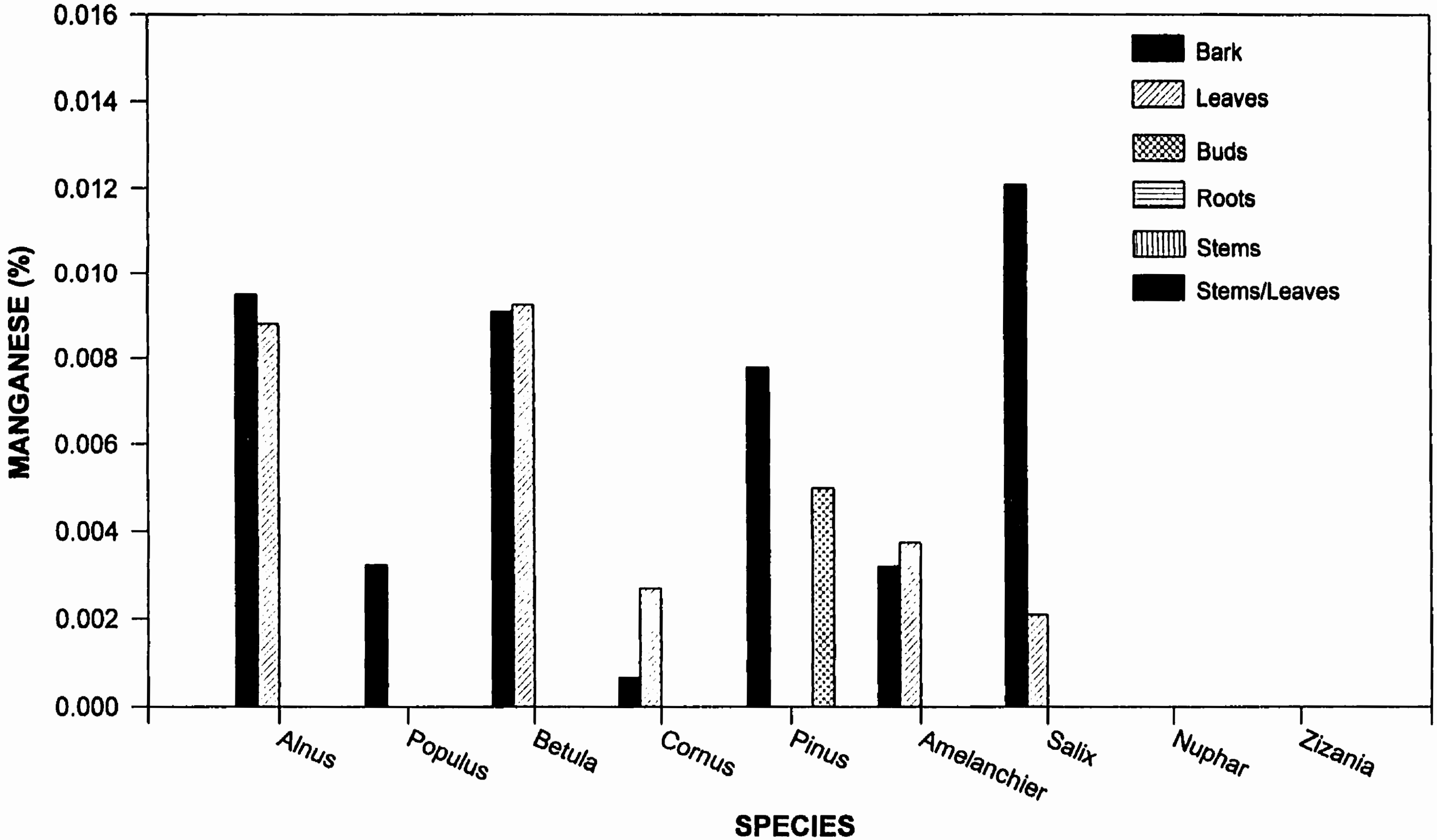

Figure 9: Manganese levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

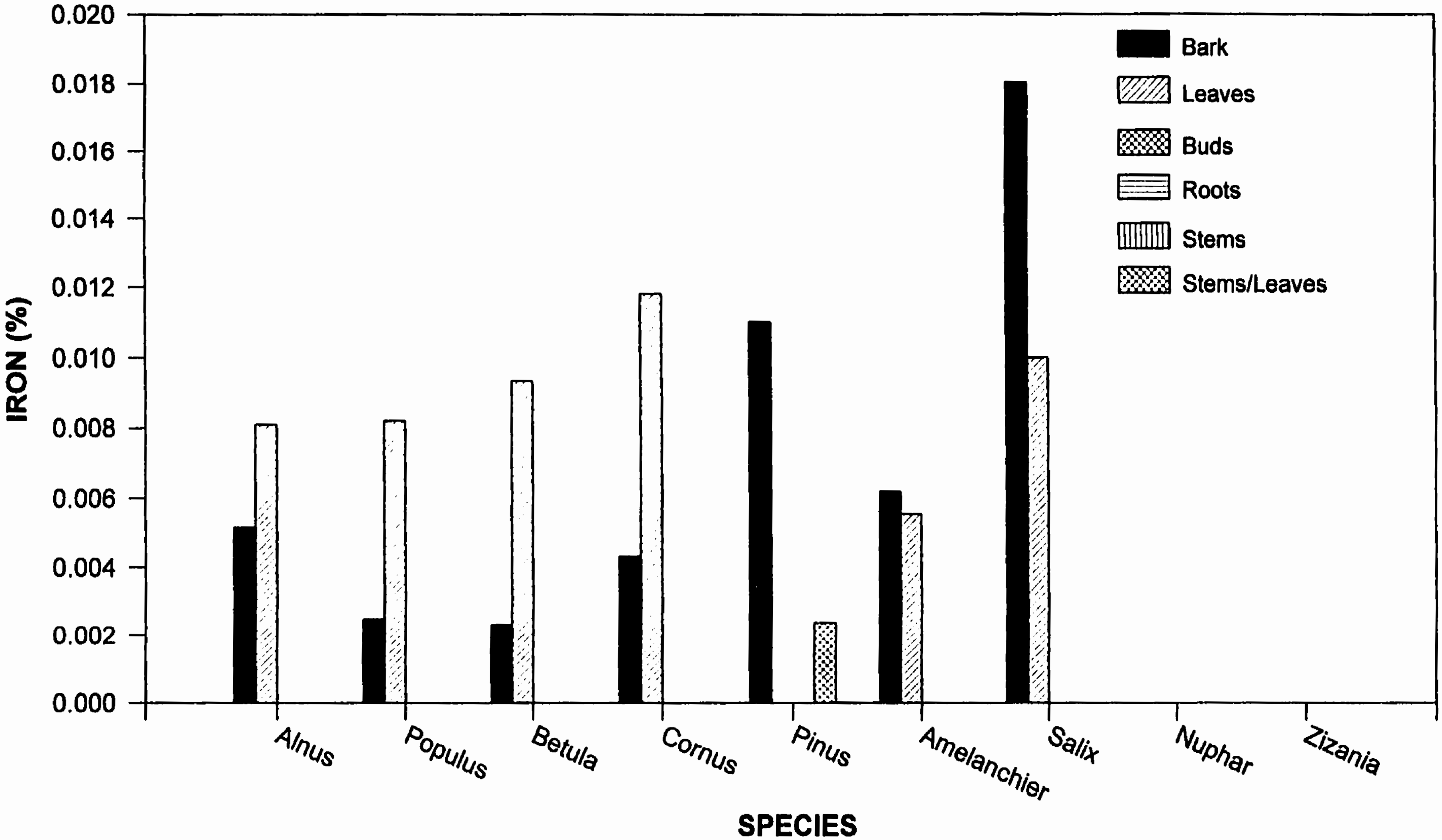

Figure 10: Iron levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

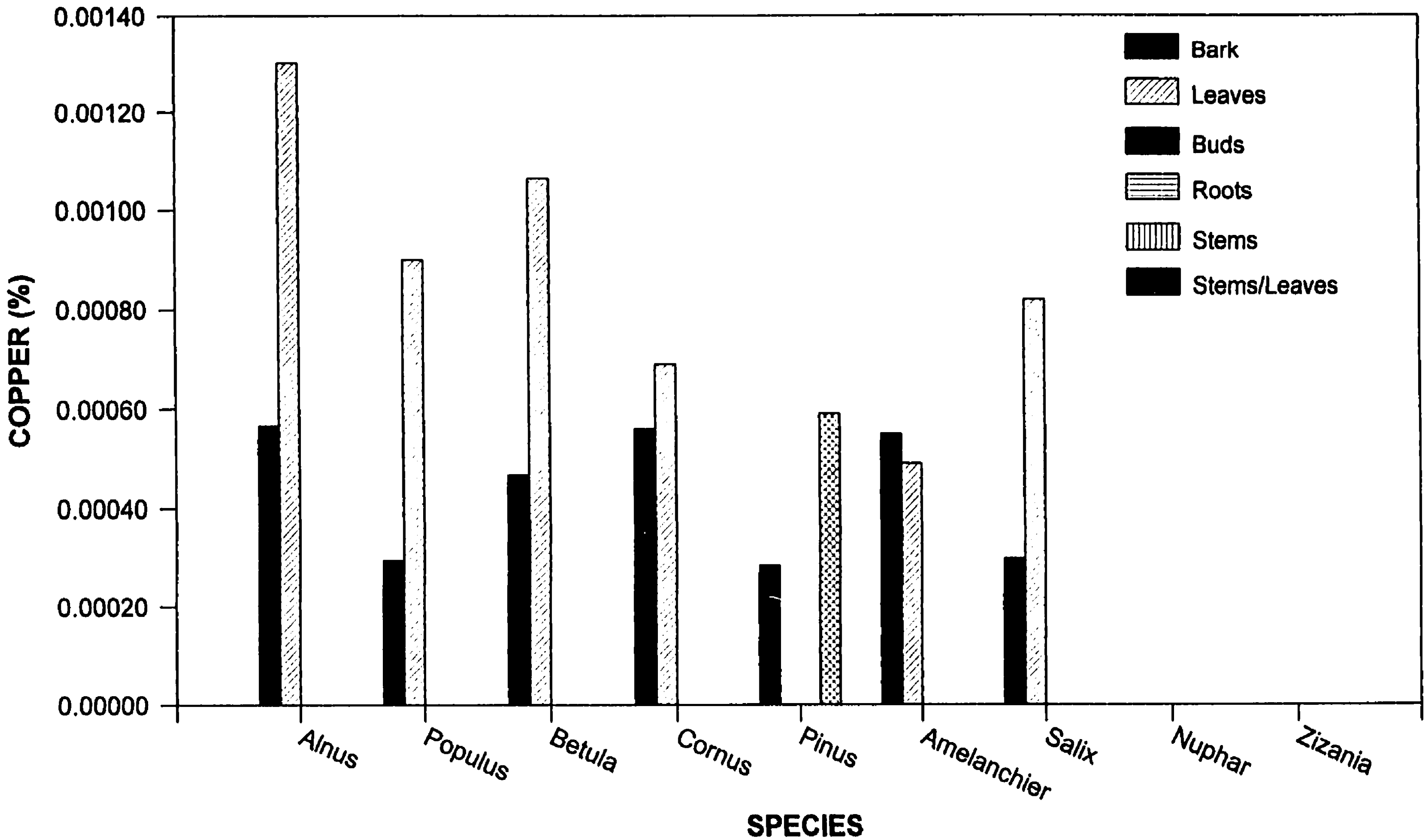

Figure 11: Copper levels (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

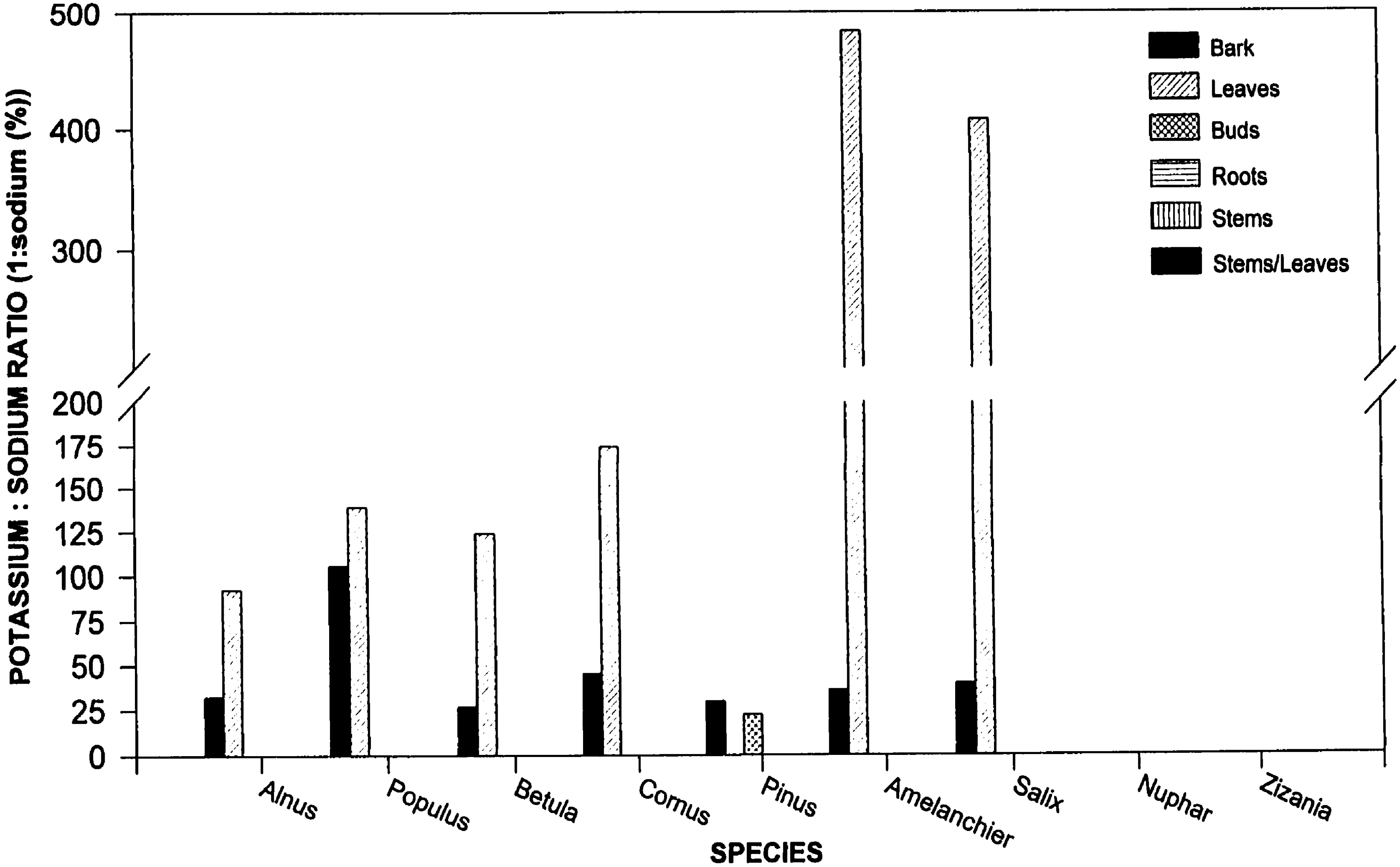

Figure 12: Potassium : sodium ratios (%) for the plant species and plant parts sampled during the growing leaf stage (May - June) of 1993.

the exception of Populus which had a higher ratio, 2-3 times more than the other species. Ratios in the leaves were more variable with Amelanchier and Salix having very high ratios of 1:475 and 1:420.

Nutrient Content During the Mature Leaf Stage

Crude Protein

Crude protein levels were lower in the bark than in the leaves in all of the tree species (67-87% lower) (Figure 13). Crude protein levels in Pinus buds were lower than in the leaves but higher than levels observed in the bark of all of the species. Crude protein levels in the bark were similar for all of the species while levels in the leaves were more variable. Salix had the highest levels for leaves while Cornus had the lowest (with the exception of Pinus needle leaves). Crude protein concentrations in the aquatic species were similar to levels observed in the leaves in the tree species. Levels of crude protein in the aquatic species plant parts were similar with the exception of Nuphar leaves which had higher levels.

Macro Elements

Magnesium, phosphorus (except Alnus), potassium and sulphur (except Alnus) levels were higher in the leaves than in the bark in all of the tree species (Figures 15, 16, 17, 19). Calcium levels in the bark of Alnus, Pinus, Amelanchier and Salix were higher than levels observed in those species' leaves while levels in the bark of Populus, Betula and Cornus were similar or lower than the levels of

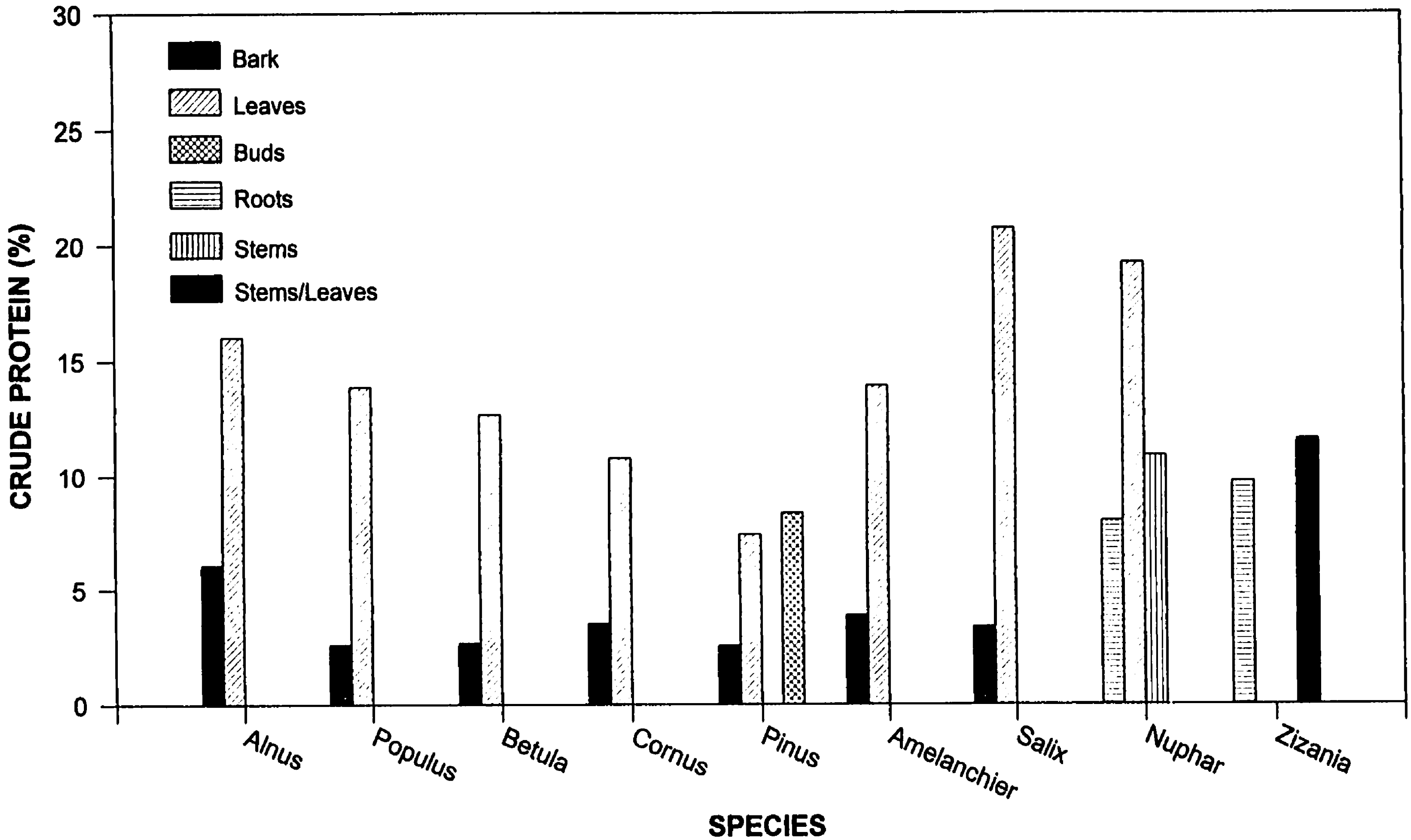

Figure 13: Crude protein levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

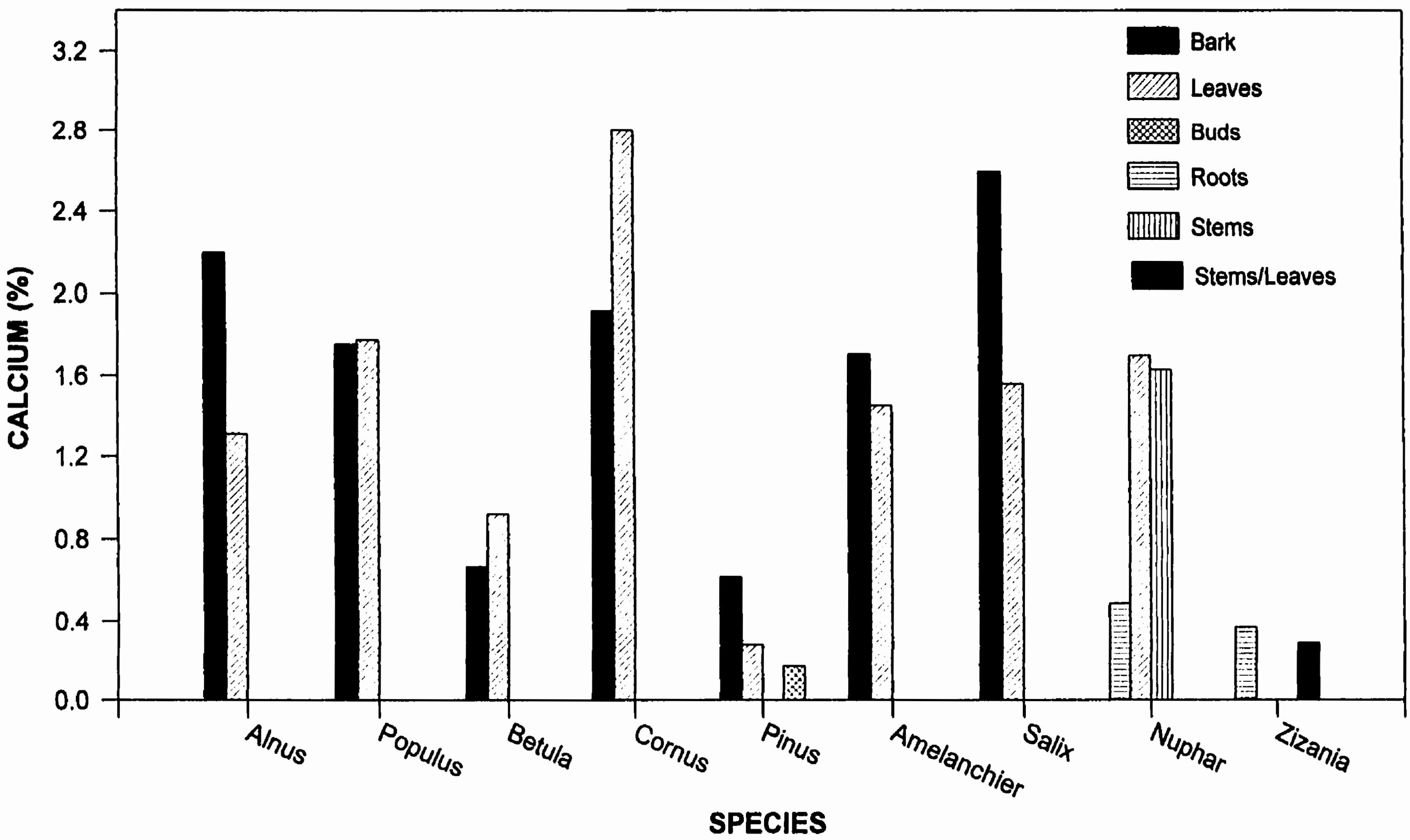

Figure 14: Calcium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

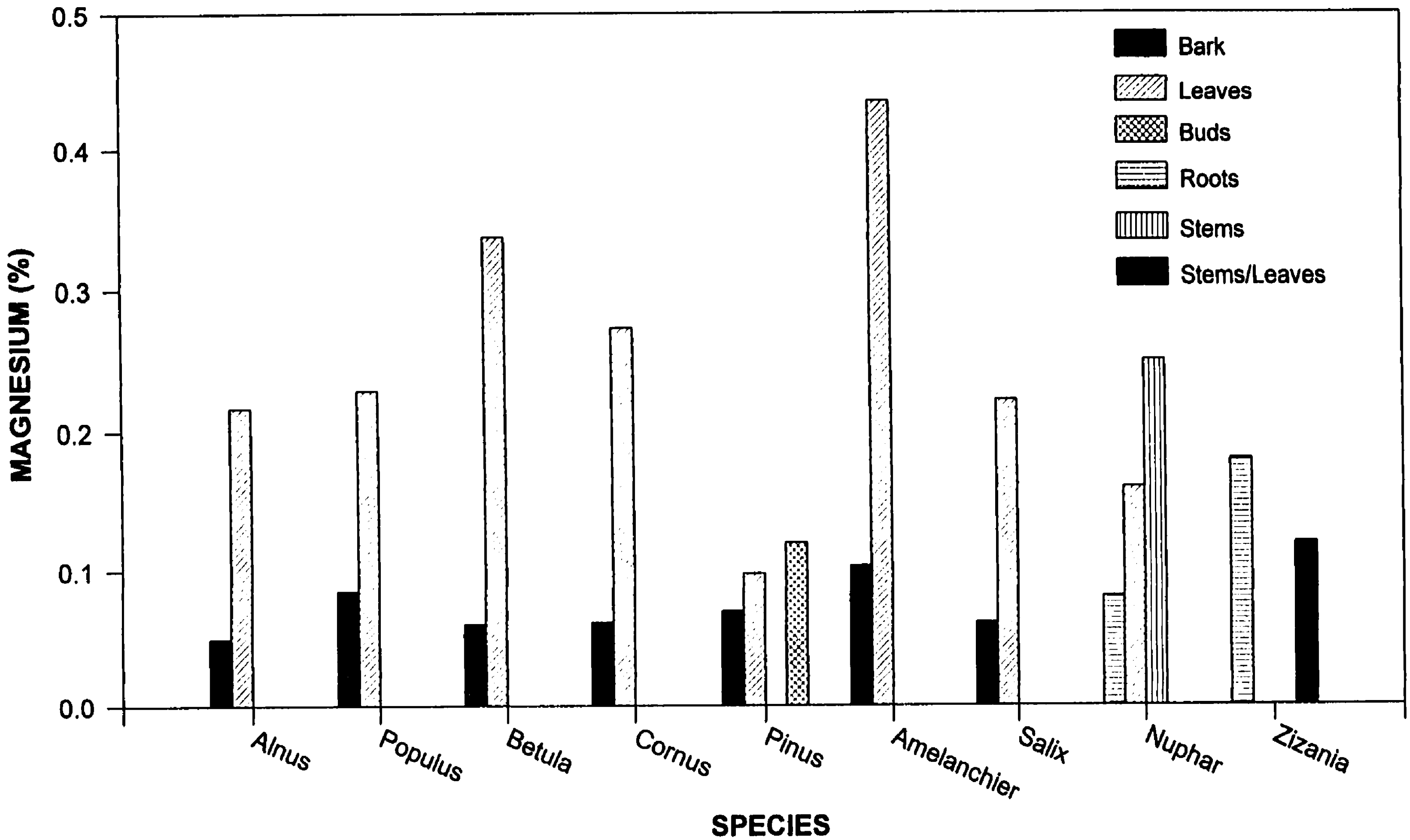

Figure 15: Magnesium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

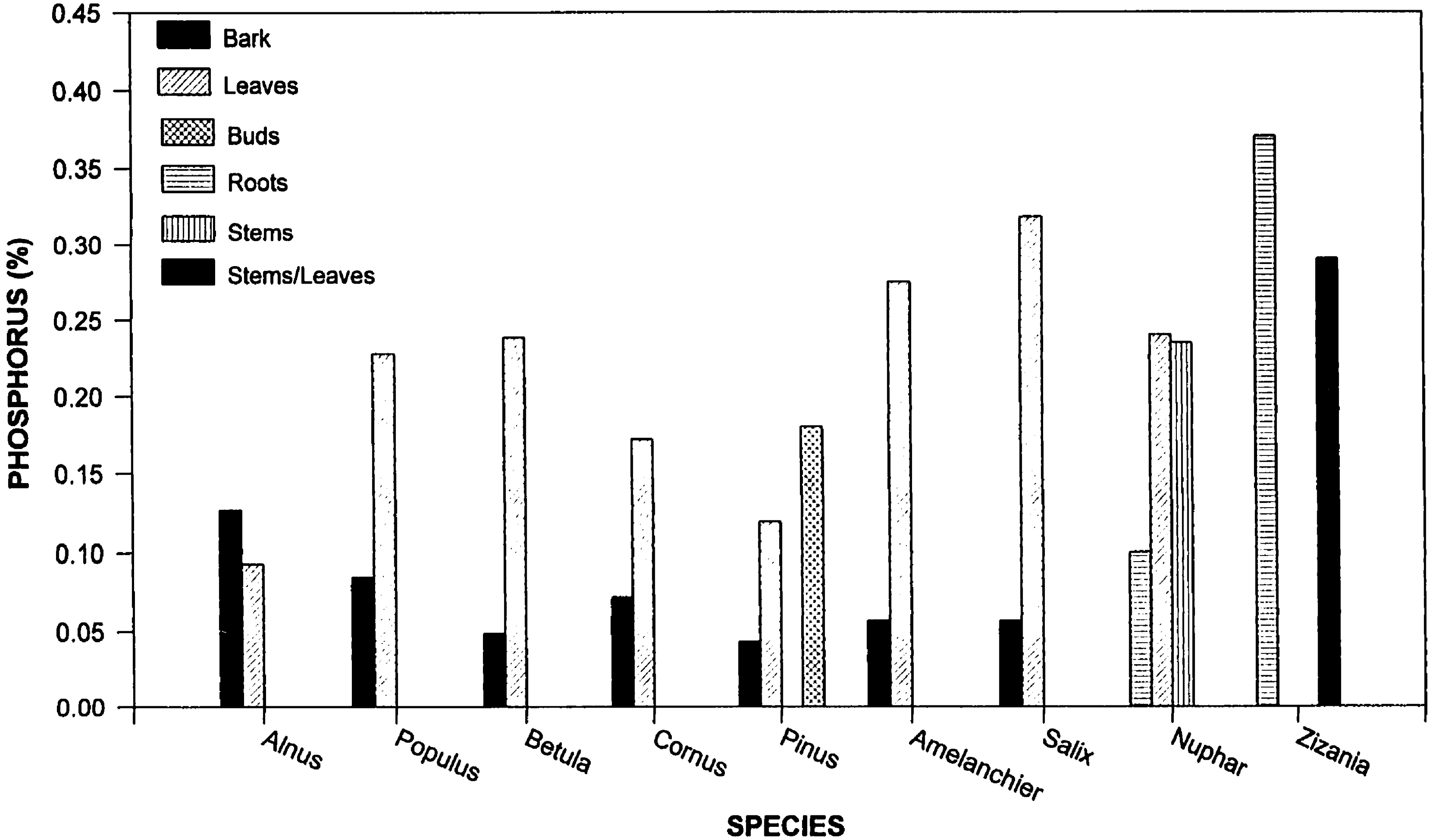

Figure 16: Phosphorus levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

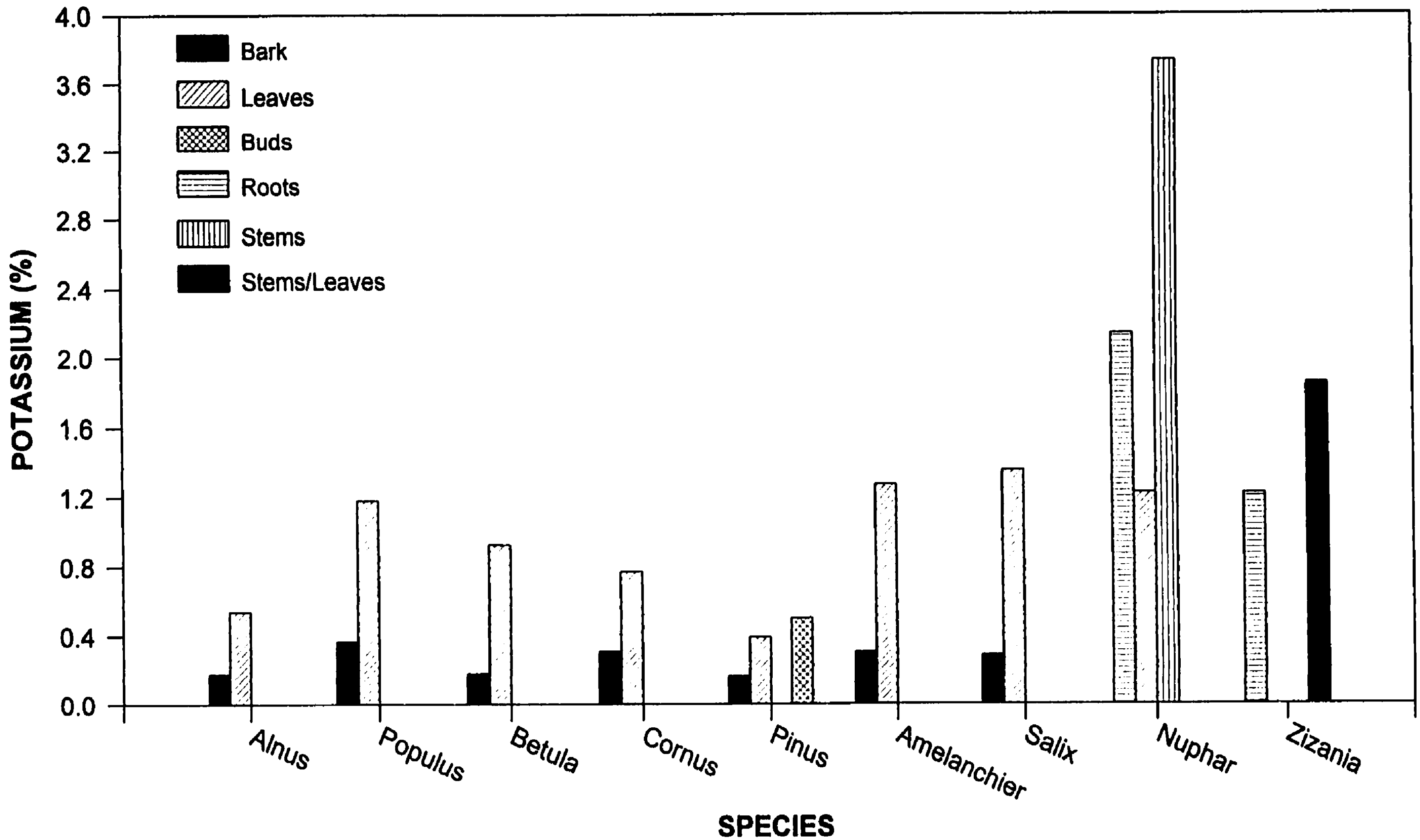

Figure 17: Potassium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

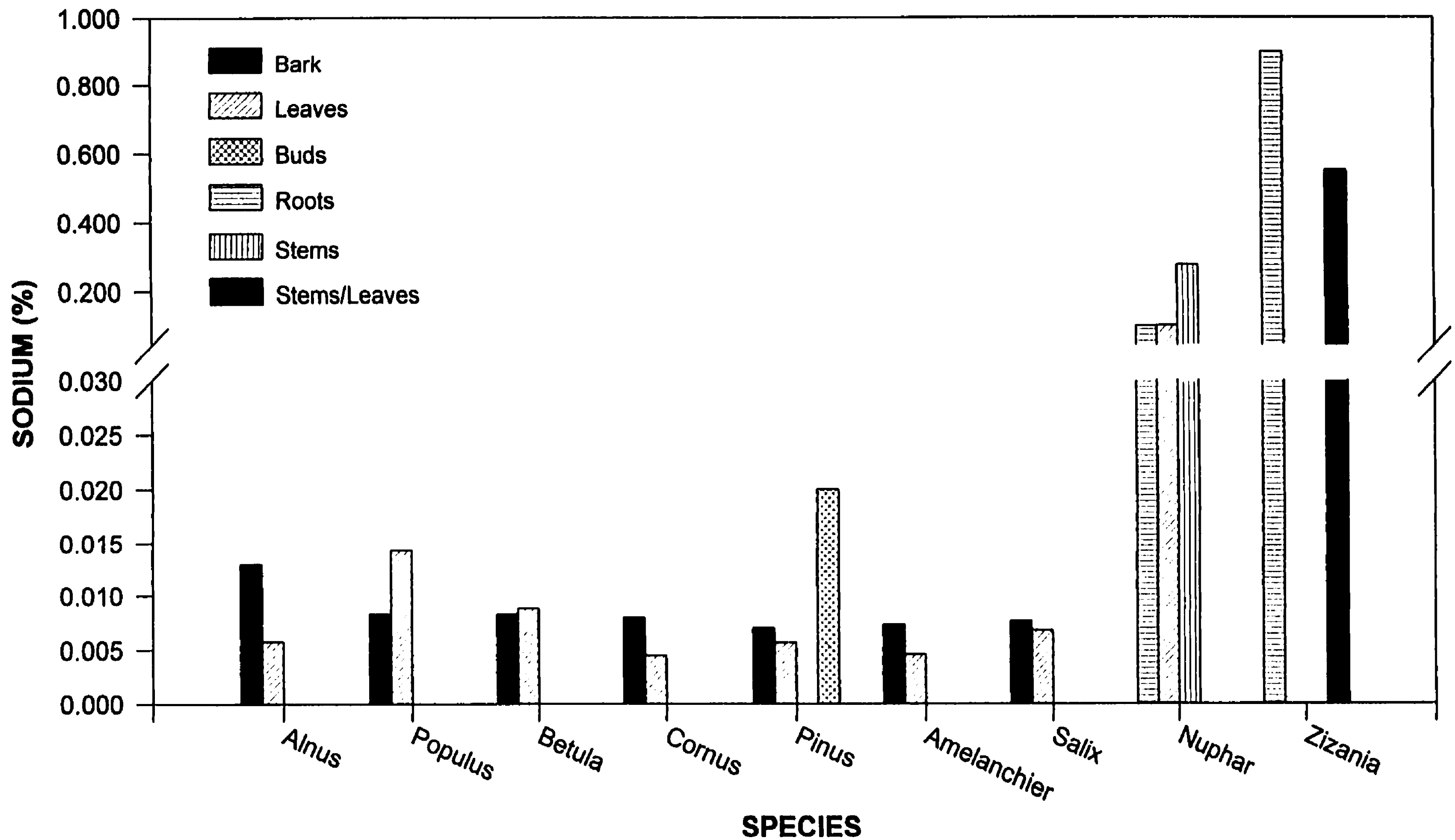

Figure 18: Sodium levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

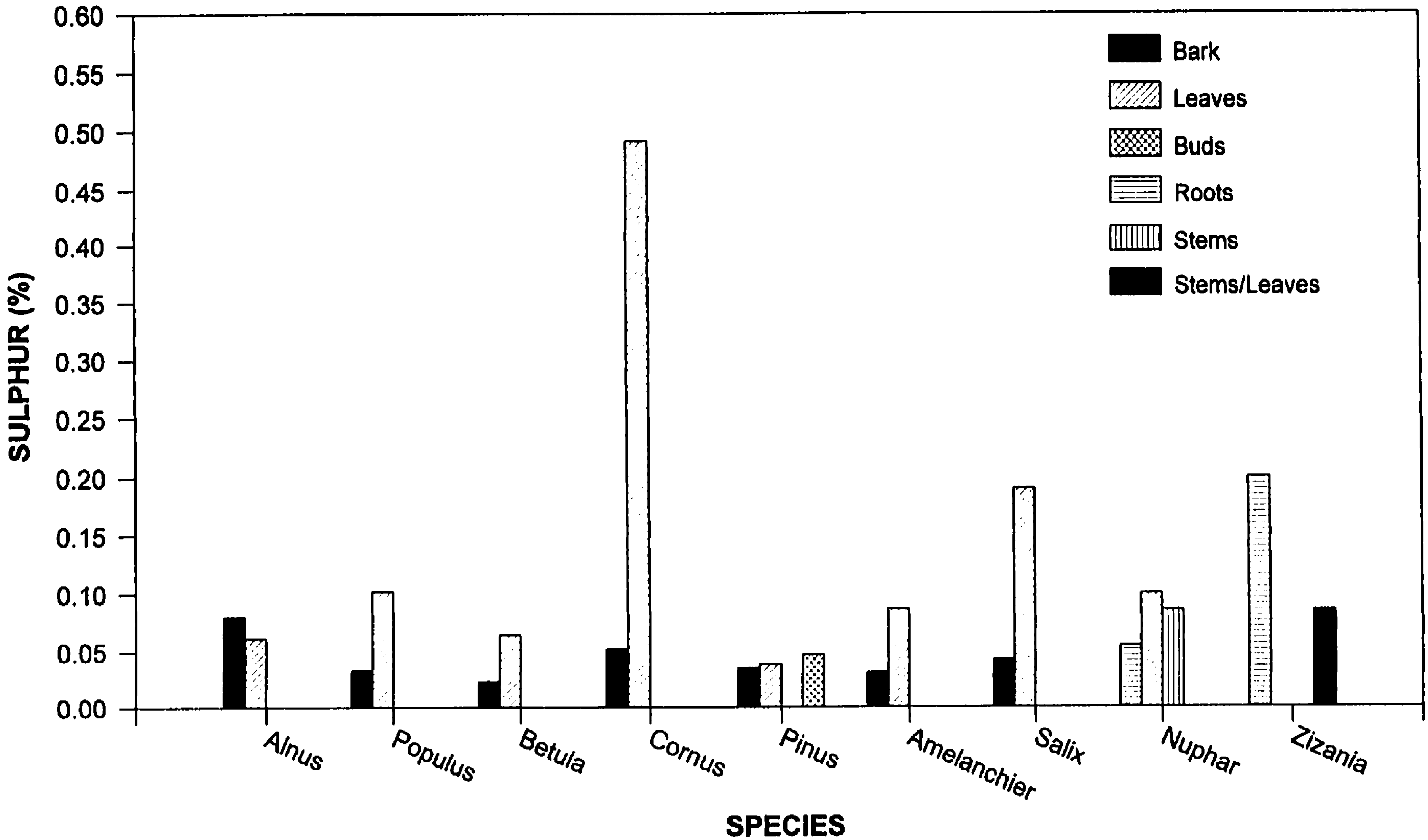

Figure 19: Sulphur levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

their leaves (Figure 14). Sodium levels were similar in both the bark and the leaves of all of the tree species (Figure 18).

Pinus buds had low levels of calcium, magnesium and sulphur, similar to levels of these nutrients in the bark (Figures 14, 15, 19). As well, moderate levels (levels higher than in the bark but lower than in the leaves) of phosphorus and potassium were observed in Pinus buds (Figures 16, 17). Pinus buds also had a high level of sodium, 1.5-5x higher than for the bark or leaves of the deciduous species (Figure 18).

Macro element levels were similar in the bark between species for magnesium, phosphorus, potassium, sodium and sulphur while calcium levels were variable (Figures 14, 15, 16, 17, 18, 19). Sodium levels in the leaves were similar between species, however, levels of calcium, magnesium, phosphorus, potassium and sulphur were more variable (Figures 14, 15, 16, 17, 18, 19). Cornus leaves had a very large amount of sulphur (2.5-10x higher than that observed for the other species).

Calcium levels in Zizania roots and stems/leaves and Nuphar roots were low while levels in Nuphar leaves and stems were moderate, at levels similar to those observed in the tree leaves (Figure 14). Magnesium and phosphorus levels were moderate for the two aquatic species and fell within the ranges observed for bark and leaves with the exception of Zizania roots which had the highest levels of phosphorus of all the species and plant parts sampled (Figures 15, 16). Levels of potassium in the aquatic species were very high with Nuphar stems having a potassium level 2.7x more than the highest potassium levels in the leaves of the tree species. Nuphar roots and Zizania stems/leaves had levels 1.4x more than the highest levels in the leaves of the tree species while Zizania roots and Nuphar leaves had levels similar to that for the highest levels observed for tree leaves (Figure 17). The aquatic species also had very high levels of sodium. Zizania roots and stems/leaves had 45 and 25x more sodium respectively compared to the highest level observed in the tree species (Pinus buds). As well, Nuphar stems, leaves and roots had 15, 5 and 5x as much sodium as the highest level observed in the tree species respectively (Figure 18). In addition, Zizania roots had a high level of sulphur, with levels that were greater than those observed in the leaves of all of the tree species except Cornus. Levels of sulphur in Zizania stems/leaves and Nuphar roots, leaves and stems were within the range observed in the tree bark and leaves (Figure 19).

Trace Elements

Levels of manganese, iron (except Pinus) and copper (except Cornus) were lower in the bark compared to the leaves of the tree species (Figures 21, 22, 23). Zinc levels were more variable with Alnus and Populus having slightly lower zinc levels in the bark compared to the leaves while the remaining tree species had higher zinc levels in the bark (Figure 20).

Pinus buds had low levels of manganese and copper and moderate levels of zinc and iron, lower than levels in the leaves but higher than levels in the bark of the tree species (Figures 20, 21, 22, 23).

Manganese, iron and copper levels in the bark were similar between species while zinc levels were variable (Figures 21, 22, 23). Likewise,all of the

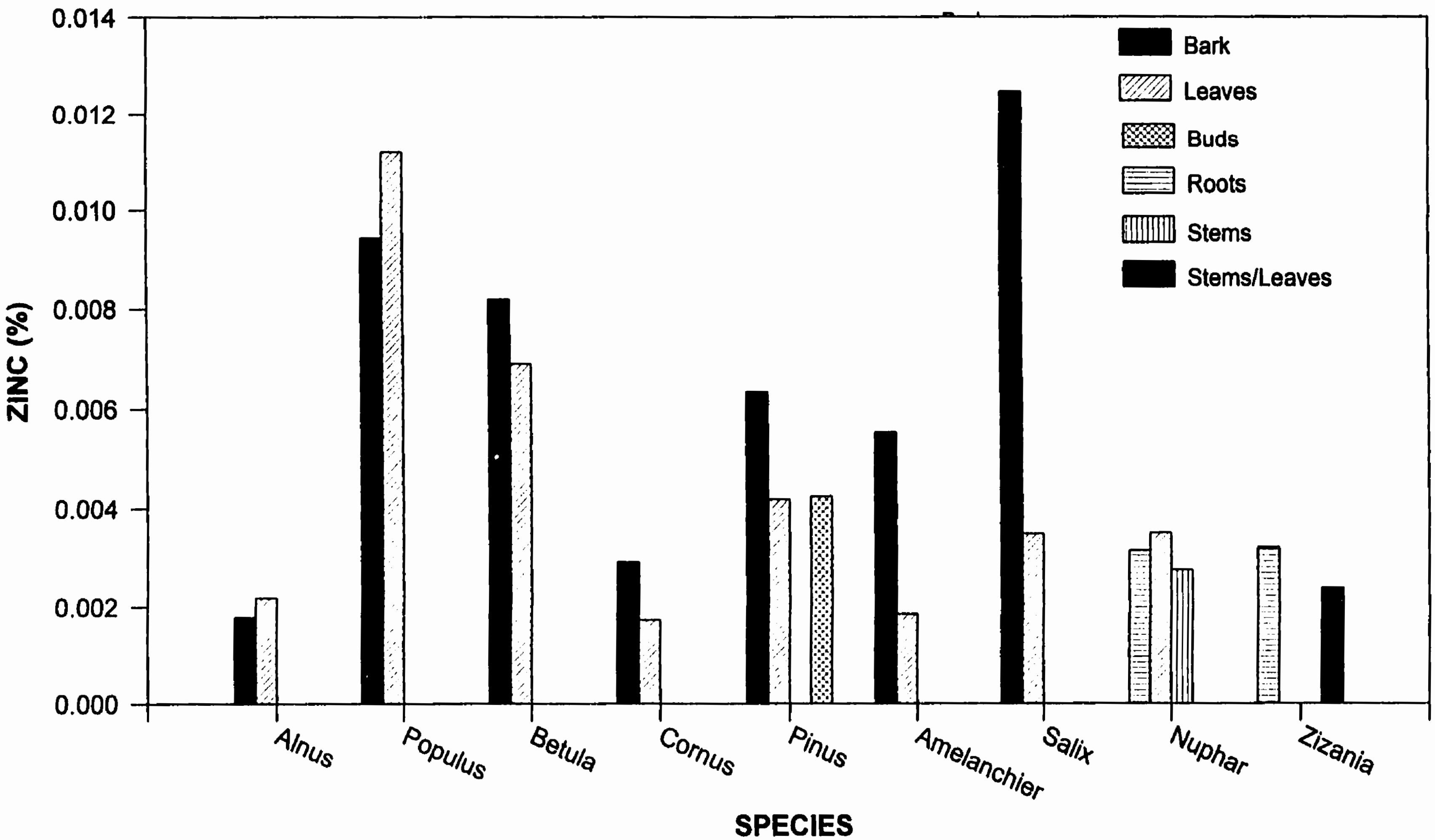

Figure 20: Zinc levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

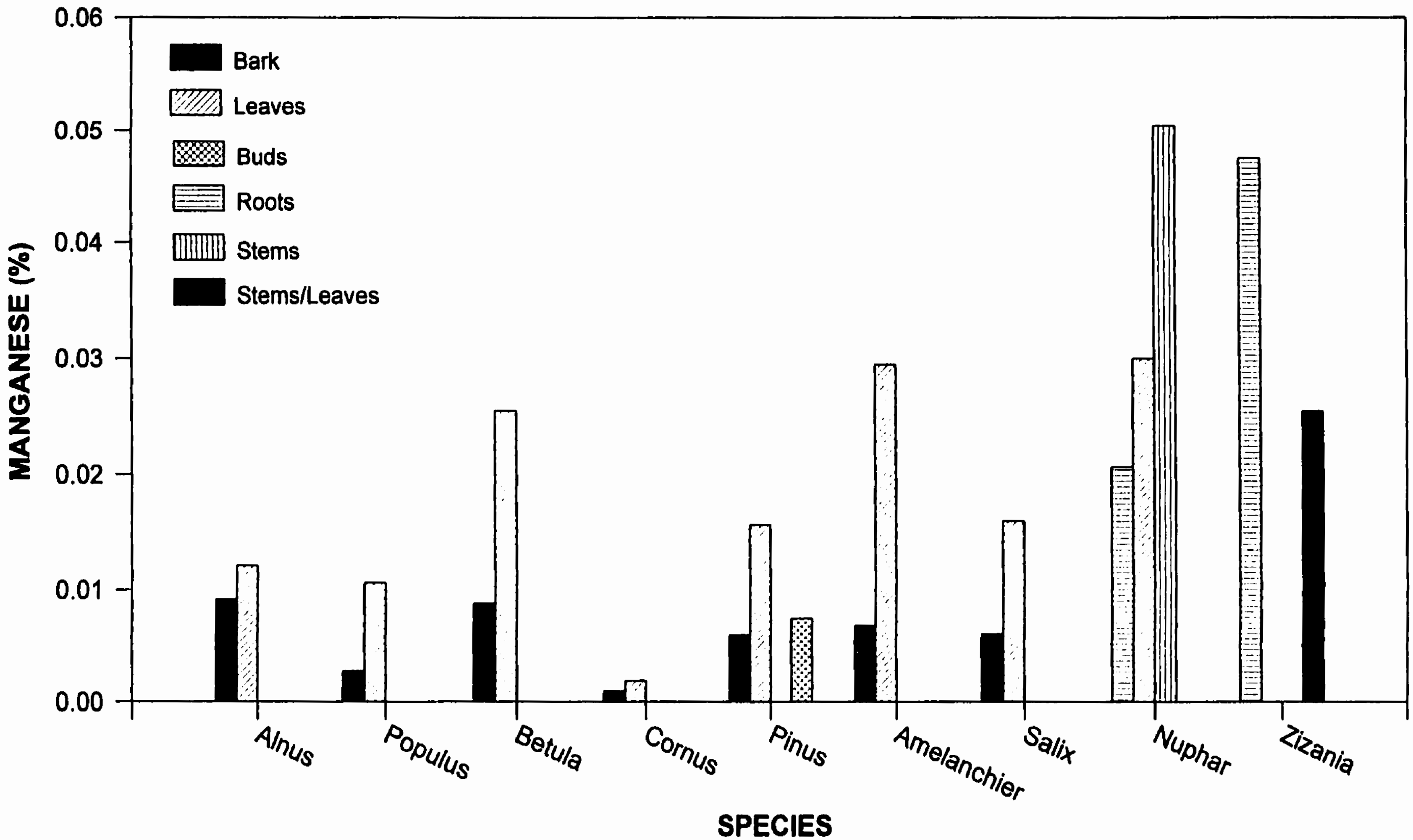

Figure 21: Manganese levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

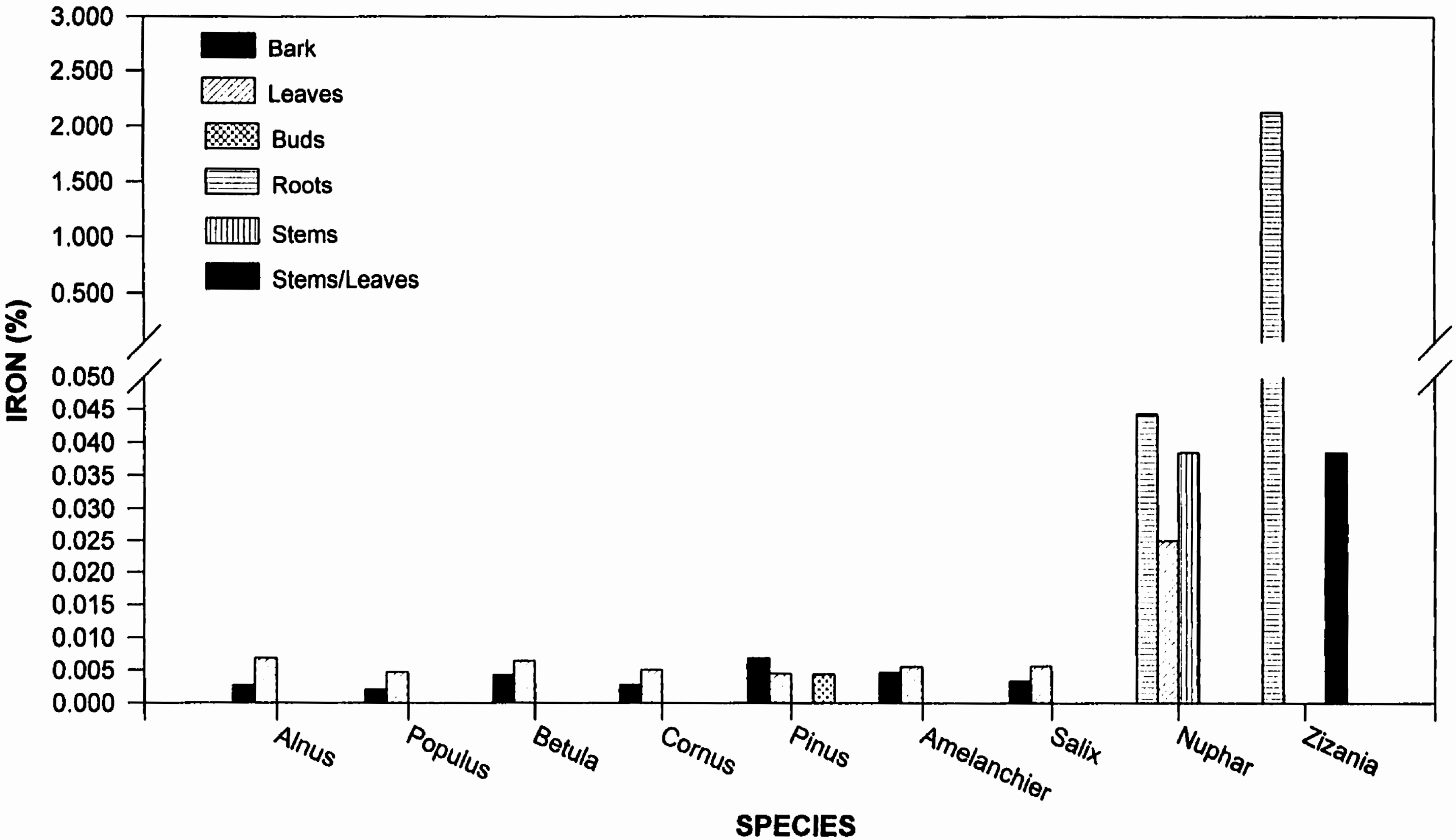

Figure 22: Iron levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

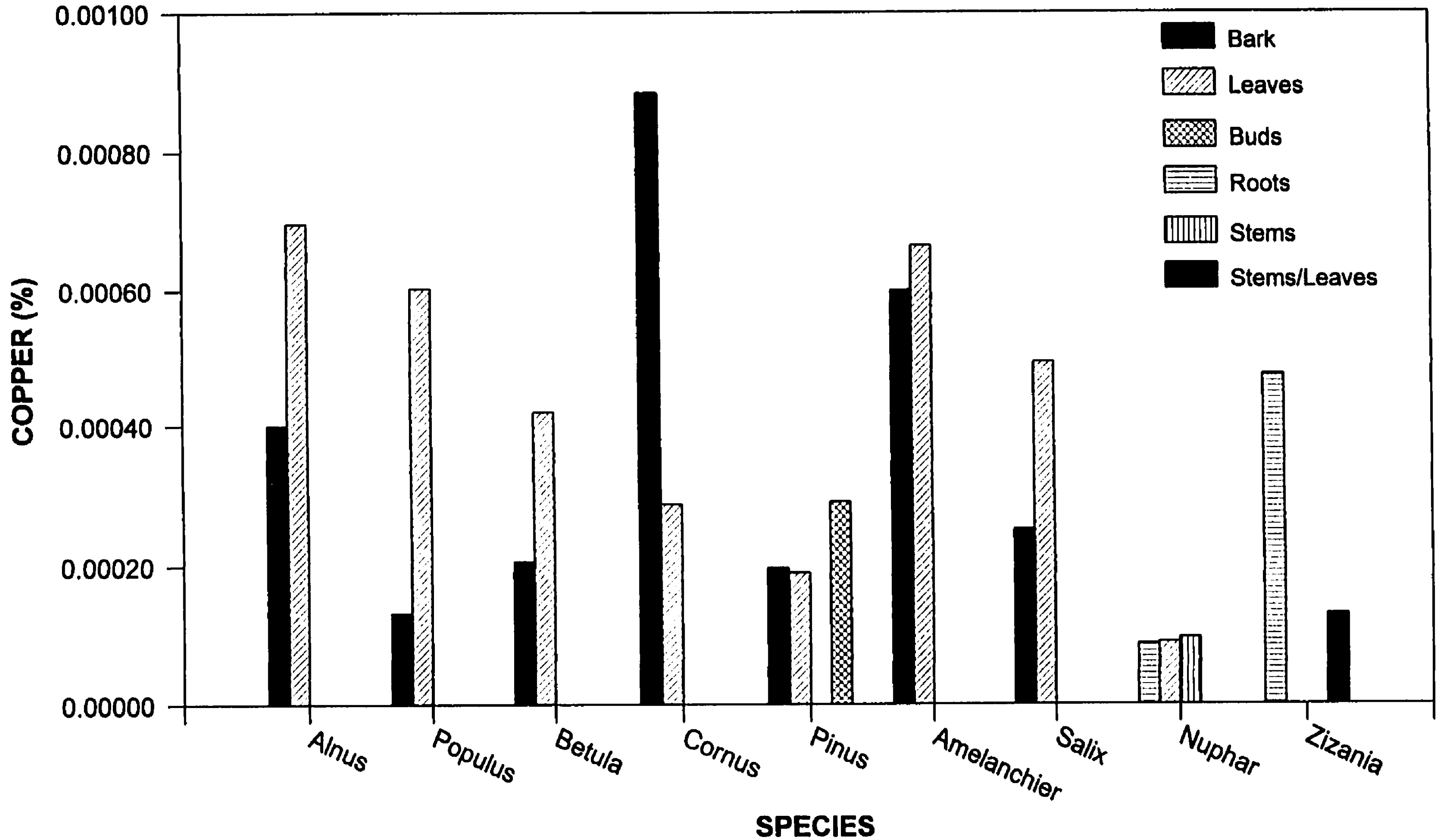

Figure 23: Copper levels (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

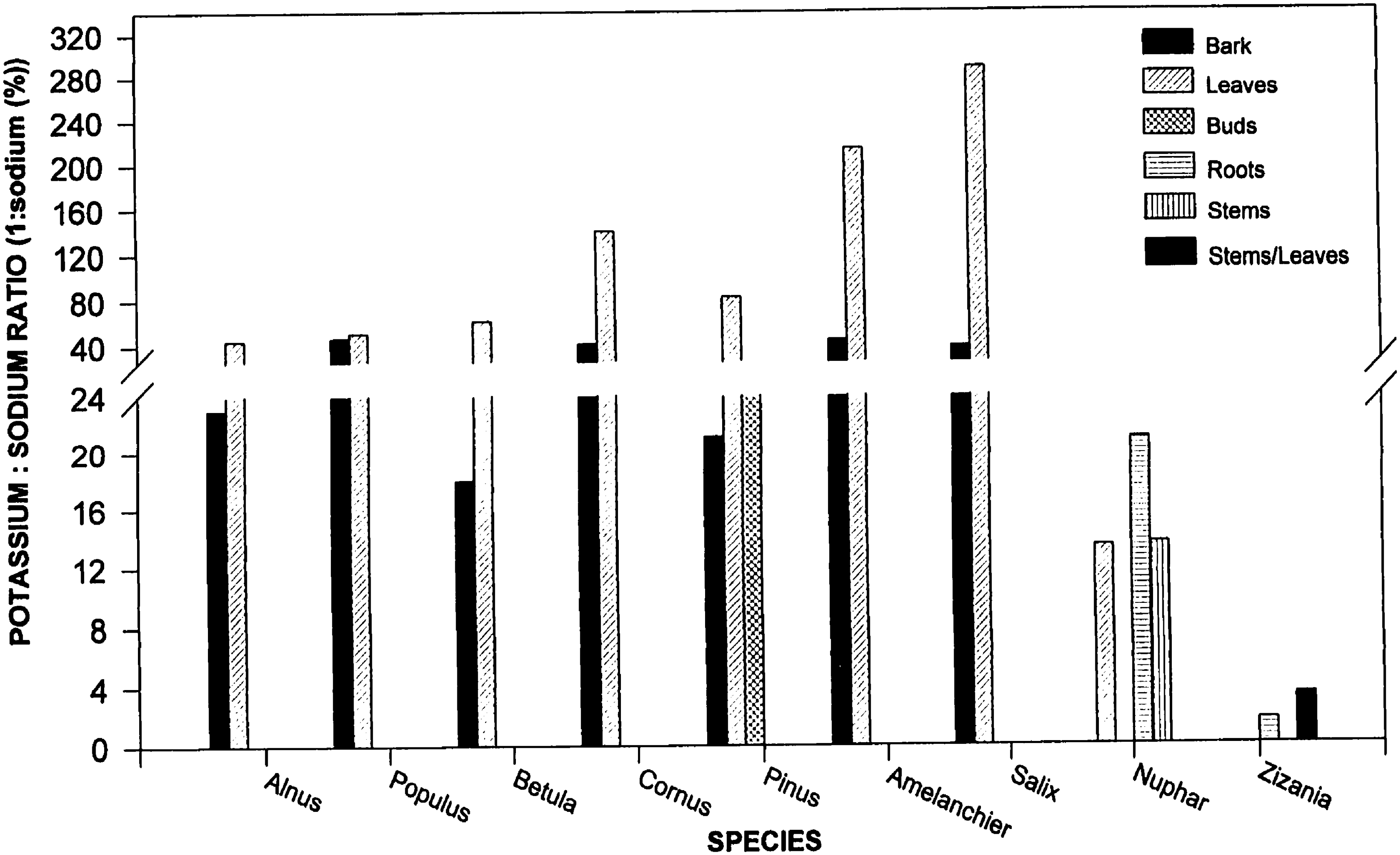

Figure 24: Potassium : sodium ratios (%) for the plant species and plant parts sampled during the mature leaf stage (July - August) of 1993.

trace elements were variable in the leaves between species (Figures 20, 21, 22, 23).

The aquatic species had low levels of zinc and copper with levels comparable to the lowest levels in the tree species and comparable to the range observed in the bark and leaves respectively (Figures 20, 23). The aquatic species had higher levels of manganese with Nuphar stems and Zizania roots having approximately 2.0x more manganese than the highest level observed for the tree species. Nuphar leaves and roots and Zizania stems/leaves had levels of manganese similar to the higher levels observed in the leaves of tree species (Figure 21). Zizania roots had the highest iron level, 314x greater than the highest level observed in the tree species. Zizania stems/leaves and Nuphar stems had 8.6x more iron and Nuphar roots and leaves had 6.4 and 4.2x more iron respectively than the tree species (Figure 22).

Potassium : Sodium Ratio

Bark potassium:sodium ratios were lower than those levels observed for the leaves in all of the tree species (Figure 24). During the mature leaf stage, the potassium:sodium ratios for the bark for all of the tree species are fairly similar, less than 1:50. The ratios observed in the leaves, however, are more variable with Salix leaves having a potassium:sodium ratio of 1:400, much higher than the other species. Populus and Amelanchier also had high ratios. Pinus buds had a low ratio similar to the ratios observed for the bark at 1:25 (Figure 24).

The potassium:sodium ratios for the aquatic species show that they have very low potassium:sodium ratios, especially Zizania compared to the bark and leaves of the tree species (Figure 24). The roots of Zizania have a 1:2 ratio while the stem/leaves have 1:3 ratio. Nuphar has higher ratios (3-5x more) in its roots, stems and leaves at ratios ranging from 1:14 to 1:22.

Nutrient Content During the Senescence Leaf Stage (September - October)

Crude Protein

Crude protein concentrations were lower in the tree species' bark compared to the leaves (34-63% lower). Levels were similar in the bark and in the leaves between species (Figure 25).

The aquatic species had crude protein levels similar to those observed in the tree species' leaves with Nuphar leaves having the highest crude protein level of all of the species and plant parts (Figure 25).

Macro Elements

Magnesium (except Alnus), phosphorus, potassium (except Alnus) and sulphur levels were higher in the bark than in the leaves for all of the tree species (Figures 27, 28, 29, 31). Calcium levels were variable with Alnus, Amelanchier and Salix leaves having higher levels and the remainder of the species having higher levels in the bark (Figure 26). Sodium levels were similar in both the bark and the leaves of the tree species (Figure 30).

Phosphorus, potassium, sodium and sulphur levels were similar in the bark between species while calcium and magnesium levels were variable

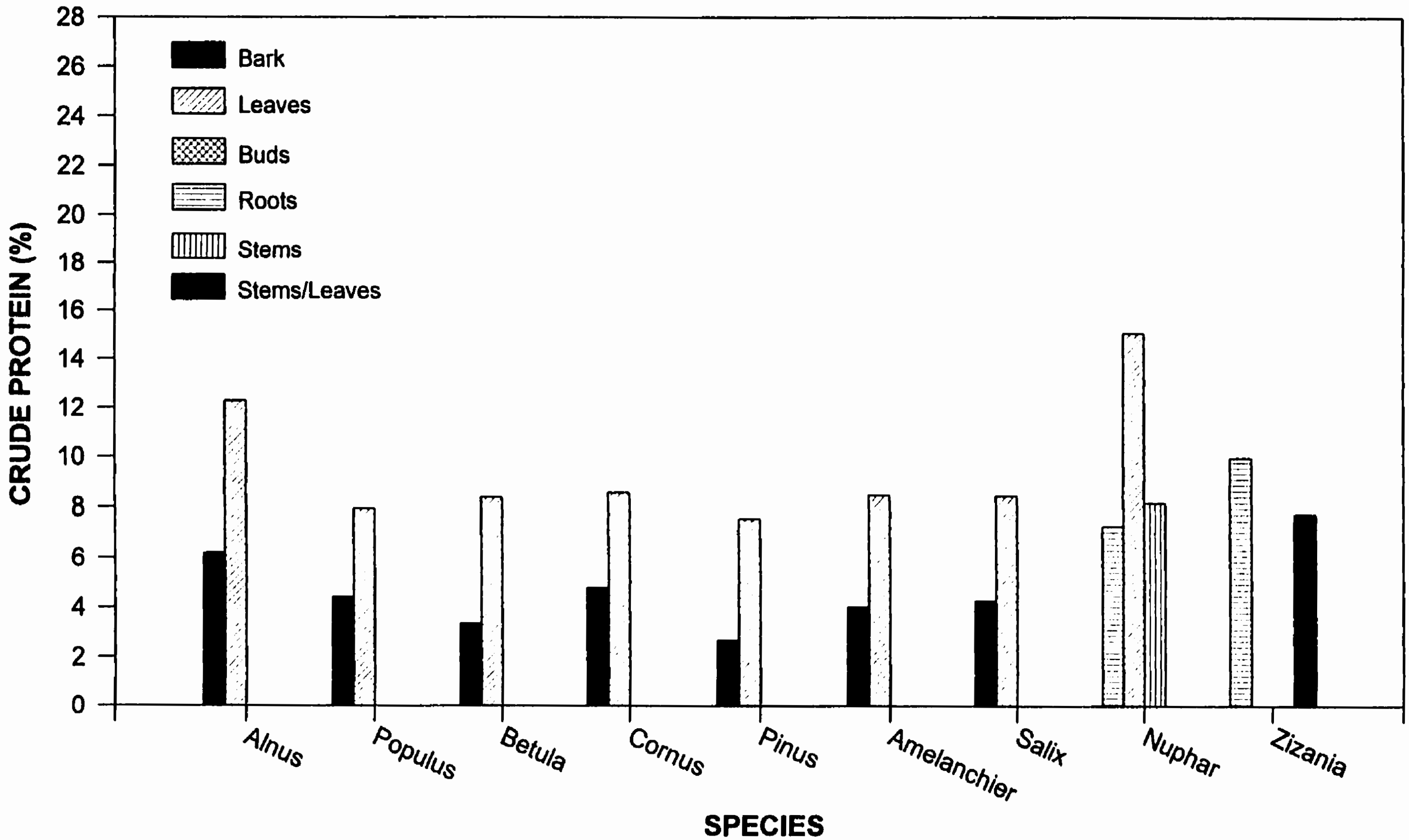

Figure 25: Crude protein levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

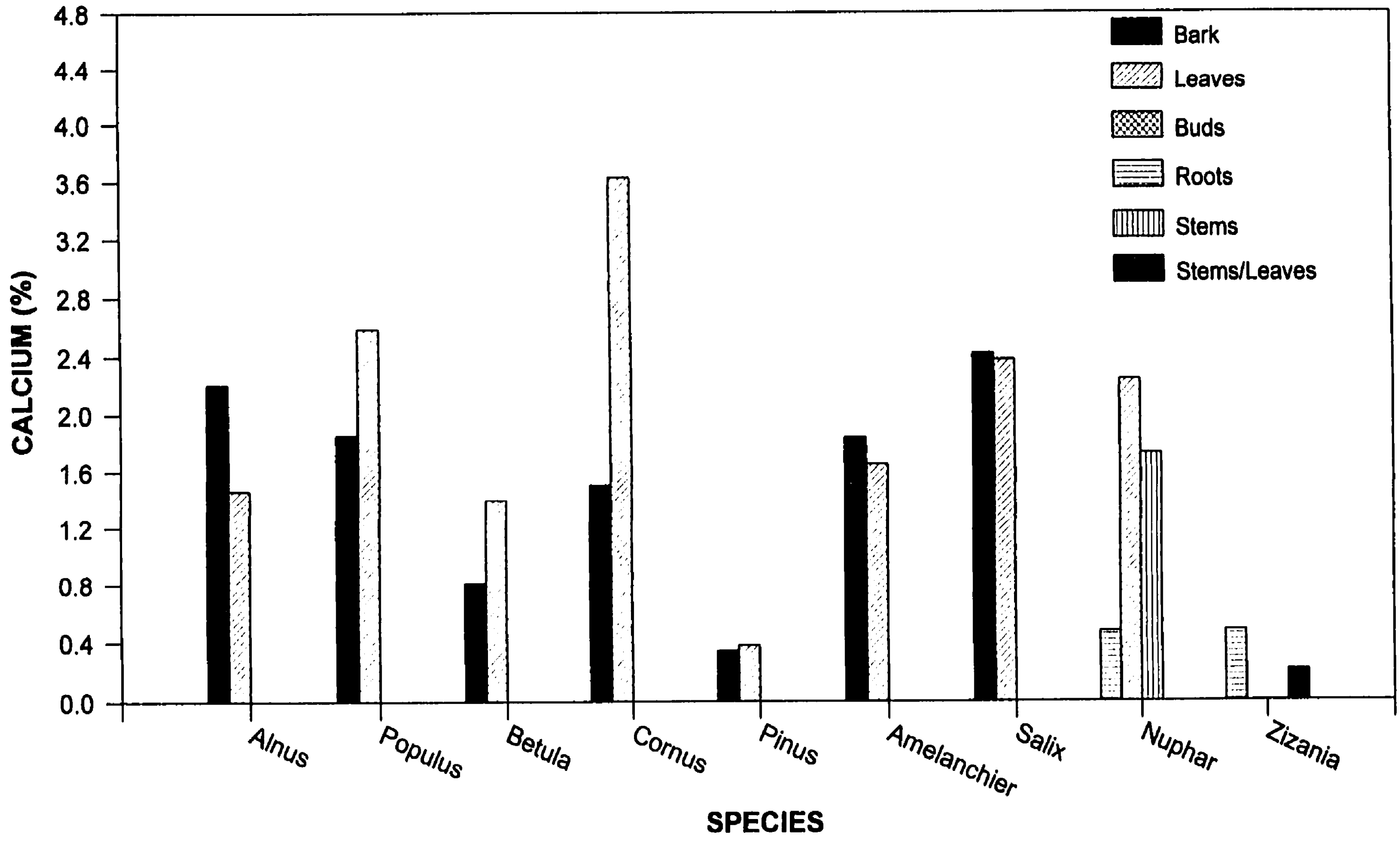

Figure 26: Calcium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

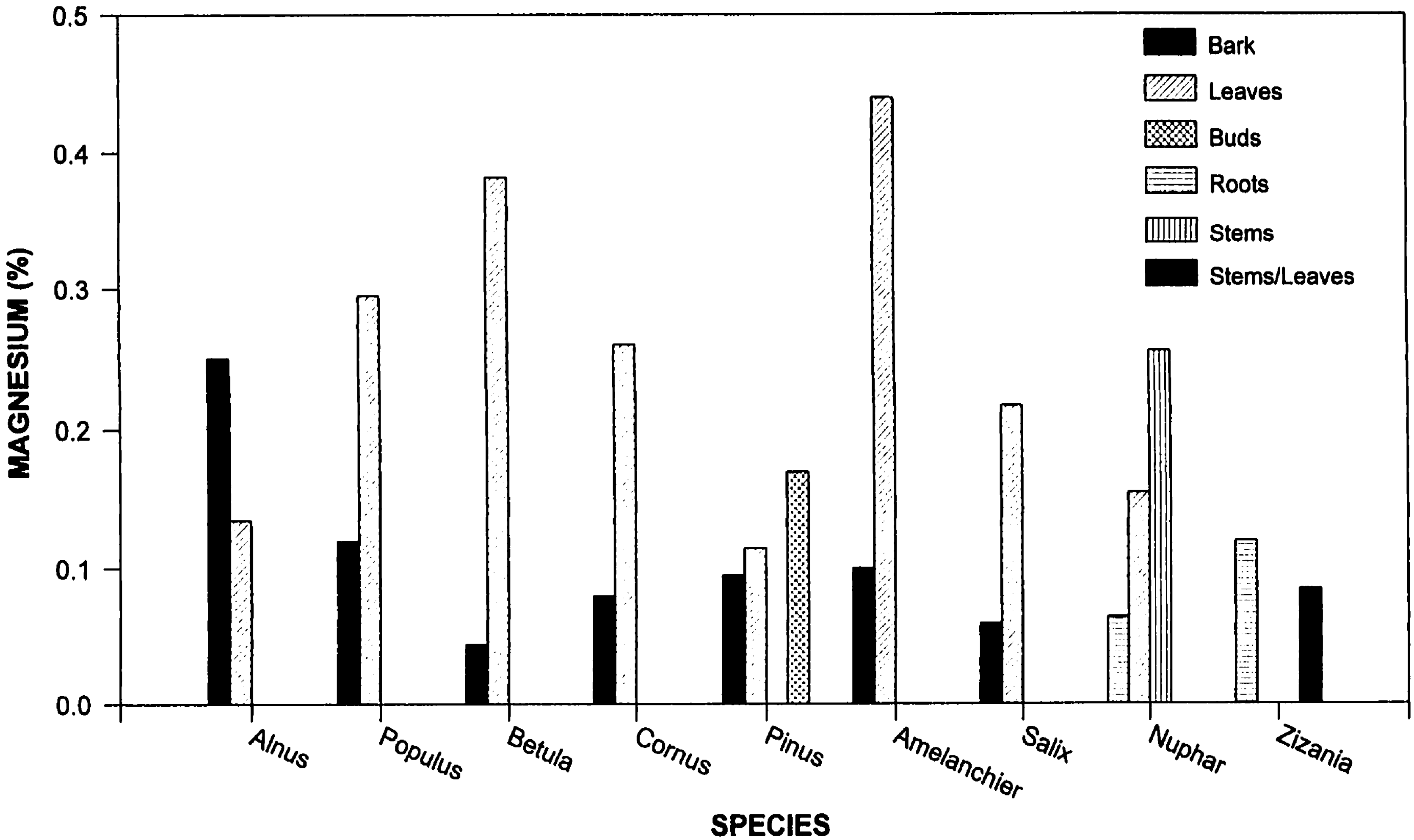

Figure 27: Magnesium levels (%) for the plant species and plant parts during the senescence leaf stage (September - October) of 1993.

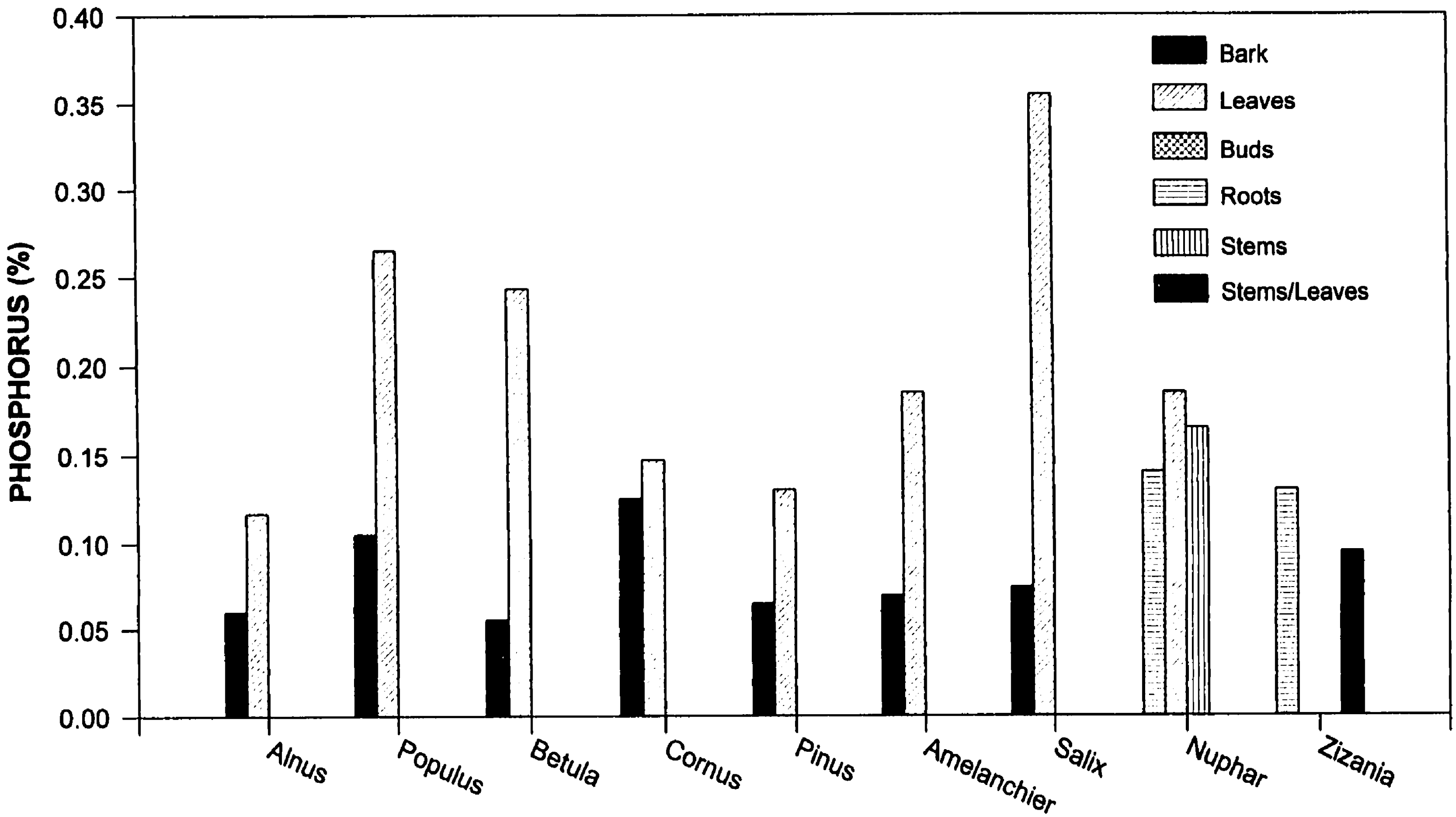

Figure 28: Phosphorus levels (%) for the plant species and plant parts during the senescence leaf stage (September - October) of 1993.

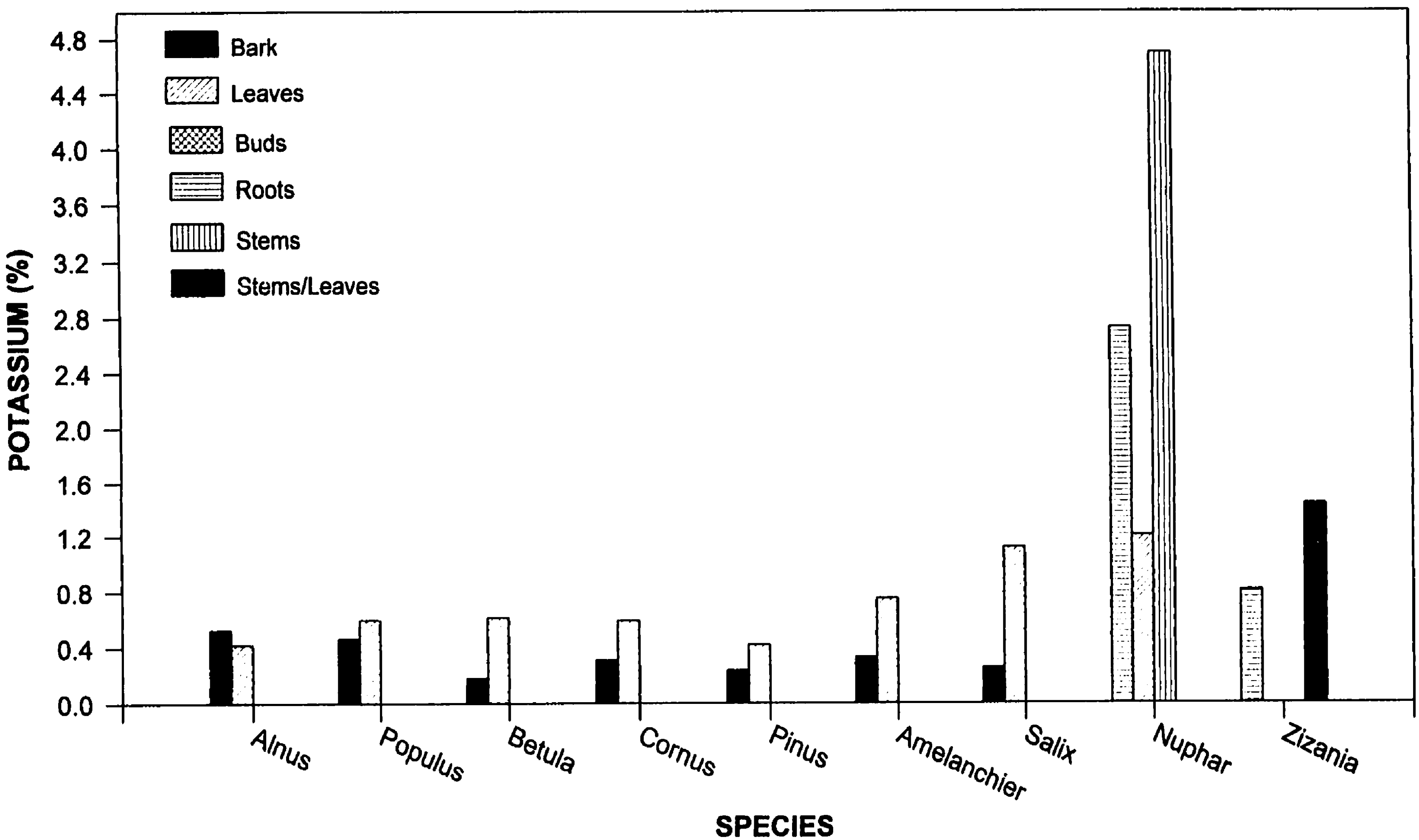

Figure 29: Potassium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

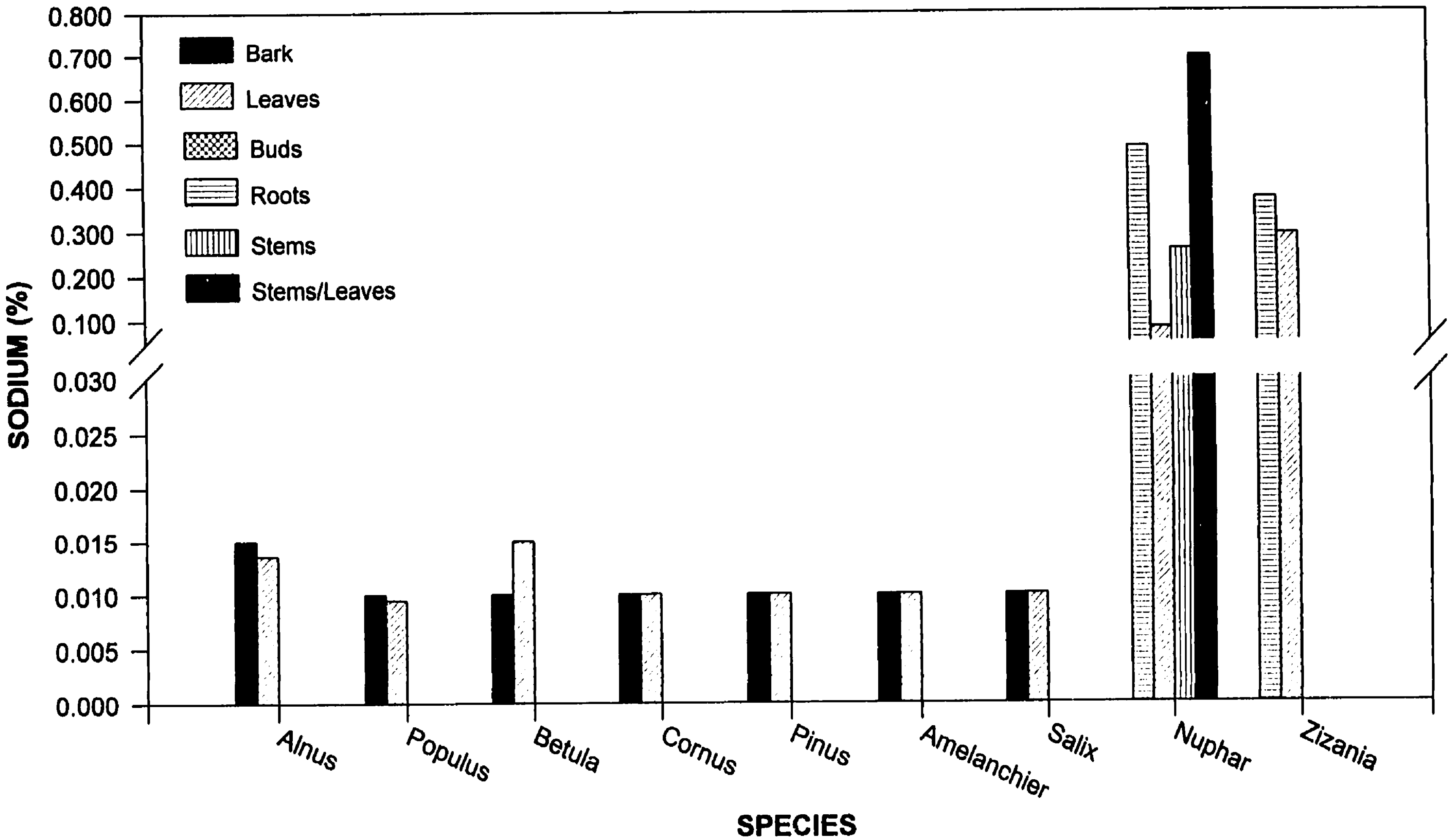

Figure 30: Sodium levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

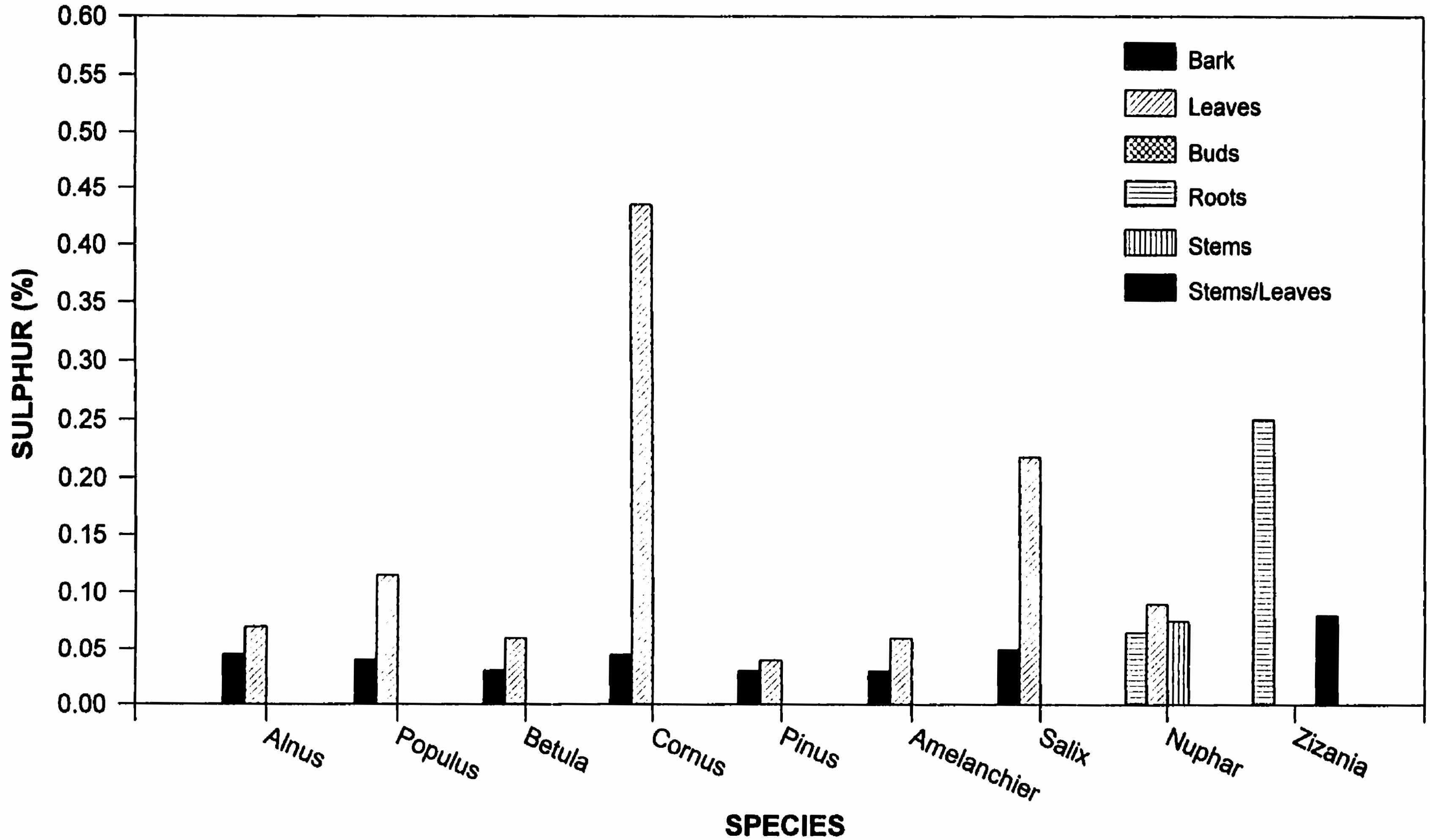

Figure 31: Sulphur levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

(Figures 26, 27, 28, 29, 30, 31). Levels of calcium, magnesium, phosphorus and sulphur were variable between species with Cornus having a very high level of sulphur (Figure 31). Potassium and sodium levels were similar in the leaves between species.

Zizania roots and stems/leaves and Nuphar roots had low levels of calcium while Nuphar leaves and stems had moderate levels within the ranges observed for the trees' bark and leaves (Figure 26). Magnesium levels were low to moderate and fell within the ranges observed for the bark and leaves of the tree species (Figure 27). Phosphorus and sulphur levels in the aquatic species were also moderate and fell into ranges observed in the tree species (Figures 28, 31). The aquatic species had very high levels of potassium (Figure 29). Nuphar stems and roots had 3.6 and 2.0x as much potassium as the highest level of potassium observed for Salix. Zizania roots, stem/leaves and Nuphar leaves had potassium levels comparable to the highest levels observed in the tree species. Sodium levels in the aquatic species were also very high with Nuphar stems and Zizania stems/leaves having approximately 35x more sodium than the highest level observed in the tree species (Figure 30). Zizania roots and Nuphar leaves and roots had levels 15, 14 and 4x greater respectively than the highest level observed in the tree species.

Trace Elements

Zinc levels were higher in the bark than in the leaves of the tree species with the exception of Populus (Figure 32). Iron levels were lower in the bark than in the leaves and manganese and copper had variable levels between the bark and the leaves (Figures 33, 34, 35).

Iron levels in both the bark and the leaves were similar between the tree species while levels of zinc, manganese and copper were variable (Figures 32, 33, 34, 35).

The aquatic species had low to moderate levels of zinc, similar to levels observed in the tree species' bark and leaves. Nuphar roots had moderate levels of manganese while the roots and stems/leaves of Zizania and the stems and leaves of Nuphar had 1.3 to 1.8x more manganese than the highest level observed for the tree species (Figures 32, 33). Likewise, iron levels in the aquatic species were very high (Figure 34). Zizania roots had the highest iron level, 314x greater than the highest level observed in the tree species. Zizania stems/leaves and Nuphar stems had 8.6x more iron and Nuphar roots and leaves had 6.4 and 4.2x more iron respectively than the tree species. Nuphar roots, stems and leaves and Zizania stems/leaves had low levels of copper while Zizania roots had high levels (Figure 35).

Potassium : Sodium Ratio

The potassium:sodium ratios for the bark of all of the species with the exception of Populus were lower than ratios observed for the leaves (Figure 36).

Ratios in the bark were less than 1:40 while Populus had a slightly higher level at 1:50. The ratios in the leaves were also variable with Salix having the highest ratio at 1:135.

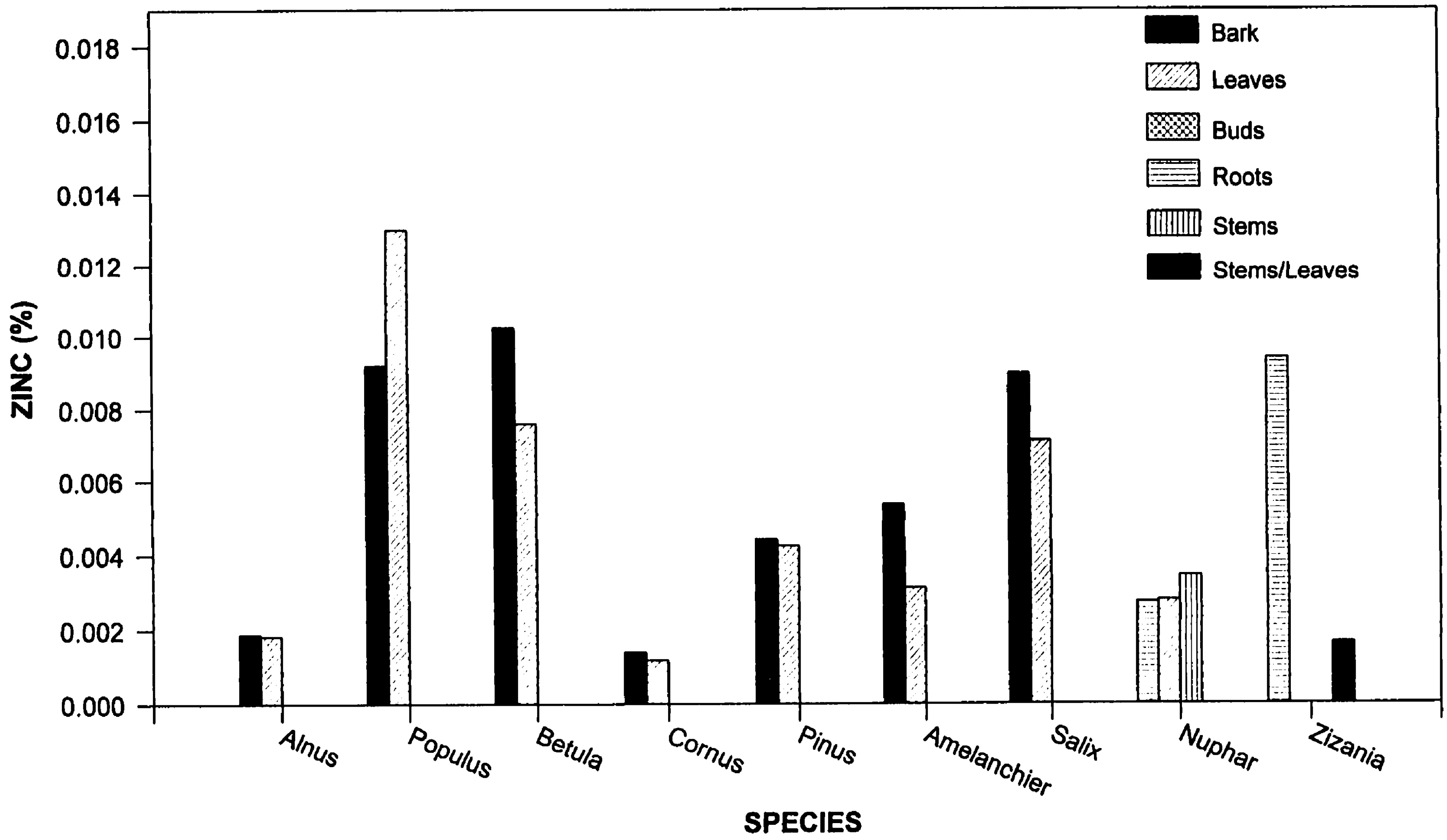

Figure 32: Zinc levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

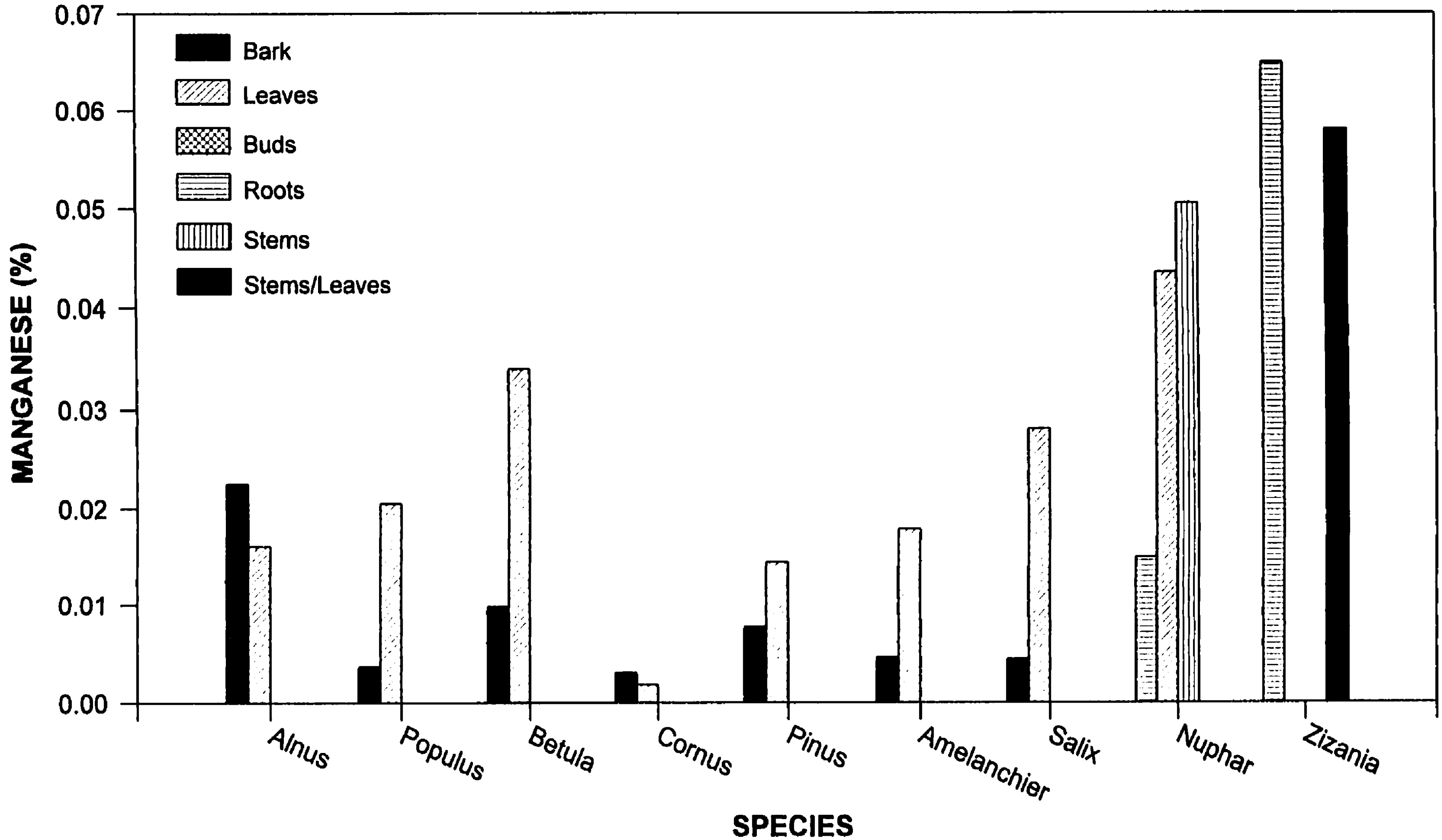

Figure 33: Manganese levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

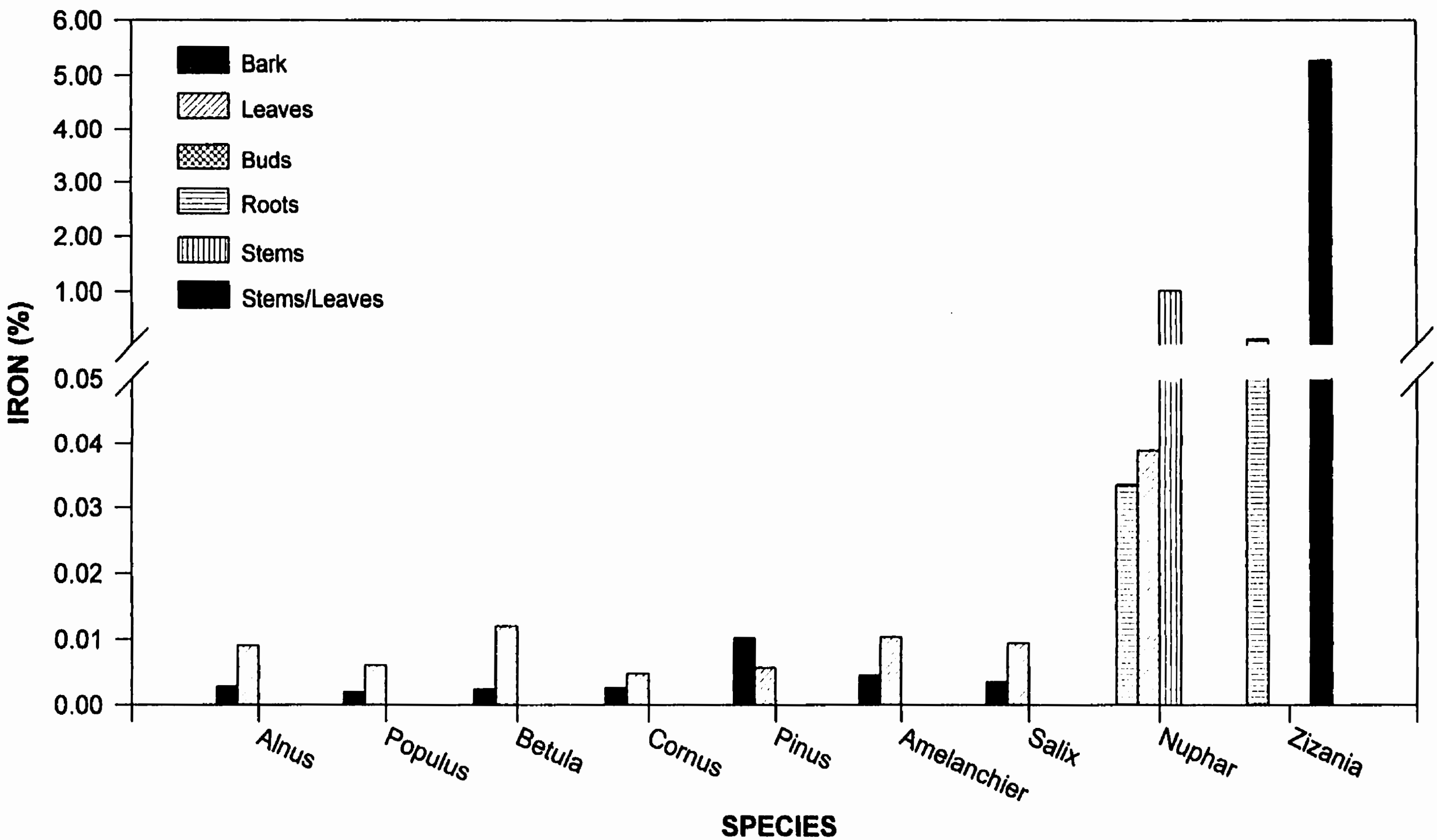

Figure 34: Iron levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

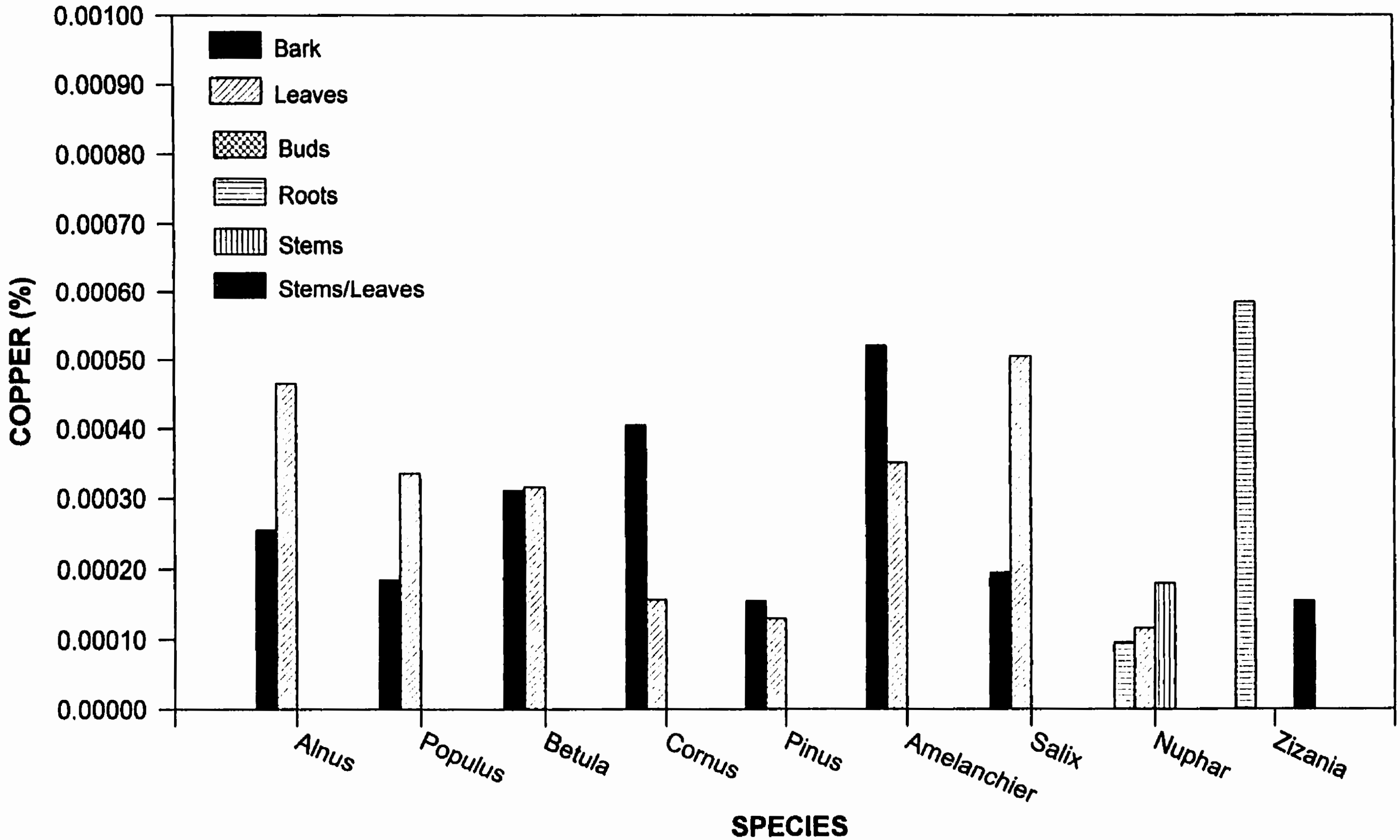

Figure 35: Copper levels (%) for the plant species and plant parts sampled during the senescence leaf stage (September - October) of 1993.

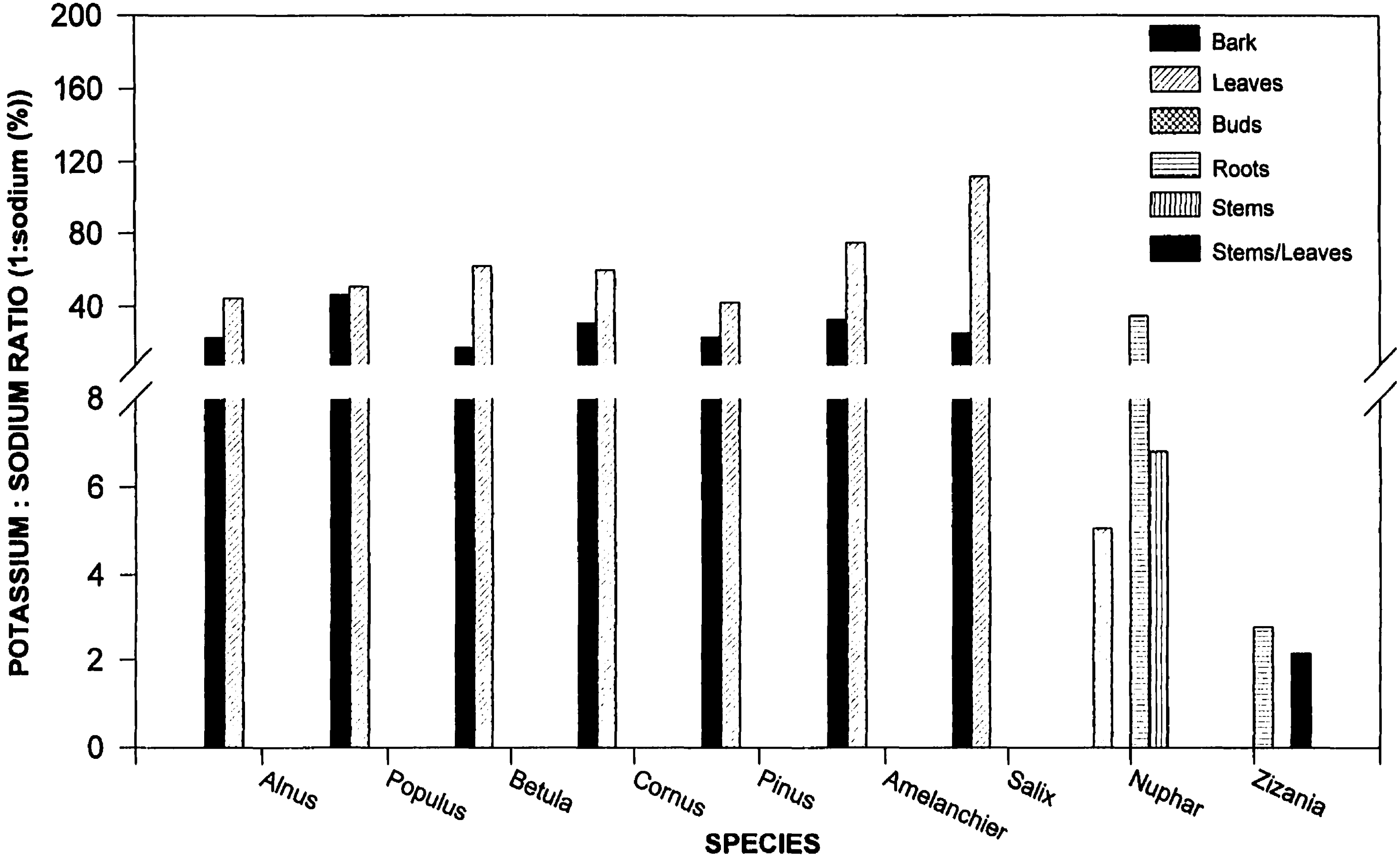

Figure 36: Potassium : sodium ratios (%) for the plant species and plant parts sampled during the senesence leaf stage (September - October) of 1993.

Potassium:sodium ratios in the aquatic species showed that Zizania had the lowest ratios in the roots and stems/leaves at ratios of approximately 1:2.5 (Figure 36). Ratios in the stems and leaves of Nuphar were slightly higher at 1:5 and 1:7 respectively. Nuphar roots, however, had a much higher ratio at 1:35, 5-14x higher than the ratios observed in its other plant parts and the plant parts of Zizania.

YEARLY VARIATIONS IN FOOD SELECTION

Yearly variations in food selection were evident. In the growing leaf stage of 1992 leaves were heavily utilized over bark (Figure 37). Betula leaves were consumed in the highest amounts while Cornus leaves were not utilized. As well, only the bark of Populus and Betula were observed to be utilized. In contrast, in 1993, the beaver utilized bark and leaves in fairly similar proportions (Figure 40). Also, the beaver utilized Cornus leaves in the highest amounts but did not utilize Betula leaves. As well, the bark of all seven tree species were utilized in 1993, especially Pinus bark. In addition, Pinus buds were observed to be utilized in small proportions in 1992 but in 1993 they were utilized in very high amounts.

During the mature leaf stage, bark was consumed in a high proportion in 1992 compared to 1993 (Figures 38, 41). As well, in 1993 a more diverse number of tree species were utilized. In 1992, however, aquatic plants were utilized in fairly high proportions compared to 1993.

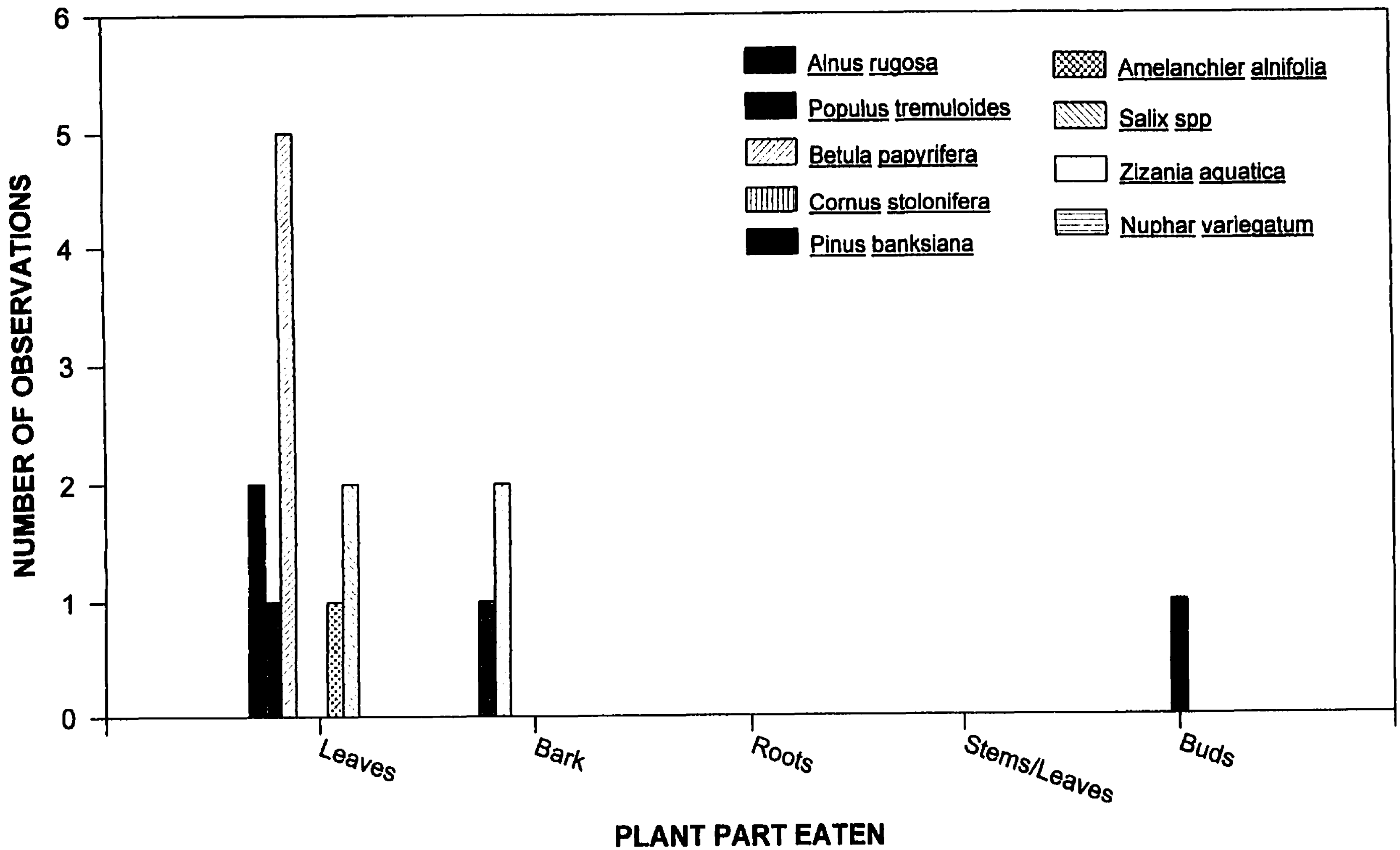

Figure 37: Frequency distribution of the plant parts consumed by the beaver family during the growing leaf stage (May - June) of 1992.

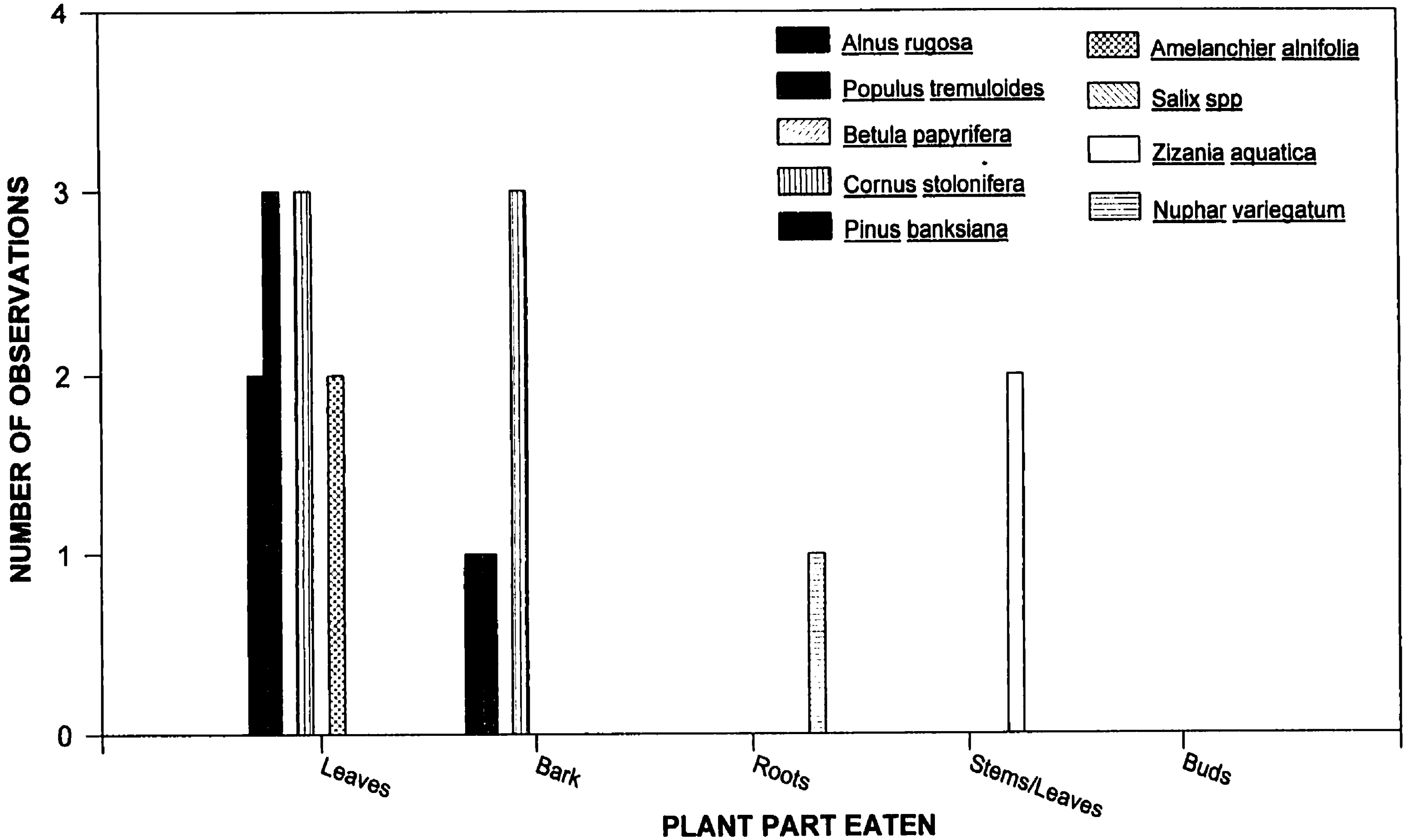

Figure 38: Frequency distribution of the plant parts consumed by the beaver family during the mature leaf stage (July - August) of 1992.

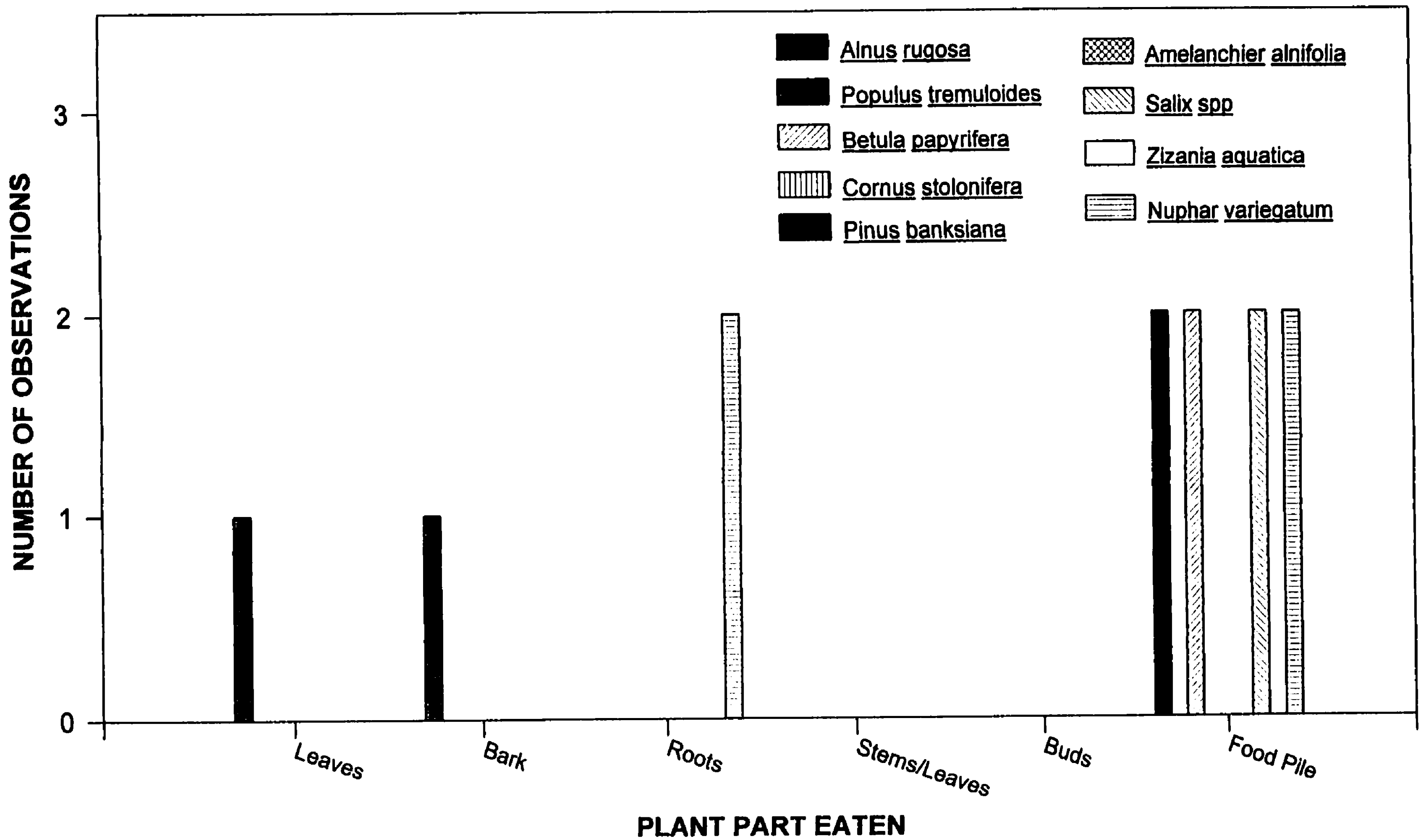

Figure 39: Frequency distribution of the plant parts consumed by the beaver family during the senescence leaf stage (September - October) of 1992.

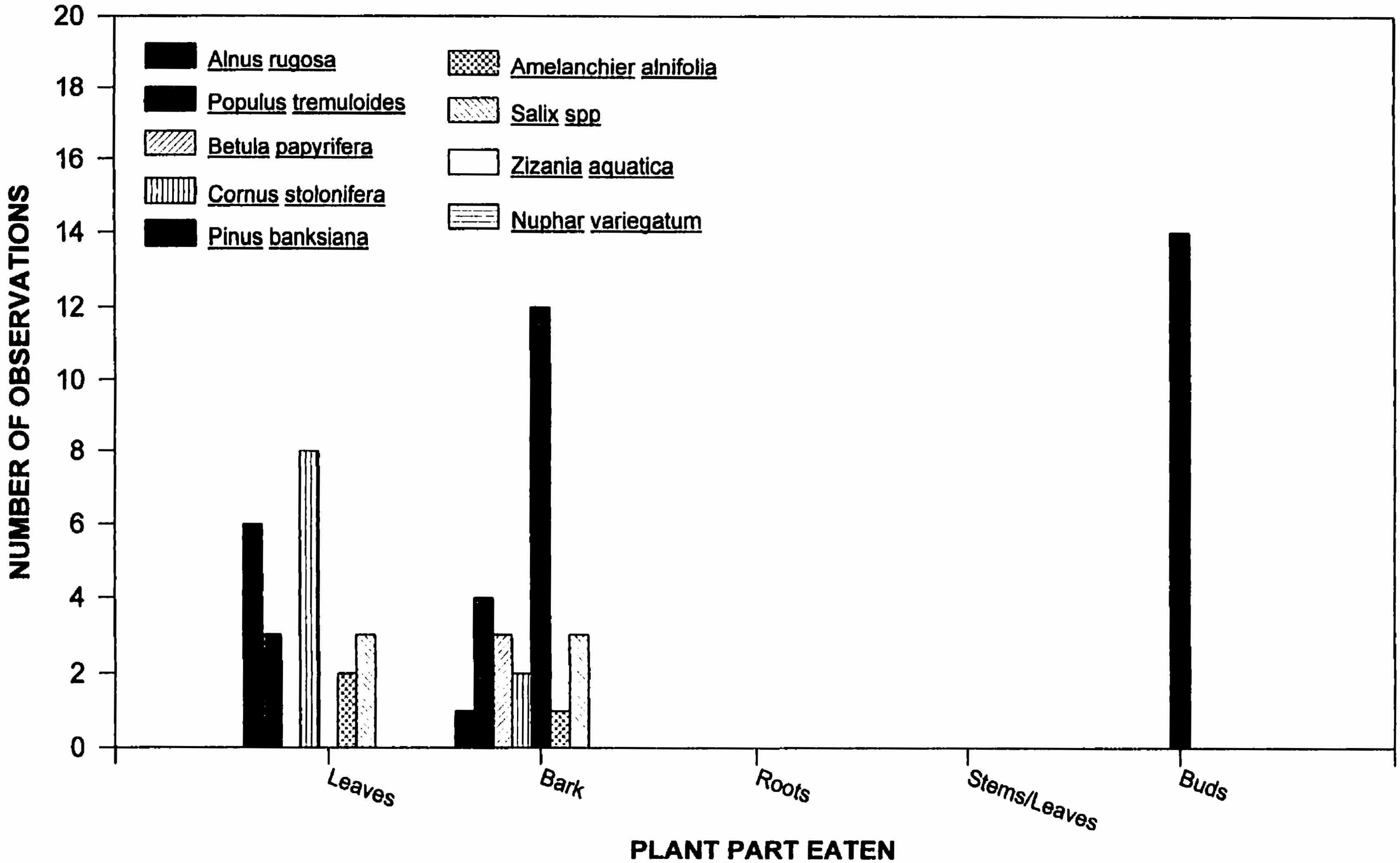

Figure 40: Frequency distribution of the plant parts consumed by the beaver family during the growing leaf stage (May - June) of 1993.

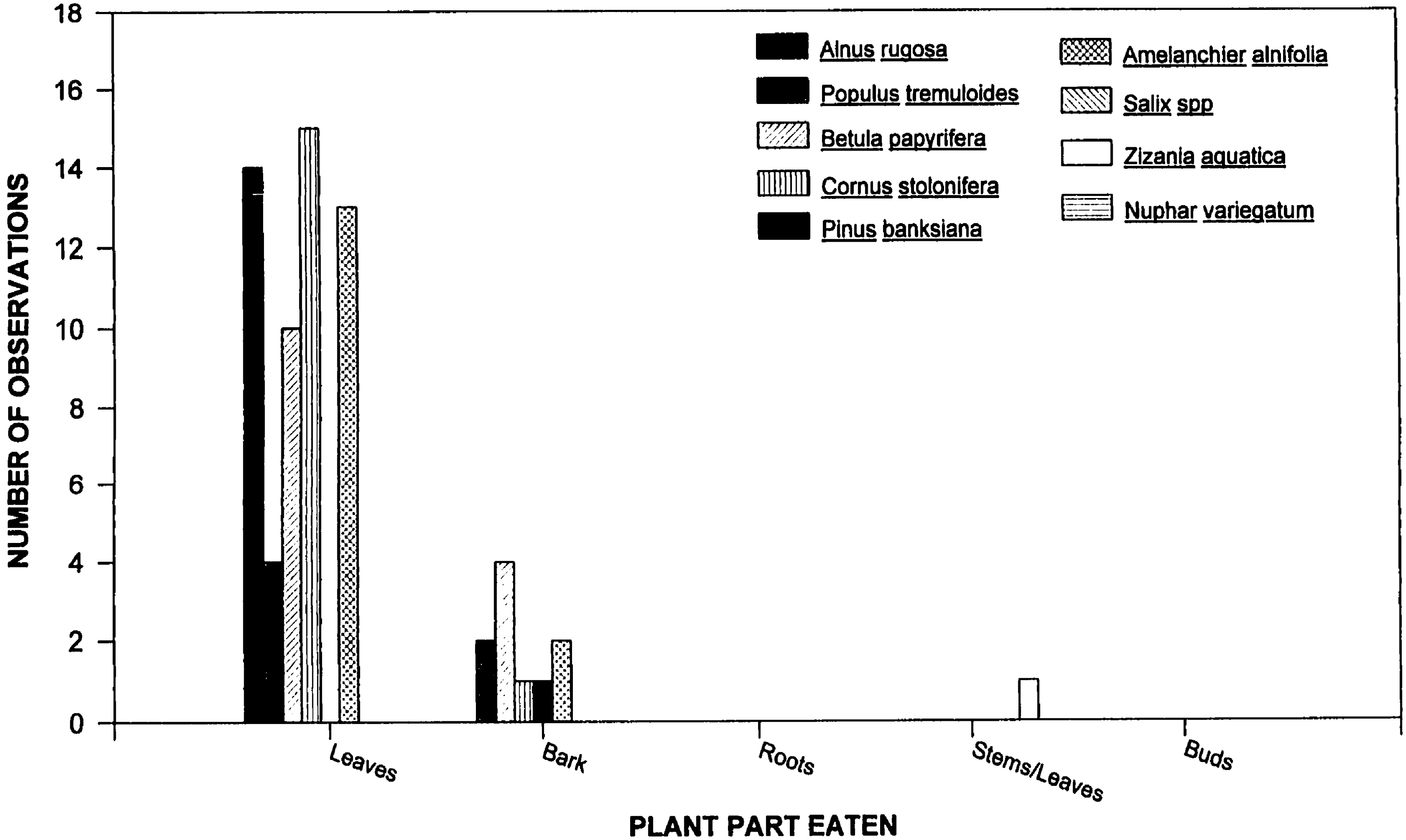

Figure 41: Frequency distribution of the plant parts consumed by the beaver family during the mature leaf stage (July - August) of 1993.

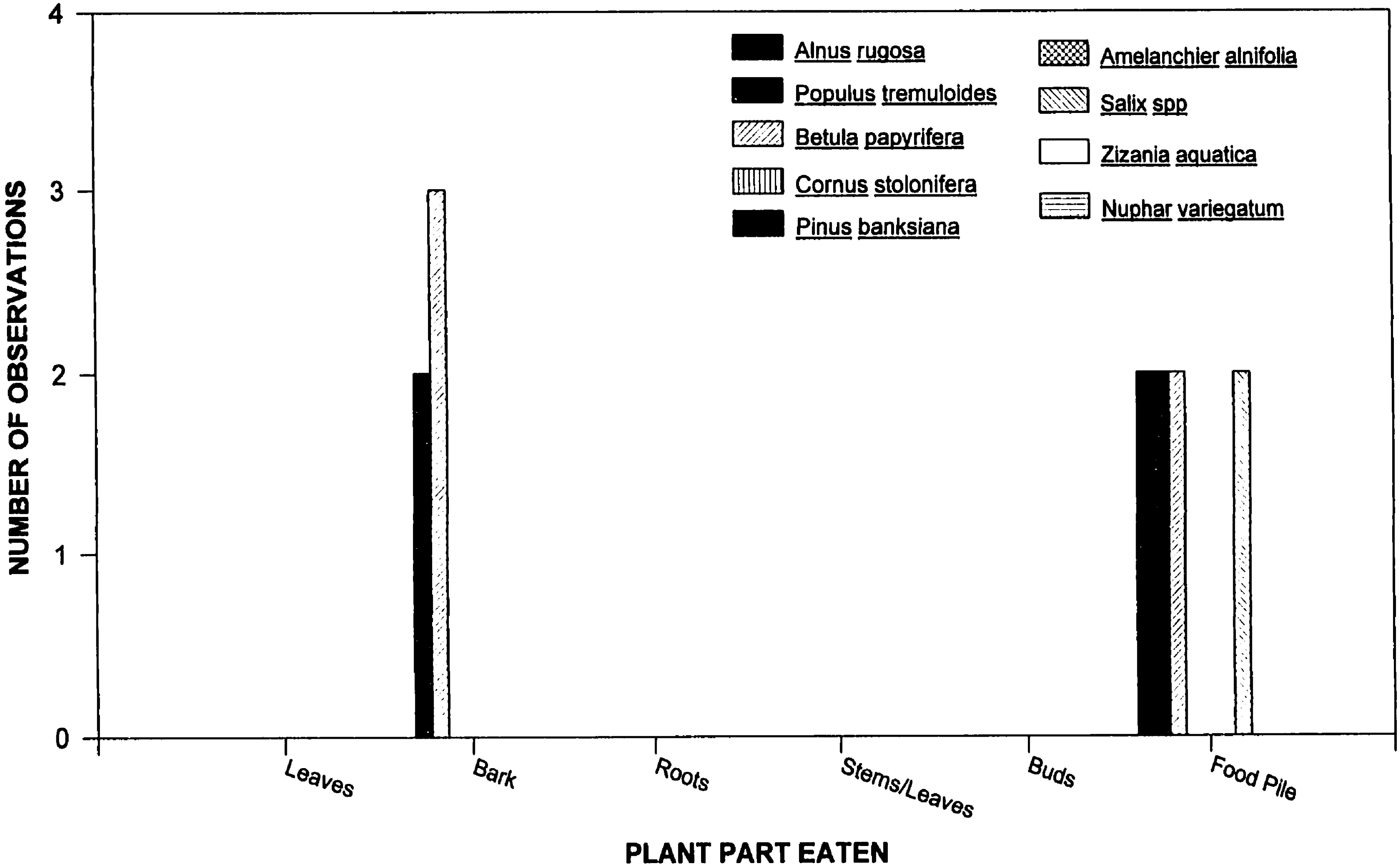

Figure 42: Frequency distribution of the plant parts consumed by the beaver family during the senescence leaf stage (September - October) of 1993.

The number of observations during the senescence leaf stage was low, thus comparisons are difficult (Figures 39, 42). However, variations were noted in that leaves and Nuphar roots were utilized in 1992 and not in 1993. Differences in species added to the winter food pile were also evident.

SEASONAL VARIATIONS IN FOOD SELECTION

Data from 1993 were more complete and will thus be utilized in this section.

During the growing leaf stage of 1993 I observed that leaves and bark were eaten in similar proportions (32 and 42% respectively) (Figure 40). As well, the beaver were also observed to feed on the bark of all seven of the tree species. Of particular note is the high proportion of Pinus bark consumed (46% of total feeding observations). The beaver were also observed to feed on the leaves of all of the deciduous species with the exception of Betula. The use of Pinus buds in the growing leaf stage was high as well (23% of total feeding observations). No observations were made of beaver feeding on either of the aquatic species as these species had not yet grown to a state to be accessible to them.

During the mature leaf stage of 1993 the beaver were observed to feed mainly on leaves (75% of the feeding observations, 15% for bark) (Figure 41). The bark of 5 of the deciduous species was observed to be consumed (excluding Salix bark). The consumption of Pinus bark was very low during this stage (1% of feeding observations). Again, the beaver were observed to feed on the leaves of all of the deciduous species, however, with the exception of Salix during this time period. Pinus buds were not observed to be utilized. The beaver were also noted to feed on the stems and leaves of Zizania in small proportions (1% of feeding observations).

During the senescence leaf stage, bark was the primary source of food for the beavers (Figure 42). Due to the decrease in hours of light, I only made three direct observations of plant part food choice by the beaver during this period of 1993. They were observed to feed on Populus and Betula bark. Direct observations of food material added to the winter food pile included branches from Alnus, Populus, Betula and Salix. No aquatic plants were observed to be utilized during this time period.

It should be noted, that in the case of the early growing leaf stage and late senescence leaf stage, the beavers fed primarily on the plant parts available to them at that particular point in time.

DIFFERENCES IN FOOD CHOICE BETWEEN BEAVERS

There were also observed differences between the male and female beavers in terms of what plant species and proportions of each species they consumed. Female beavers fed upon Alnus, Populus, Betula, Cornus, Pinus, Amelanchier, Salix and Zizania. Males were observed to consume the same species with the exception of Zizania.

The data were combined for 1992 and 1993 with the male food choices combined to include the observations of the two yearlings males in 1992 and the one two-year old male in 1993. Likewise, the data for the female food choices were combined to include the observations of the one yearling female in 1992, one two-year old female in 1993 and the adult female in both years.

However, chi-square analysis shows that the observed differences in food selection between male and female beavers is not statistically significant (X^2 = 11.09 at P = 0.05 with 8 degrees of freedom).

Dardaillon (1989) studied age-class differences on feeding choices in wild boars (Sus scrofa) and found that there were differences in food choice between juvenile, yearling and adults wild boars, primarily in the fall and winter. Studies on the beaver to date have not quantified differences in food choice between age classes nor sex of the beaver.

DISCUSSION

NUTRIENT ANALYSIS

For healthy growth, development and maintenance, animals have specific nutritional requirements. These requirements include energy, protein, water, minerals, vitamins and essential fatty acids. As well, the mineral content and requirements of an animal vary with age, species, sex, maturity level, season and reproductive condition (Robbins 1993).

There are two categories of minerals, the macro elements and the trace elements. Macro elements are required in fairly large amounts (mg/g) and include calcium, phosphorous, sodium, potassium, magnesium, sulphur and chlorine. Trace elements are required in very small amounts, parts per million (ppm) and include iron, zinc, manganese, copper, cobalt, molybdenum, iodine, selenium, fluoride and chromium (Robbins 1993). Robbins (1993) discusses in detail the nutrient requirements of various species of animals and the physiological effects that nutrient deficiencies may have. As well, Roze (1989) discusses the detailed nutrient requirements by the porcupine (Erethizon dorsatum).

Crude Protein

In my study crude protein levels were found to be higher in the leaves compared to the bark of all of the tree species over all three leaf stages (Figures 1, 13, 25). The aquatic species also had crude protein levels similar to those observed in the leaves of the tree species.

Robbins (1993) notes that browsers on average require their diet to contain at least 6% protein. During all three leaf stages the bark of all of the tree species was found to be below this level. Protein levels in the leaves, Pinus buds and the aquatic species however, exceeded this level.

Macro Elements

Requirements of calcium and phosphorous range between 0.4 - 1.2% and 0.3 - 0.6% respectively for growing mammals and birds (Robbins 1993).

Calcium levels in the tree species were found to be variable both between plant parts and between species over all three leaf stages (Figures 2, 14, 26). As well, levels of calcium in the Pinus buds were very low (less than 0.1%). The calcium levels in Zizania were very low and Nuphar had lower to moderate levels.

With the exceptions of Pinus buds, bark and needle leaves and Zizania stems/leaves, the species and plant parts tested had levels of calcium which fall within and/or exceeded those listed by Robbins (1993) as being adequate for proper growth.

Phosphorus amounts in the bark of the tree species were for the most part much lower than levels observed in the leaves (Figures 4, 16, 28). Levels of phosphorus in the bark of the tree species was also roughly similar in each of the three seasons. Levels of phosphorus in the leaves were more variable between the tree species in each season. As well, phosphorus levels observed in the aquatic plants mainly fell within the ranges observed for the bark and leaves of the tree species.

Levels of phosphorus were adequate, as suggested by Robbins for growing mammals, only in the leaves of the deciduous trees during the growing leaf stage.

Magnesium requirements for rodents were listed as 0.04 to 0.3% (Robbins 1993). The levels of magnesium observed in the bark of the tree species were lower than the levels observed in the leaves over all three leaf stages (Figures 3, 15, 27). Levels of magnesium in the bark and leaves were variable between the species in all three seasons. Pinus buds had low levels of magnesium similar to the levels observed in the bark of the tree species. The aquatic species had magnesium levels that fell within levels observed in the tree species.

All of the plant species and plant parts meet the minimum requirements of 0.04% for magnesium.

Growing plants often have a very high potassium content. Potassium requirements range from 0.3 to 0.6% (Robbins 1993). Potassium levels in the bark of the tree species were, with one exception, significantly lower than levels observed in the leaves (Figures 5, 17, 29). Levels in the bark between the tree species was fairly constant in each season. Levels of potassium observed in the leaves was however, much more variable in each season. Levels of potassium in the aquatic species were very high with potassium levels similar to the highest observed levels in the tree species or exceeding these levels by 1.4 - 3.6x.

The observed levels of potassium surpassed the lowest requirements listed by Robbins with the exception of some of the tree species' bark which had potassium levels lower than the minimum listed level.

Requirements of sodium by domestic and lab animals is estimated to range from 0.05 - 0.4% of the dry diet. Very few plants require sodium and do not concentrate it in their tissues; thus, there is a potential for animals, particularly herbivores, to develop sodium deficiencies (Roze 1989, Robbins 1993).

Levels of sodium observed in the bark and leaves were variable both within and between species in the growing leaf and mature leaf stages (Figures 6, 18, 30). As well, the sodium levels in the fall are all at almost the same level of 0.01% for all of the species and all three of the plant parts. Pinus buds were observed to have a very high level of sodium. The aquatic species also exhibited very high levels of sodium, up to 15x higher than the highest level observed in the tree species.

Sodium levels observed in the tree species were within the lower range listed by Roze (1989) and Robbins (1990) as being adequate for mammals.

Robbins (1993) does not give a minimum requirement for sulphur in animals. Levels of sulphur in the bark of the tree species were lower than those observed in the leaves with two exceptions (Alnus in the growing leaf and mature leaf stages) (Figures 7, 19, 31). Of particular note are the high levels of sulphur in Cornus leaves over all three leaf stages. Levels of sulphur in Pinus buds were low. As well, levels in the aquatic species fell within the range observed for the tree species.

Trace Elements

Zinc is required at levels in rodents of 9.2 to 30 ppm (0.0009 to 0.0003%), manganese is required at levels of 3.7 to 50 ppm (0.00037 to 0.0005%), iron is required at levels of 25 to 140 ppm (0.00025 to 0.0014%) and rodents require low copper levels of 1.6 to 6 ppm (0.000016 to 0.00006%) (Robbins 1993).

Zinc, manganese and copper levels in the bark and leaves were variable both within and between species over all three leaf stages (Figures 8, 9, 11, 20, 21, 23, 32, 33, 35). Iron levels were lower in the bark of the tree species compared to the leaves with the exception of Salix in the growing leaf stage (Figures 10, 22, 34). Pinus buds had moderate levels of zinc and copper and low levels of iron and manganese.

Levels of zinc in the aquatic species were low for the most part and fell within levels observed in the tree species while copper levels were very low compared to the tree species. As well, the aquatic species had high levels of manganese and iron, up to 2.0x and 393x as much as the highest level observed in the tree species respectively.

The observed zinc, manganese, iron and copper levels for all of the species in all three leaf stages greatly exceeded those given by Robbins (1993).

Potassium : Sodium Ratios

In herbivorous species it is essential that the nervous and muscle tissues maintain a 1:1 ratio of potassium to sodium ions. However the plant tissues that herbivores consume only need to maintain a saline environment inside their cells with the results that plants may contain potassium:sodium ratios up to 500:1 (Roze 1989).

The bark of the tree species had similar or lower potassium:sodium ratios compared to the leaves in all three leaf stages (Figures 12, 24, 36). Ratios in the bark were below 1:55. Ratios in the leaves were often very high, at ratios as high as 1:475 in the leaves of Amelanchier. Pinus buds had a lower ratio similar to the ratios observed in the bark of the tree species. The aquatic species had the lowest potassium:sodium ratios ranging from 1:2 up to 1:35.

Overall, the family of beaver under study was probably not constrained by nutrient limitations. By feeding on a wide variety of species and plant parts over the seasons, the beaver ensure that they obtain the necessary amounts of nutrients required for proper growth and maintenance.

YEARLY VARIATIONS IN FOOD SELECTION

I found that the colony of beaver I was studying consumed a diverse

Salix spp., (Green 1936, Aleksiuk 1970, Ingle-Sidorowicz 1982, Doucet and Ball 1994), Betula papyrifera (Ingle-Sidorowicz 1982), and Nuphar variegatum (Aleksiuk 1970).

Yearly variations in food choice by the beaver in this study may be due to a variety of factors including species availability, nutrient content, accessibility, etc. Belovsky (1984) speculates that beaver may select food based on the quantity of items (leaves, bark, etc.) available per plant rather than items per unit area and item size, whereas Haseltine (1950), Aleksiuk (1970), and Jenkins (1979 & 1981) state that food availability is the most important factor in food selection.

SEASONAL VARIATIONS IN FOOD SELECTION

I also observed seasonal variations of the plant species selected by the beaver with Pinus being utilized primarily in the growing leaf stage and Amelanchier being utilized mostly in the growing leaf and mature leaf stages (Figures 40 & 41). Similar findings for Pinus spp., were observed by Jenkins (1979 & 1981) and Wheatley (1994). Jenkins (1975 & 1979) also found year to year and seasonal differences in tree selection by beaver. Furthermore, he also found that tree size and genus both influence food selection by beaver.

I also observed that Nuphar and Zizania were utilized in the summer and early fall once they became available to the beaver. Likewise, Aleksiuk (1977) observed that Nuphar variegatum was utilized by the beaver when available in the summer on some lakes. Bradt (1938) and Brenner (1962) also found that during the summer months the beaver fed primarily on herbaceous aquatic vegetation.

The beaver were observed to construct food piles starting in late August and continuing until freeze-up (Figure 42). Species added to the winter food cache included the branches of Alnus, Populus, Betula, and Salix. Likewise, Green (1936) found that the beaver in his study constructed winter food caches consisting of Salix spp., and Populus tremuloides and Aleksiuk (1970) found that Salix spp., Populus balsamifera (Poplar) and Alnus rugosa were utilized in foodpile construction in his study.

Variations in plant part selection were also observed in my study. During the early growing leaf stage the beaver were observed to feed primarily upon the bark and growing shoots of the deciduous species and on the growing buds of Pinus. During the late growing leaf and mature leaf stages, as leaves became available to the beaver, a shift was noted towards leaves. As well, during the summer Nuphar and Zizania plants became available to the beaver and were utilized as food sources. In the senescence leaf stage the beaver primarily consumed deciduous tree bark (Figures 40, 41, 42).

Aleksiuk (1970 & 1977) also found that beaver diets vary on a seasonal basis and that once the beaver emerged after spring thaw, bark was primarily consumed. Then, in the summer he noticed a shift in food habits whereby no bark was observed to be consumed. In the fall he observed that as the plant growth ceased and leaves fell from the trees the beaver reverted back to feeding on bark. Green (1936), Brenner (1962) and Jenkins (1981) also noted that, when available in the spring and summer, stems, leaves and aquatic vegetation were preferred by beaver over the coarser woody bark. But in the fall when the leaves had begun senescence they observed that the beaver selected Populus tremuloides branches for food.

As well, the beaver in my study were observed to consume only the petioles of leaves in small amounts and only for the species Populus, Alnus, Cornus and Amelanchier. Thus observations on leaf plus petiole use were combined with the data for leaves. The low use of petioles may possibly be due to low nutritional values of the petioles as evidenced in the nutrient analysis by the lack, for the most part, of a significant difference in nutrient levels between leaves and leaves plus petioles (nutrient results of leaves plus petioles were also combined with the results of the leaves). Another possibility may be the presence of certain phenolic compounds in the petioles which are not palatable to the beaver. During his study on the porcupine (Erethizon dorsatum), Roze (1989) found that they do not consume the petioles of leaves.

The use of particular food types by the beaver during certain seasons of the year may be related to a number of factors. Ingle-Sidorowicz (1982) discusses that food type, distribution and accessibility are important and may determine the number of beavers in a colony. Jenkins (1981) attributes the beavers' preference for leaves and herbaceous vegetation over bark to the high fiber content and low protein:fiber ratio of bark.

Hay (1958) noted that food quality may affect fertility in beaver. He found that Populus tremuloides stands appeared to support a larger number of beaver than did those of Salix spp. Masslich et al (1988) compared nutritive values of Populus tremuloides bark, twigs and sprouts and found that the twigs contained significantly higher levels of nitrogen, phosphorus, potassium, magnesium, iron and manganese. Calcium was found to be highest in the bark while copper was not found to be significantly different between bark, twigs and sprouts. Wheatley (1994) found that, in general, primary food items (parts from Populus tremuloides and Pinus banksiana) had higher levels of protein in the spring and summer. She also found that for similar plant parts, protein levels were higher in the summer than in the spring. In addition, she observed that primary foods had adequate levels of macro elements (sodium, magnesium, and calcium) in the summer but that primary food items did not have adequate levels of sodium in the spring and phosphorus in both spring and summer. She also found that only Populus tremuloides had sufficient levels of calcium in the spring. She likewise found levels of trace elements (zinc, copper, iron and manganese) to be sufficient in the primary foods in both seasons sampled. Finally, Wheatley (1994) observed that, while individual sodium and potassium levels were high in primary foods in the summer, the overall potassium:sodium ratios were low.

Inducible chemical products developed by tree species as an anti-herbivory device may be another factor influencing food selection by beaver. Basey et al (1990) found that beaver avoided feeding on "juvenile-form" sprouts (sprouts characterized by large leaves and no lateral branching) of Populus tremuloides when "adult-form" sprouts (characterized by small leaves and heavy lateral branching) were available. They attributed this finding to a new compound that was found in higher concentrations in the juvenile-form sprouts. As well, Muller-Schwarze et al (1994) found that Red Maple (Acer rubrum) develops a chemical compound which renders this species unpalatable to beaver. Roze (1989) also found that porcupine (Erethizon dorsatum) food selection was governed by the amounts of phenolics present in leaves and growing buds and that they also avoided Acer rubrum.

In my study nutrient levels may have played a role in food selection by the beavers. High levels of crude protein and sodium in Pinus buds may be an important factor governing the use of Pinus buds by the beaver in early spring before leaf-out. As well, higher levels of potassium, magnesium, phosphorus, sulphur and copper were found in the leaves of the deciduous tree species and may thus be factors influencing the high usage of leaves by the beaver compared to bark. The aquatic species were observed to have high levels of crude protein, sodium, potassium, copper and iron, which may be contributing factors in the use of aquatic species such as Nuphar and Zizania by the beaver family.

Finally, the low potassium:sodium ratios observed in the aquatic species and tree bark may be a factor in the use of aquatic species by the beaver and in the continued use of bark by the beaver after leaf-out has occurred.

Aleksiuk (1977) found that beaver in the Mackenzie Delta feed primarily on Salix spp., leaves and growing shoots which were found to have high protein levels. He speculates that the high protein leaves and shoot tips are utilized exclusively by the beaver to promote rapid growth during the short summer period.

Botkin et al (1973), as reported in Belovsky (1984), states that beaver do not have any sodium constraints due to the consumption of aquatic plants during the summer. As well, Belovsky and Jordan (1981) observed that moose (Alces alces) fed heavily on aquatic plants which are high in sodium.

CONCLUSIONS

The family of beaver under study consumed a diverse number of plant species including trees and aquatic plants and were selective in their food habits both in terms of species consumed and plant part consumed seasonally and yearly. These findings suggest that boreal beaver may be opportunistic herbivores (as Jenkins, 1975 suggests) when the food supply is diverse, choosing those species which meet their energy and nutritional requirements at a particular point in time.

While beavers may have different nutritional requirements over the course of a year (i.e.: lactating females in the spring), differences in food selection by male and female beaver were not found to be statistically significant in this study.

Beaver at Wallace Lake do not appear to be constrained by nutrient availability in the plant species they consume. Most of the plant species and plant parts had adequate levels of nutrients as described by Robbins (1993) with two exceptions. Potassium levels in the bark of some of the plant species did not meet minimum requirements and adequate phosphorus levels were found only in the leaves of deciduous tree species in the growing leaf stage.

Nutrient levels in food consumed by beaver is hypothesized as a probable factor influencing food selection in terms of species and plant part selection. Noticeable differences in potassium, sodium, copper and iron levels and the potassium:sodium ratio between tree species and the aquatic plants were observed, with the aquatic species having much higher levels of these nutrients and much lower potassium:sodium ratios. As well, there were observed differences in some of the nutrient levels between the bark and leaves of the tree species The leaves were noted to have greater levels of potassium, magnesium, phosphorus, sulphur and copper than in the bark for each tree species while the bark had a much lower potassium:sodium ratio. Pinus buds were also noted to have very high levels of crude protein and sodium.

By consuming a wide variety of species and plant parts the beaver in this study may be ensuring that they will not be affected by nutrient deficiencies. Thus, determining food selection based on nutrient contents in plants appears to be much more complex and may involve several factors at play at once, including soil fertility, moisture regimes and topography at each site.

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CHAPTER 3: FEEDING SITE SELECTION BY BEAVER

ABSTRACT

Feeding site selection and the distance traveled from the water's edge for food harvesting by a beaver colony were studied. The study area was divided into experimental sites that were extensively utilized by the beaver colony at the time of this study and control sites which were not. Five of each site type were then randomly chosen and sampled for the following; tree species, tree density and the diameter at a height of 20 cm from the ground (DLH) as factors influencing feeding site selection, and the presence of cut stumps as a function of distance traveled for food harvesting.

Tree species, density and diameter were not found to influence feeding site selection in this study.

The beavers were observed to harvest trees 11-30 m from the lakeshore in experimental sites and old cut stumps were found in control sites at a distance of 21-30 m. Food availability, topography and site history are postulated as factors that may have influenced the distance traveled from the lakeshore by the beaver colony for food harvesting.

INTRODUCTION

Most research on beaver in the past has focused on their general ecology and social habits with most papers including some discussion on food preferences by beaver in a particular study area. More recently, food habit studies have attempted to determine what factors define how beaver make the food choices they do in terms of temporal, spatial, species and plant part selection. Jenkins (1975, 1979, 1981), Pinkowski (1983), Belovsky (1984), McGinley and Whitman (1985), and Fryxell and Doucet (1991) have studied tree size-distance relationships in terms of selection by beaver. Findings are divided, however, as Jenkins and Pinkowski found that relatively more smaller trees were cut at increasing distances from the water's edge whereas McGinley and Whitham and Fryxell and Doucet found that with increasing distance from the water's edge, beaver cut a larger percentage of large trees and branches. Belovsky found no difference between the average diameter of cut trees and distance from the shore. In addition, Belovsky found that up to a distance of 30 m from shore, beavers did not change their preferences for tree species. In contrast Bradt (1938) found that at distances greater than 40 m from shore beavers were more selective. As well, Jenkins found that beavers exhibit generic selectivity at different feeding sites.

This study was conducted to provide further insight into some of the factors that may influence feeding site selection by beavers including species density, total tree density and the diameter of trees at a height of 20 cm from the ground. Distance from the water's edge for food harvesting by the beavers was also measured as a function of cut stump density.

METHODS

The area on Wallace lake utilized by the family of beaver varied in topography, soil characteristics and fire history, all of which in turn influenced the tree species composition in the study area. During the study, I noted that around the lake the beavers used particular feeding sites which were fairly conspicuous. Comparisons of the vegetative characteristics of beaver run sites (experimental sites), which I define as sites at which trails or canals have been created by the beavers into the forested lake shoreline for food collection purposes, and sites that contained little or no beaver activity (non-beaver run sites) (control sites) were made.

All the beaver run and non-run sites within the beaver colony's home ranges were marked on an enlarged aerial photograph with a 100 m x 100 m UTM grid overlay. I then randomly chose five sites of each type for closer examination.

At each site, two 30 meter tapes were placed 1 m apart and strung perpendicular to the shoreline 30 m back into the bush, creating a 30 m x 1 m belt transect. Within this transect tree species, density, diameter at 20 cm off the ground, and diameter at breast height were measured. Any cut stumps left by beaver were also measured for height from ground to cut and diameter at 20 cm (as I observed that most cuts by beavers were made at 20 cm from the ground).

Comparisons were made between beaver run sites and non-run sites to determine whether total tree density and diameter at lower height (DLH) (20 cm from the ground) influenced beaver feeding site selection. Sites were also assessed for distance from the lakeshore for food harvesting in terms of stump density.

RESULTS

TREE DENSITY AS A FUNCTION OF FEEDING SITE SELECTION

Figures 1, 2 and 3 show that there are observed differences in density for each tree species between control (non-beaver run sites) and experimental sites (beaver run sites). At a distance from the water of 0-10 m the experimental sites have lower densities of each species than the control sites with the exception of Cornus (Figure 1). As well, control sites are observed to contain Pinus and Picea glauca trees which are absent from the experimental sites at this distance. In addition, Alnus trees were found in the experimental sites but were absent from the control sites. However, chi-square analysis reveals that the observed differences in tree species density between control and experimental sites at the 0-10 m distance is not statistically significant ($X^2 = 4.39$ at $P = 0.05 = 14.07$).

At the 11-20 m distance both experimental and control sites contained the same species with the exception of Alnus which was again found only in the experimental sites (Figure 2). At this distance, both sites also contained Picea glauca trees. Experimental sites were also observed to contain Pinus saplings. Densities for each species at this distance were also similar with the exceptions of Betula, Amelanchier and Picea glauca for which the control sites had 14, 55 and 78% more of these species m^{-2} respectively. Chi-square analysis reveals that the observed differences in tree density between control and experimental sites at the 11-20 m distance are not statistically significant ($X^2 = 1.25$ at $P = 0.05 = 14.07$).

At the 21-30 m distance the control sites had from 50-80% more trees m^{-2} than did the experimental sites with the exception of Cornus for which the experimental sites had 71% more (Figure 3). As well, Amelanchier and Alnus were found only in the control sites at this distance. Chi-square analysis reveals that the observed differences in tree density between control and experimental sites at the 21-30 m distance are not statistically significant (X^2 = 4.53 at P = 0.05 = 14.07).

Control sites were also noted to contain a larger percentage of coniferous species (Pinus and Picea glauca), 14, 33 and 34% for 0-10 m, 11-20 m and 21-30 m respectively compared to experimental sites with 0, 17 and 14% respectively. Both the control and experimental sites were observed to have the highest percentage of Alnus and Cornus at the 0-10 m distance. In addition, the 21-30 m distance was observed to have the highest level of Populus for the control sites (17%). Moreover, the total average tree density in the experimental sites was highest at the 21-30 m distance while the 11-20 m distance in the control sites had the highest density.

A chi-square test for independence was also conducted to determine whether observed differences in total average tree density of all species between control sites and experimental sites was significant. The results of the chi-square test reveal that the observed differences are not statistically significant (X^2 = 0.89, P at 0.05 = 5.99).

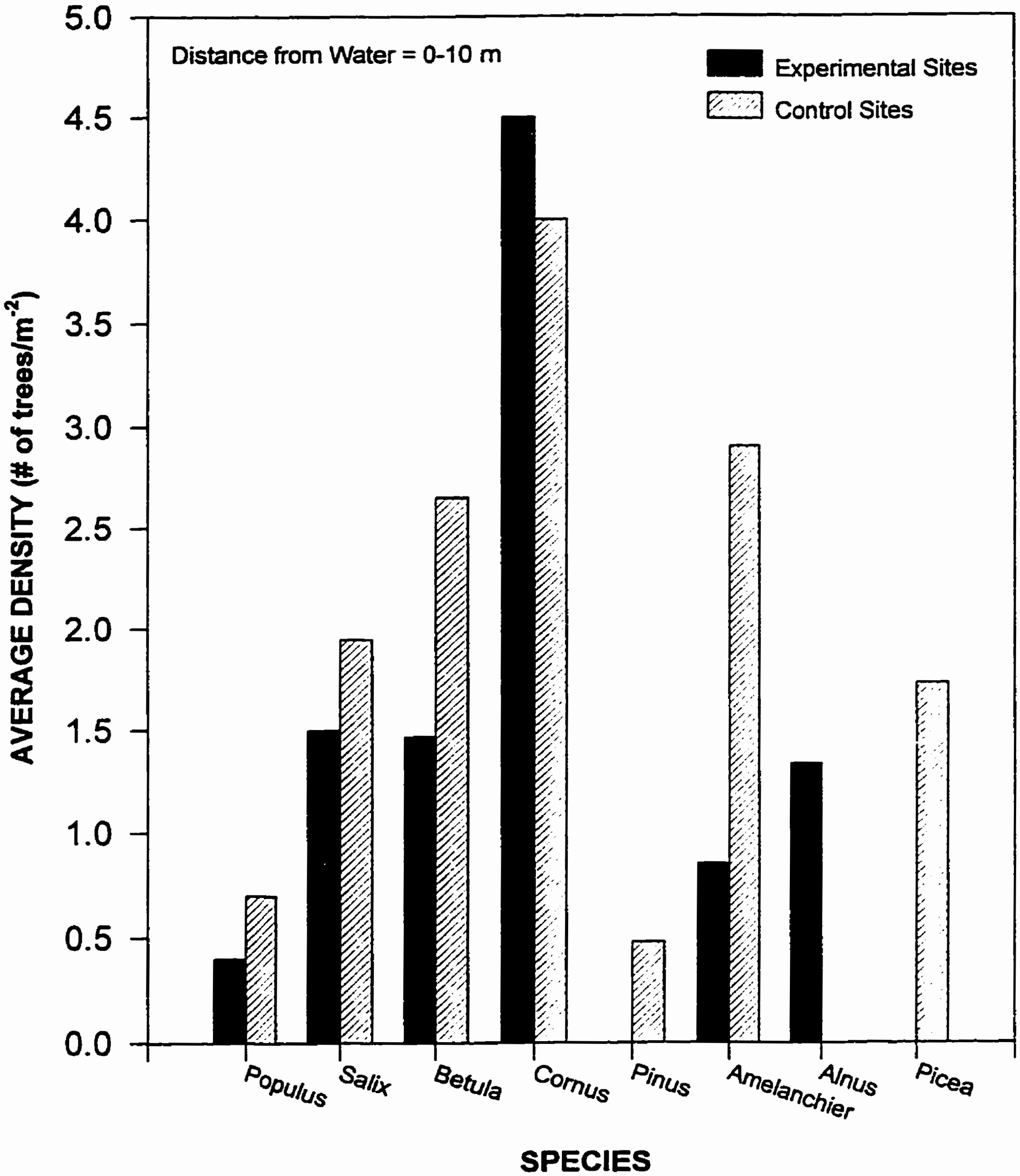

Figure 1: Tree density in control and experimental sites at a distance of 0 - 10 m from the lake's edge.

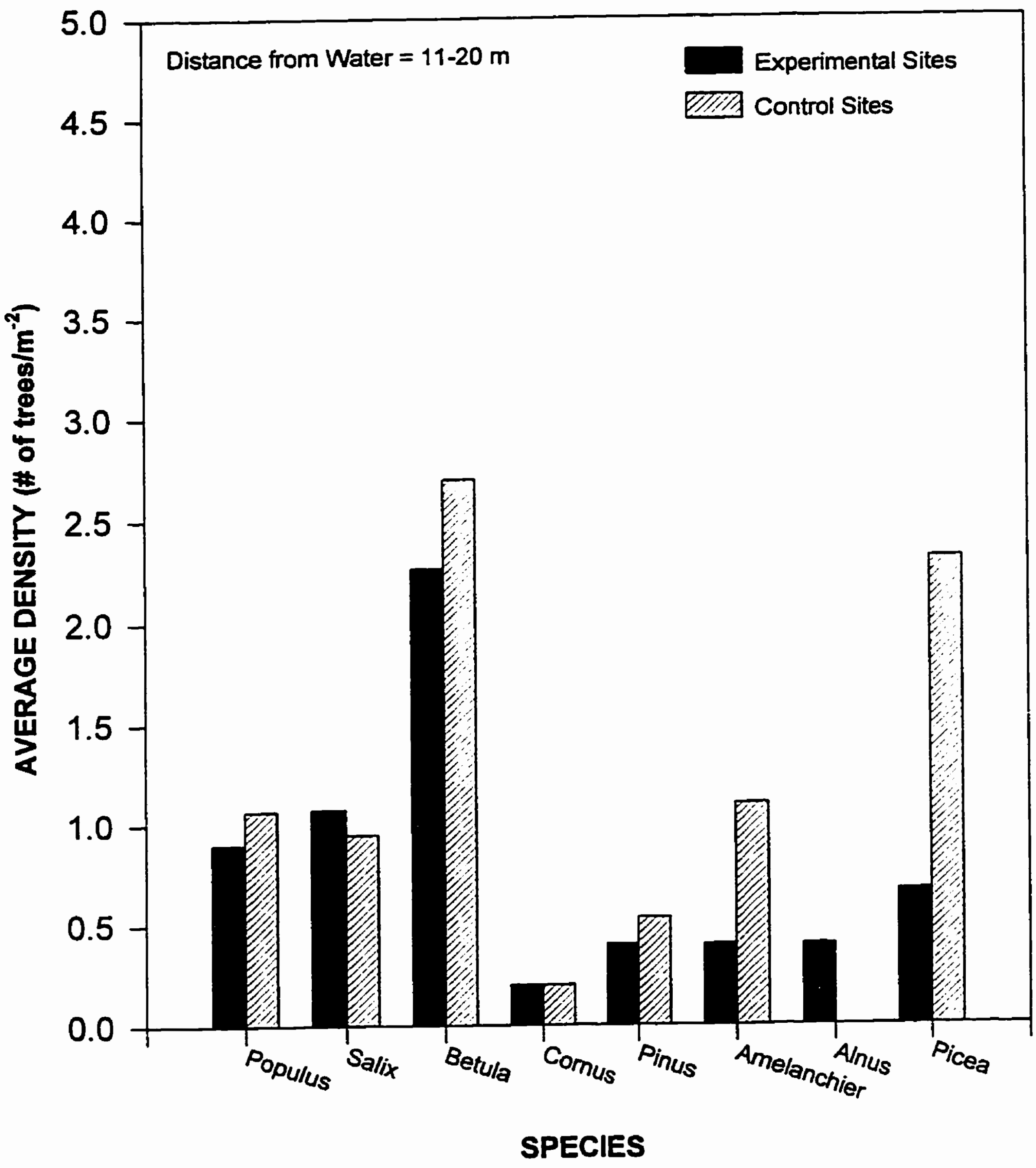

Figure 2: Tree density in control and experimental sites at a distance of 11 - 20 m from the lake's edge.

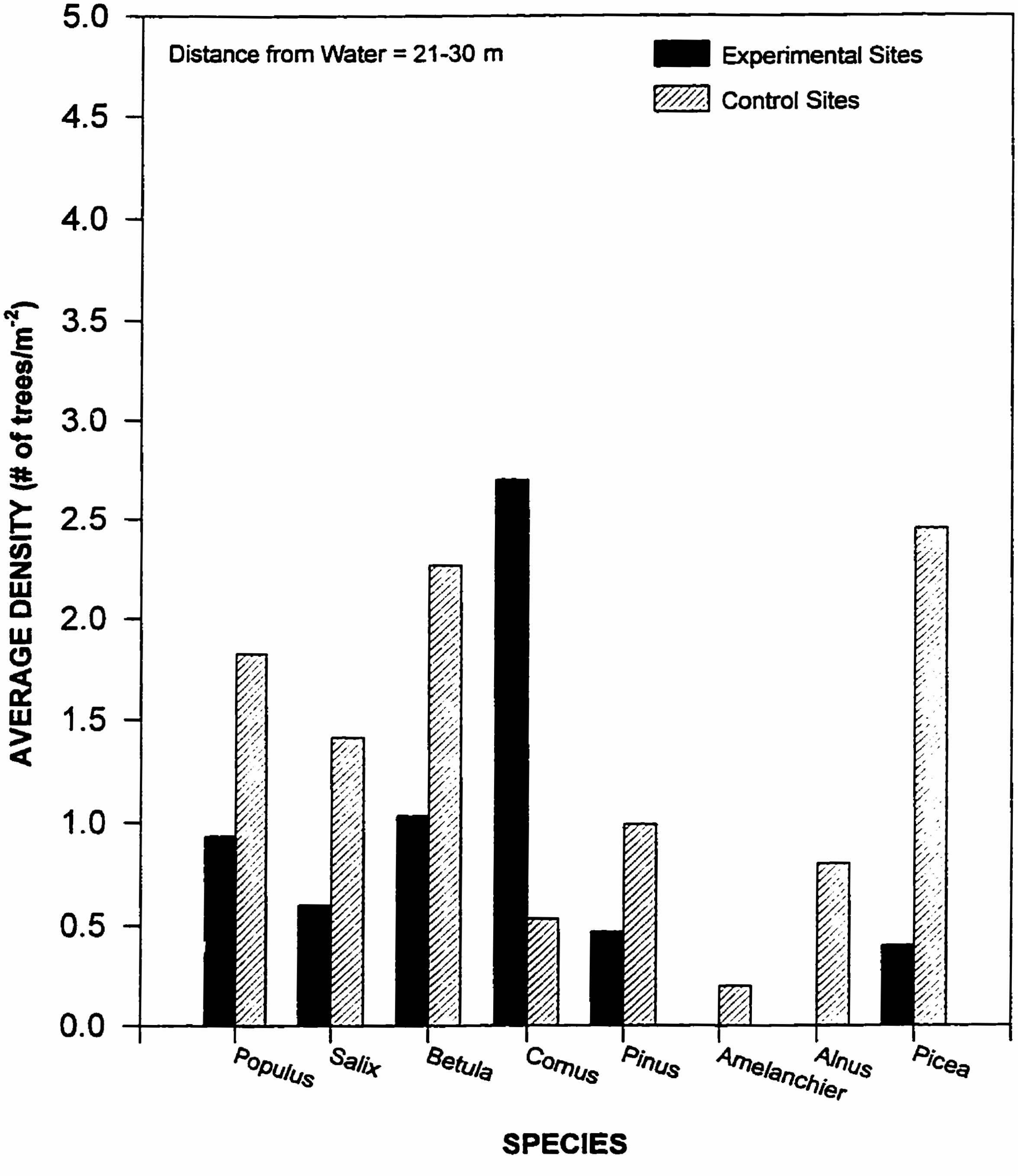

Figure 3: Tree density in control and experimental sites at a distance of 21 - 30 m from the lake's edge.

DIAMETER LOWER HEIGHT (DLH) AS A FUNCTION OF FEEDING SITE SELECTION

Differences in the diameter lower height (diameter of trees at 20 cm from the ground) for each species were also examined to determine whether this factor plays a role in feeding site selection by the beavers.

At a distance of 0-10 m from the water's edge differences are observable between control and experimental site DLH (Figure 4). Salix., Betula, Cornus and Amelanchier trees in the experimental sites had larger DLH than in the control sites (40, 40, 32 and 31% greater respectively). In contrast, Populus in control sites had a 97% larger DLH. Chi-square analysis reveals that the observed differences in DLH between control and experimental sites at the 0-10 m distance are not statistically significant (X^2 = 2.83 at P = 0.05 = 14.07).

At the 11-20 m distance Populus, Salix., and Amelanchier in the control sites had larger diameters compared to the experimental sites (40, 77 and 50% larger average DLH respectively) (Figure 5). In contrast, Betula, Cornus, Pinus and Picea glauca in the experimental sites had larger diameters (21, 60, 52 and 33% greater average DLH). Chi-square analysis reveals that the observed differences in DLH between control and experimental sites at the 11-20 m distance are not statistically significant (X^2 = 1.4 at P = 0.05 = 14.07).

At a distance of 21-30 m the control sites had larger DLH for the species found at both sites with the exception of Cornus for which the experimental sites had trees with larger diameters (67% greater) (Figure 6). Chi-square analysis reveals that the observed differences between control and experimental sites at

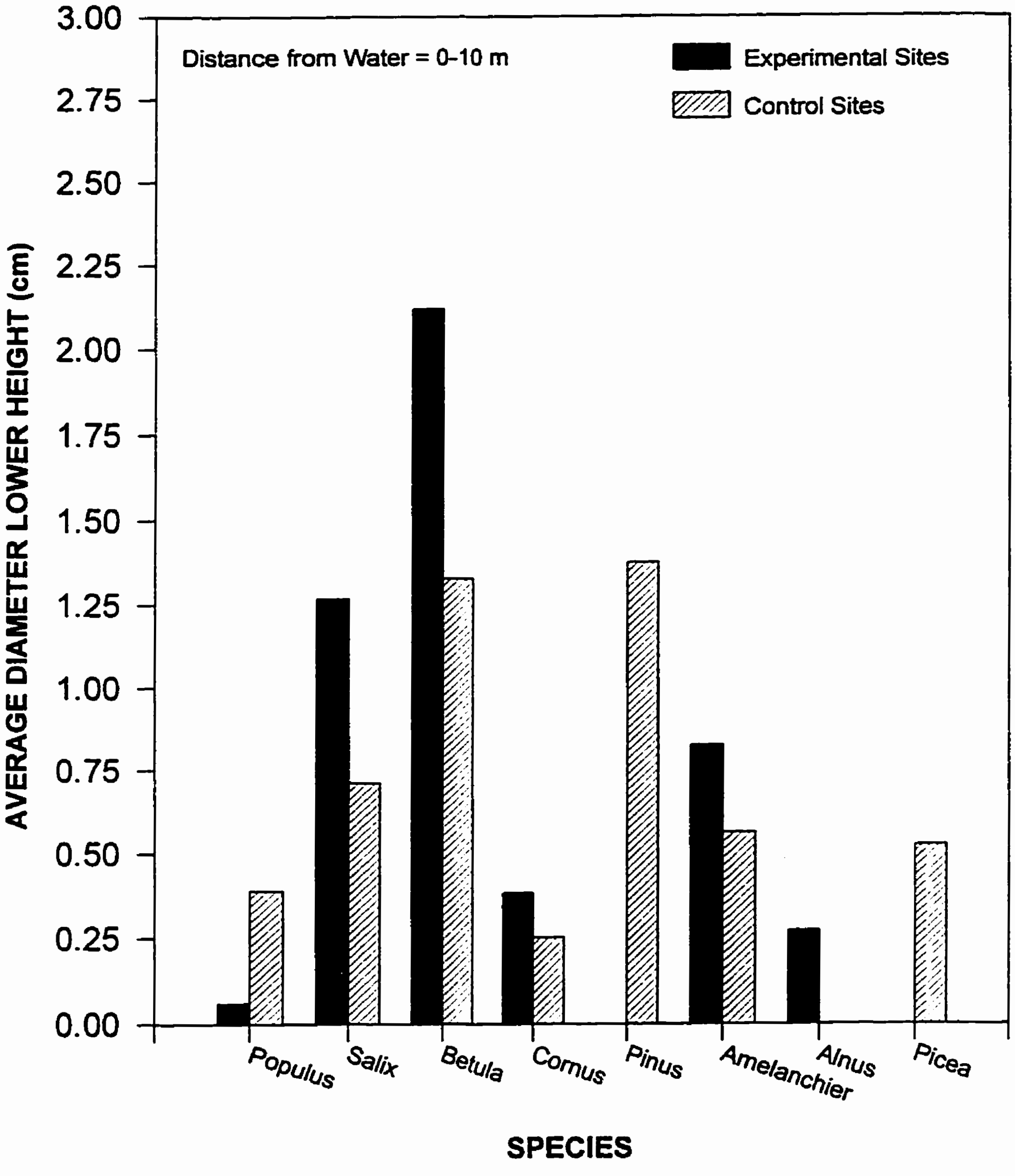

Figure 4: Diameter lower height in control and experimental sites at a distance of 0 - 10 m from the lake's edge.

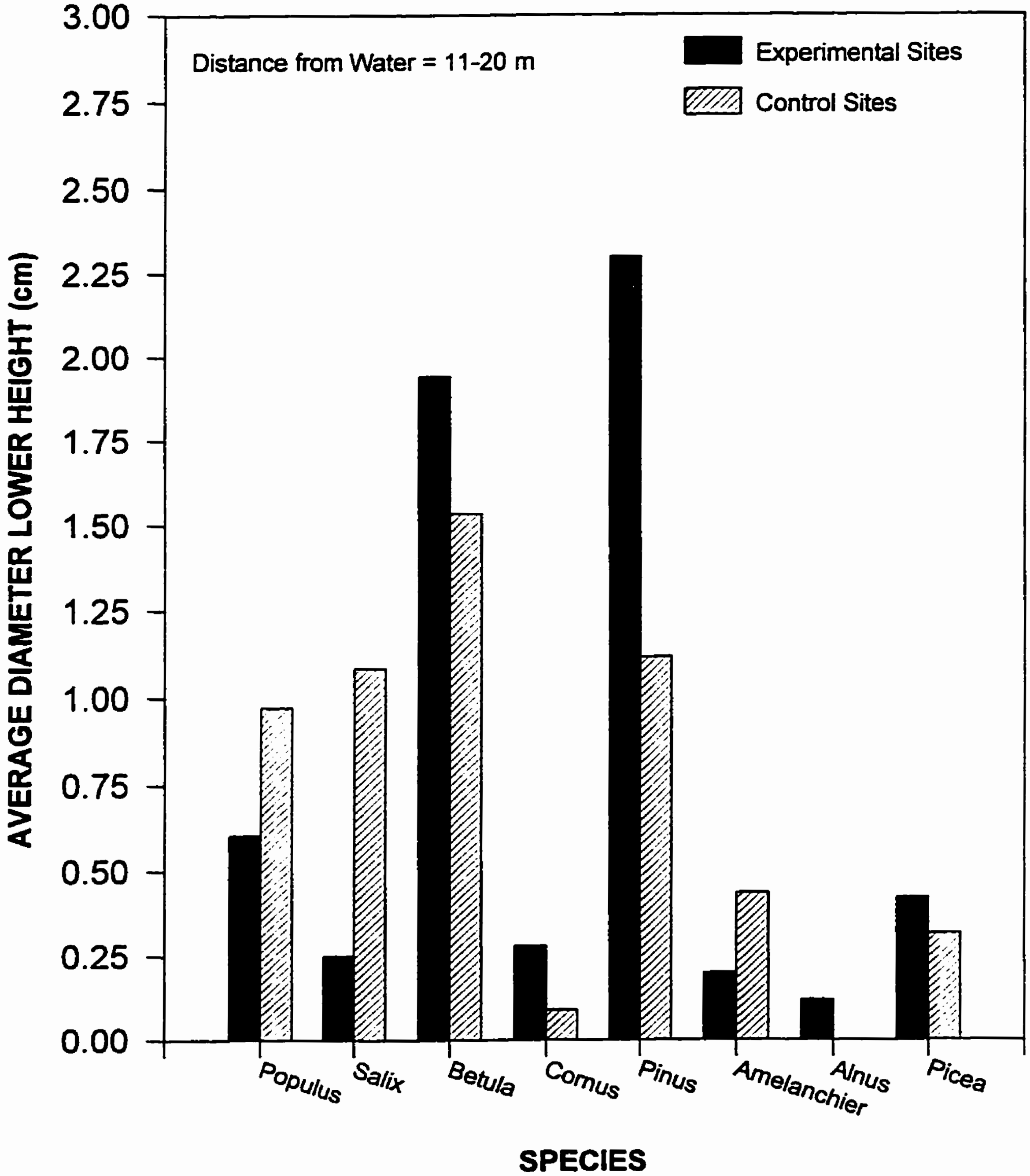

Figure 5: Diameter lower height in control and experimental sites at a distance of 11 - 20 m from the lake's edge.

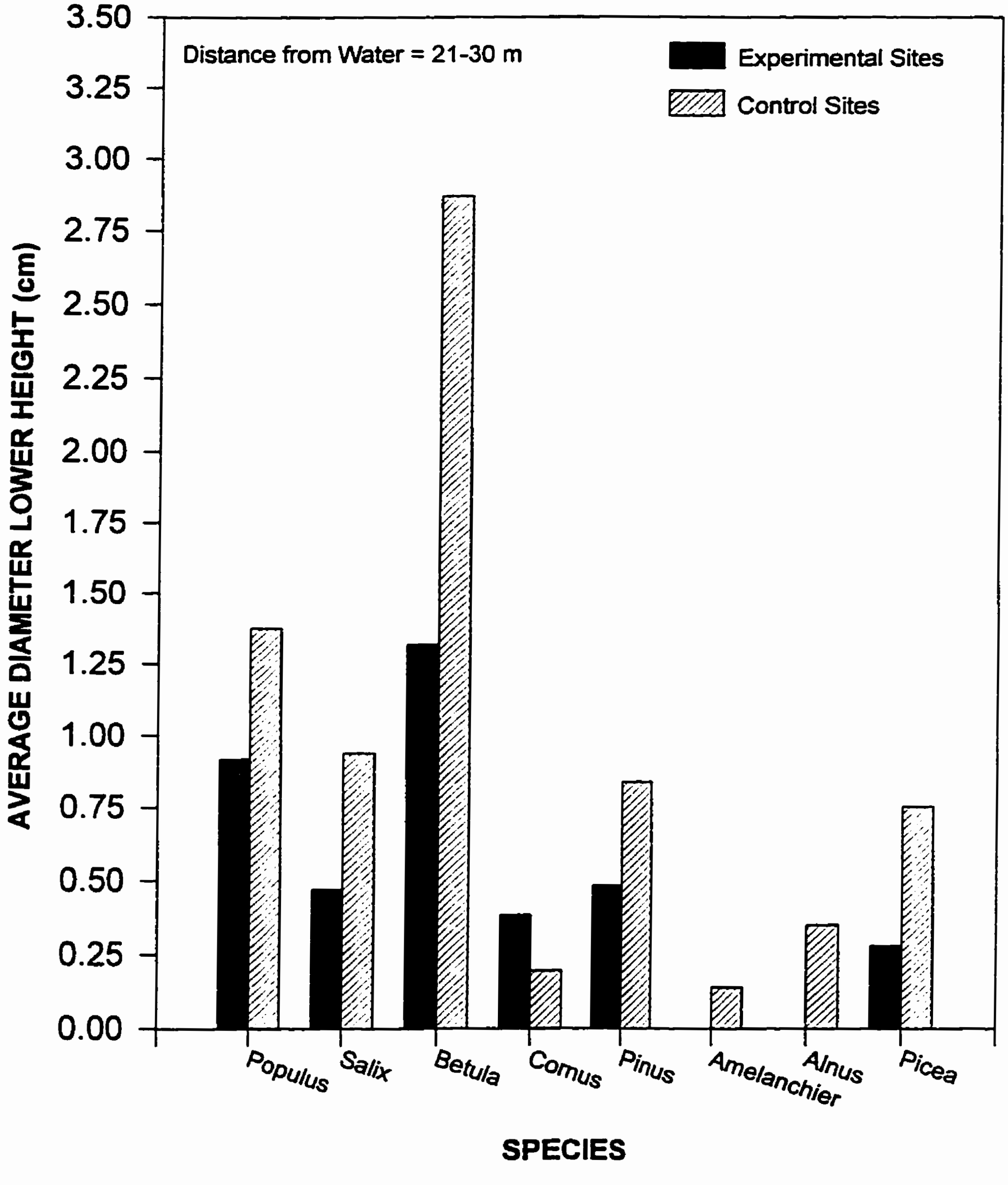

Figure 6: Diameter lower height in control and experimental sites at a distance of 21 - 30 m from the lake's edge.

the 21-30 m distance are not statistically significant ($X^2 = 0.60$ at $P = 0.05 = 14.07$).

DLH of Populus saplings at the 0-10 m distance was much lower than at the other two distances for both control and experimental sites. As well, Betula saplings had a greater DLH at the 11-20 m distance compared to the other two distances in the control sites.

A chi-square test for independence also revealed that the observed differences in total average diameter lower height for all species between control and experimental sites was not significant ($X^2 = 0.05$, P at $0.05 = 5.99$).

DISTANCE TRAVELED FOR FOOD HARVESTING AS MEASURED BY STUMP DENSITY

Comparisons were also made of differences in average stump density for each species between control and experimental sites (Table 1). As expected, there are a larger number of stumps in the experimental sites. There were no stumps observed at the 0-10 m distance for both control and experimental sites. As well, no stumps were observed in the control sites at the 11-20 m distance. Stumps were however observed at the 11-20 and 21-30 m distances for the experimental sites and at the 21-30 m distance for control sites.

Betula had the highest stump density at 11-20 m with 2.36 stumps m^{-2} and Cornus had the highest stump density (2.74 stumps m^{-2}) at 21-30 m in the experimental sites. Alnus had the highest stump density for the control sites at a density of 1.68 stumps m^{-2}.

DISTANCE FROM THE WATER	STUMP DENSITY (Stumps m^{-2})															
	Populus		Salix		Betula		Cornus		Pinus		Alnus		Amelanchier		Picea	
	E	C	E	C	E	C	E	C	E	C	E	C	E	C	E	C
0-10 m	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11-20 m	0.78	0.00	0.30	0.00	2.36	0.00	1.10	0.00	0.20	0.00	0.17	0.00	0.67	0.00	0.20	0.00
21-30 m	0.78	0.94	0.55	1.07	1.49	0.00	2.74	1.00	0.08	0.30	0.08	1.68	0.08	0.00	0.13	1.35

- E = experimental sites
- C = control sites

Table 1: Stump density of control and experimental sites at 0 - 10, 11 - 20 and 21 - 30 m.

DISCUSSION

TREE DENSITY AS A FUNCTION OF FEEDING SITE SELECTION

There were observed differences in average species density at each set of distances measured, however, these observed differences were not found to be statistically significant (Figures 1, 2, 3). As well, I found no significant differences in average total species tree density between experimental and control sites in this study. Masslich et al (1988) found that average density of aspen was much greater at feeding sites utilized by the beaver than at control sites. This was not found to be so in my study.

One point of interest is the fact that the control sites were observed to have a much higher percentage of coniferous species (Pinus and Picea) compared to the experimental sites. This may be a factor in feeding site selection as Picea was never observed to be harvested by beaver in this study and Pinus was generally utilized only in the spring.

DIAMETER LOWER HEIGHT AS A FUNCTION OF FEEDING SITE SELECTION

Masslich et al (1988) observed that densities of stumps in a class size of 0-5 cm were greater in areas used by beavers than for the same size class of trees in non-feeding areas. However, in my study, observable differences in diameter lower heights of the tree species between control and experimental sites were not observed to be statistically significant (Figures 4, 5, 6). Total average diameter lower height for the tree species between experimental and control sites was also not found to be statistically significant. Thus DLH does not appear to be a factor in feeding site selection in this study. However, further studies with a larger sample size may be required to confirm this statement.

DISTANCE TRAVELED FOR FOOD HARVESTING AS MEASURED BY STUMP DENSITY

Surveys of the study area showed that most of it had been utilized by beaver at one time or another as evidenced by the presence of old cut stumps at control sites. However, only certain sites (experimental sites) were being utilized extensively during the time of this study. Jenkins (1975) postulates that beaver may sample trees of the various species present at a site to determine nutritional values. This may be a factor as to why most of the control sites in the study area had some sign of beaver activity.

Beavers are semi-aquatic mammals and therefore one would postulate that they would harvest trees as near to the water's edge as possible. Belovsky (1984) did find this to be true in that the beaver in his study limited their cutting away from the water. However, in my study I only found cut stumps at the 11-20 and 21-30 m distances in the experimental sites and only at the 21-30 m distance in control sites (Table 1). Betula and Cornus were found to have the highest stump densities in the experimental sites at 11-20 m and 21-30 m respectively. Alnus had the highest stump density in the control sites.

A possible explanation as to why beaver in this study utilized food 11+ m from the water at experimental sites is that they were observed to utilize Pinus buds and bark in the spring season. However, this species was only found to be present in experimental sites at distances greater than 11 m. This would force the beaver to travel farther from the lakeshore to reach this species. Once at a particular distance from the water's edge, beaver may "familiarize" themselves with the area for further harvesting of different species.

In addition, the beaver were only observed to cut trees for food up to a distance from the shore an average of 30 m. Likewise, Aleksiuk (1970) and Belovsky (1984) observed that beaver cuts were not common at distances greater than 20 and 30 m from the shoreline respectively. Masslich et al (1988), however, found that the beaver in his study traveled up to 100 m from the shoreline to reach Populus trees of larger diameters, while Bradt (1938) found that beaver do not cut trees more than 60 meters from the water's edge.

The harvesting of trees only to a distance of 30 m in my study may be due to the topography and vegetative characteristics of Wallace Lake. Large, often steep rock ridges exist around the lakeshore which may limit the beaver from traveling farther from the shoreline for food. As well, a fire had swept the area 12 years prior to this study which resulted in many standing dead trees falling in wind storms; this made land travel in certain areas very difficult, especially for a low bodied animal such as the beaver.

CONCLUSIONS

The comparisons conducted between beaver run (experimental) sites and non - beaver run (control) sites showed no significant differences between the sites in terms of tree densities and diameters lower height indicating that these factors do not appear to influence feeding site selection.

There were observed differences in stump densities between control and experimental sites with stumps found at 21-30 and 11-30 m from the water's edge respectively. Species availability, topography and site history were postulated as potential factors influencing the distance beaver traveled to harvest food.

However, only 5 sites of each were measured for this study. It may, therefore, be beneficial to conduct a larger survey to determine whether factors such as tree species, density and diameters influence feeding site selection and distance traveled for food harvest by beavers. As well, studies should be conducted to determine whether feeding sites and harvesting distance may be selected by the beaver based on other physical and chemical site factors.

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CHAPTER 4: EMERGENCE TIME FROM THE LODGE

ABSTRACT

During nightly observations of the beaver colony under study weather conditions and nightly emergence times from the lodge for each beaver family member were recorded. Nightly emergence from the lodge was found to be correlated with time of sunset with most of the nightly emergence occurring prior to sunset. In 1992 the beavers were observed to emerge from the lodge primarily 30 - 120 minutes prior to sunset while in 1993 the beavers were observed to leave the lodge mainly between 60 - 150 minutes prior to sunset.

Weather conditions appeared to have little influence on nightly emergence from the lodge.

INTRODUCTION

Seton (1909) was one of the early naturalists to study and write about the life history of the North American Beaver (Castor canadensis). He observed that the beaver is semi-aquatic and mainly nocturnal in habit. Beavers emerge from lodges or bank burrows in the late afternoon or early evening to commence their nightly activities of foraging, repair to the lodge and/or dams and play (Green 1936, Schramm 1968, Anonymous 1978). Beavers are active during the day, but usually only for brief periods for food gathering (Green 1936, Wheatley 1989). Studies on the order of emergence from the lodge have been conducted (Schramm 1968, Brady and Svendsen 1981), however discussions on the factors which govern daily emergence are lacking in the literature.

The objectives of this study were to determine if weather conditions and/or sunset times play a role in daily emergence time.

METHODS

EMERGENCE TIME FROM THE LODGE

Nightly emergence times from the lodge were recorded for each member of the beaver family I was studying, including the two juvenile males, the juvenile female and the adult female to determine if weather or sunset times play a role in the commencement of nightly activity.

During the first few weeks of the field research, nightly observations of the beavers commenced at the lodge between 18:00 and 19:00 hours. The beavers had usually emerged from the lodge by this time. It was ultimately determined that the beavers did not usually emerge from the lodge prior to 16:00 hours to begin their nightly activities. Thus observations of the beavers' emergence times were made from a freighter canoe I anchored 30 - 40 m the lodge prior to 16:00 hours daily.

Emergence times were usually determined by visual identification when a beaver would appear swimming in the water outside of the lodge and by radio telemetry. When the signal for a beaver inside the lodge grew weak and the beaver did not surface, this indicated that the beaver had swum underwater to a location behind where I was anchored and was not observed visually.

WEATHER DATA

Daily weather data at the site were also collected. These included:

1. Air temperature (^0C) using a 40^0C thermometer held at approximately 0.5 m from the surface of the water;
2. Water temperature (^0C) using a 40^0C thermometer held within the top 30 cm of the water;
3. Wind direction (i.e.: N, NE, WSW etc.) was noted by observing the direction of waves;
4. Wind speed (m/sec) was measured using a hand-held anemometer at approximately 1 m from the water's surface;
5. Percent cloud cover was determined as a measure in tenths between 0 - 1 with 0 being clear sky and 1 being complete cloud cover from horizon to horizon;
6. The amount of precipitation (mm) in the previous 24 hours was recorded (as measured from a rain gauge at the field station).
7. I also obtained daily sunset times for Wallace Lake ($51^o02'40''$ N latitude, $95^o20'40''$ W longitude) from the Planetarium of the Manitoba Museum of Man and Nature in Winnipeg. "Sunset" in this paper is defined as the time at which the upper limb of the sun touches the horizon for $51^o02'40''$ N latitude, $95^o20'40''$ W longitude (Valentin, 1998). As well, all sunset and emergence times recorded in this paper have been adjusted to Central Standard Time. Refer to Appendix I for a list of daily sunset times for 1992 and 1993 used in this study.

RESULTS

WEATHER AND EMERGENCE TIME

I examined each set of weather variables (1992 and 1993 combined) versus emergence time from the lodge for all of the beavers studied (two juvenile males, juvenile female and adult female) by regression analysis to determine if nightly emergence time by beavers is related to weather conditions. Regression analysis of emergence time with air temperature for all of the beavers studied revealed a low r^2 value of 0.07. Furthermore, regression analysis of water temperature, wind direction, wind speed, percent cloud cover and precipitation with emergence time revealed the following r^2 values: 0.05, 0.04, 0.03, -0.0009 and 0.02 . These low r^2 values indicate that a relationship between these weather conditions and emergence time is insignificant.

To determine if a combination of weather conditions may affect nightly emergence time, I applied multiple regression analysis to all sets of weather data versus emergence time (1992 and 1993 combined). This analysis revealed an r^2 value of 0.158, higher than the separate values obtained in the regression analysis, but still indicating little relationship between emergence time and weather.

SUNSET AND EMERGENCE TIME

I designated nightly observations of emergence times for each beaver family member into 30 minute intervals described by one of nine categories as follows: +180, 150-180, 120-150, 90-120, 60-90, 30-60 and 0-30 minutes before sunset and 0-30 and 30-60 minutes after sunset. Histograms of the 1992 and 1993 data show the distribution of these categories for each beaver family member (Figures 1 and 2).

In 1992 a total of 73 emergence time observations were made, 31 observations for the two yearling males (averaged), 16 observations for the yearling female and 26 for the adult female. The beavers primarily emerged from the lodge 30-120 minutes before sunset with 81%, 48%, and 69% of the emergence observations for the adult female, the yearling males and the yearling female occuring within this time frame (Figure 1).

In all of the 26 emergence observations made on the adult female in 1992 she was not observed to leave the lodge after sunset (Figure 1). Both the yearling males and the yearling females were observed to leave the lodge after sunset, up to 30 and 60 minutes after sunset respectively (23% and 13% of observations respectivley). Only the adult female and the yearling males were observed to leave the lodge earlier than 120 minutes before sunset (4% and 29% respectively).

In 1993 a total of 69 emergence time observations were made, 26 observations for the two-year old male, 23 observations for the two-year old female and 20 observations for the adult female.

Compared with 1992, emergence times were more variable in 1993 with all of the beavers observed to emerge from the lodge up to and including 180

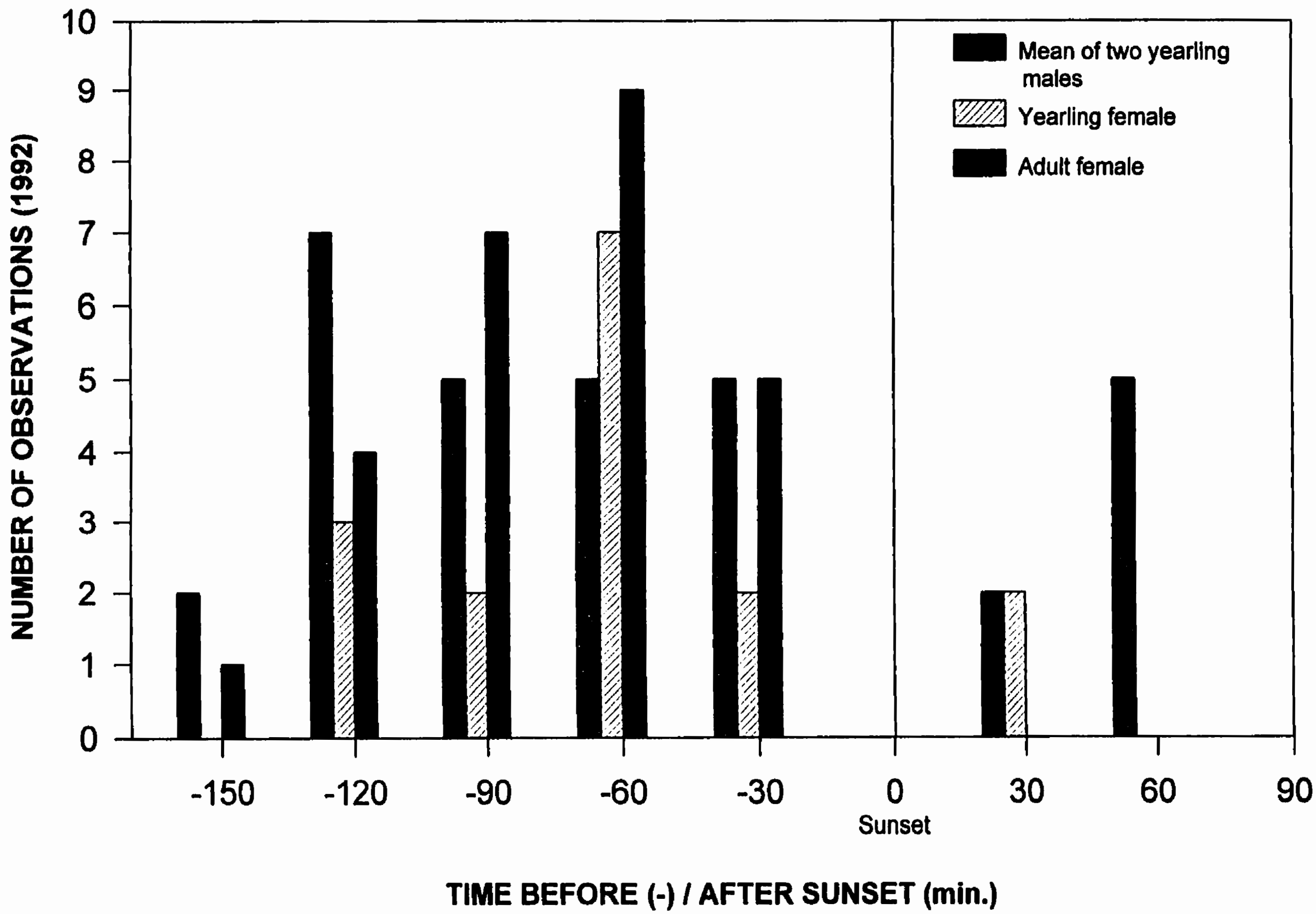

Figure 1: Comparisons of observed emergence times from the lodge for the yearling males, yearling female and the adult female beaver of the family in 1992.

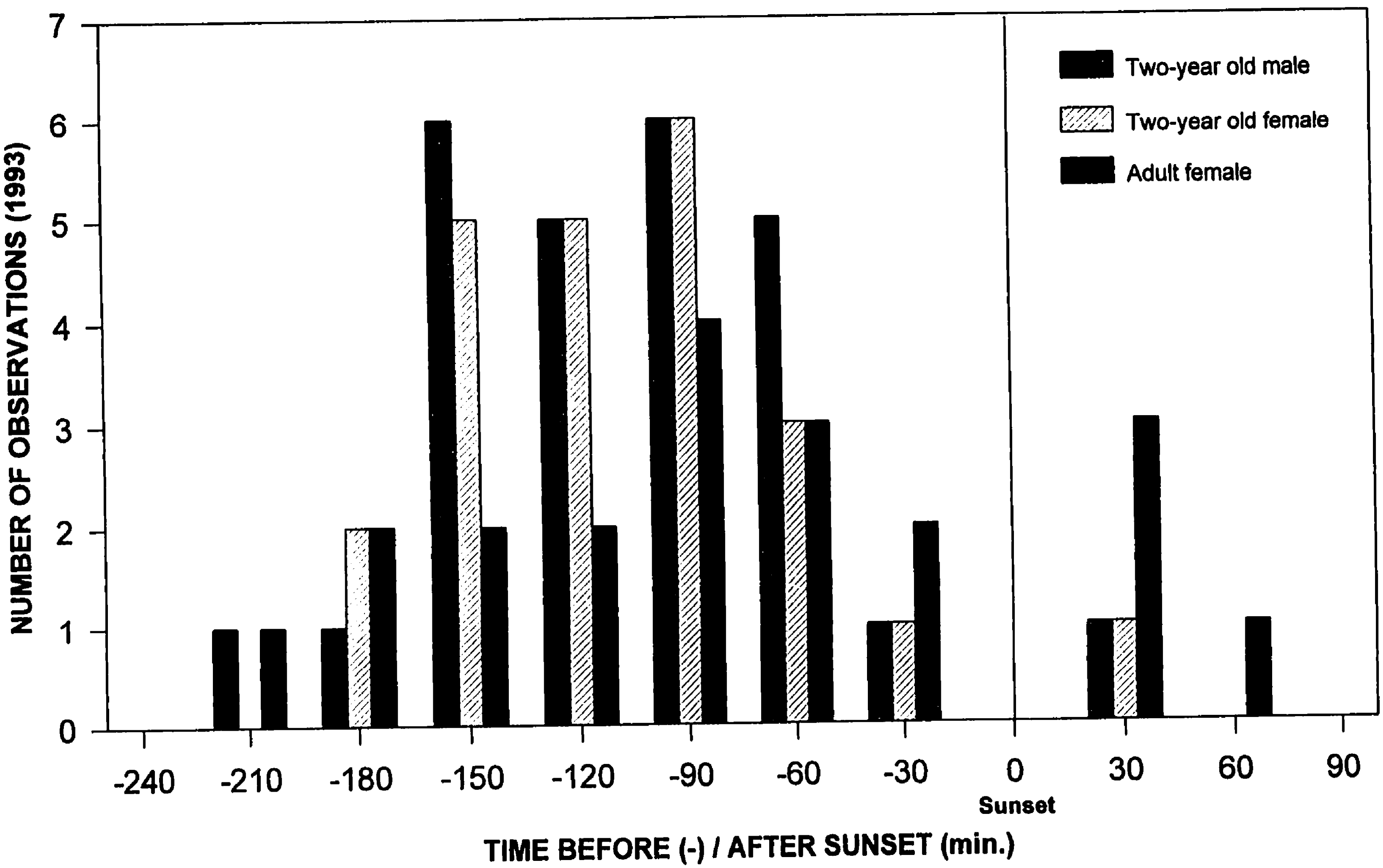

Figure 2: Comparisons of observed emergence times from the lodge for the two-year old male, two-year old female and the adult female beaver of the family in 1993.

minutes prior to sunset (Figure 2). In 1993 the beavers were observed to emerge from the lodge primarily between 30 to 150 minutes before sunset. The two-year old male, two-year old female and the adult female were observed to emerge from the lodge 30 to 150 minutes before sunset in 85, 83 and 55% of the total observations for each beaver respectively. In addition, in 1993 the two year old male and female, as well as the adult female were all observed to leave the lodge at least once after sunset. All three of these beavers were also observed to leave the lodge more than 180 minutes prior to sunset.

Chi-square analysis was conducted to determine whether the observed differences in emergence time between the adult female and the juveniles was significant (for both 1992 and 1993 combined). The results indicate that these observed differences are not statistically significant (chi-square = 8.73, $P>0.100$). However, observed differences in emergence times between the two years (for all of the beaver family members combined) was found to be statistically significant (chi-square = 15.74, $P<0.0005$).

DISCUSSION

SUNSET AND EMERGENCE TIME

The fact that beavers are mainly but not exclusively nocturnal in habit is undisputed in the literature (Seton 1909, Green 1936, Schramm 1968, Bovet and Oertli 1974, Brady and Svendsen 1981, Belovsky 1984). Reports correlating nightly beaver emergence from the lodge with environmental factors such as weather conditions and light, including sunset times, are essentially lacking. Bovet and Oertli (1974) and Potvin and Bovet (1975) have studied beavers in Canada where they found that the animals exhibit a circadian rhythm of activity that spans approximately 24 hours in the summer and 27 hours in the winter. They suggest beaver may be influenced by light intensity. Green (1936) discusses that when the sun sets there is a general movement of the colony out of the lodge but he does not discuss how soon before or after sunset the beavers leave the lodge. Brady and Svendsen (1981) report on the order of emergence from the lodge by various members of the beaver family they were studying, but they did not report on the actual times the beavers emerged nightly.

My results revealed a relationship between emergence time and time of sunset. The juvenile males and female and the adult female emerged from the lodge in 1992 usually between 30 to 120 minutes prior to sunset (Figure 1). In 1993 the emergence times were more variable with most of the emergence observations occurring between 60 to 150 minutes prior to sunset (Figure 2).

The beavers were rarely observed to stay in the lodge until the sun had set. The observed differences in emergence time by the family members was not found to be statistically significant; however, differences in emergence time between years for all of the family members combined was found to be statistically significant.

WEATHER AND EMERGENCE TIME

I found no correlation between beaver emergence time from the lodge and weather conditions including air temperature, water temperature, wind speed, wind direction, percent cloud cover and precipitation. As well, multiple regression analysis of all of the weather conditions versus emergence time also revealed no correlation.

Belovsky (1984) correlated beaver activity with the thermal environment. He found that the main activity period for beaver in his study was during the coldest ambient air temperatures, which occurred between 1900 to 0700 hours. He also found that a peak of activity sometimes occurred from 1300-1500 hours when the water was cooler than the air or at a time when the thermal environment was as amiable for foraging activity as it was for rest.

CONCLUSIONS

Nightly emergence from the lodge by beavers appears to be correlated with the time of sunset, with most emergence by the beavers occurring 30 to 150 minutes prior to sunset. Weather conditions appear to have little influence on nightly beaver emergence; however, further study may be required.

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MANAGEMENT RECOMMENDATIONS

These management recommendations are based on the information obtained from this study. However, it should be noted that this information may be relevant only to the particular family of beaver under study and additional data are required in different areas of Canada to make broad generalizations about beaver for management purposes.

1. Beaver appear to be very opportunistic in food habits and may consume a diverse array of plant species. Therefore a survey of beaver habitat should be conducted to determine which plant species the beaver are utilizing prior to any habitat management decisions being made.

2. A variety of factors such as nutritional value of plant species, soil fertility, moisture regimes and topography should be taken into account when developing management programs for beaver.

3. When preparing habitat management designs for beaver, changes in yearly and seasonal food choice should be taken into account.

4. When conducting research on beaver in northern climates it is best to start daily studies 90 minutes prior to sunset.

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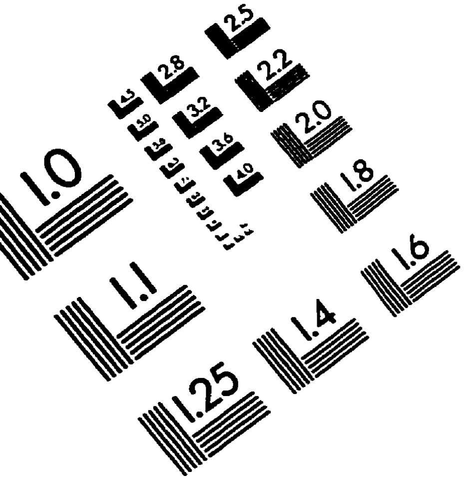
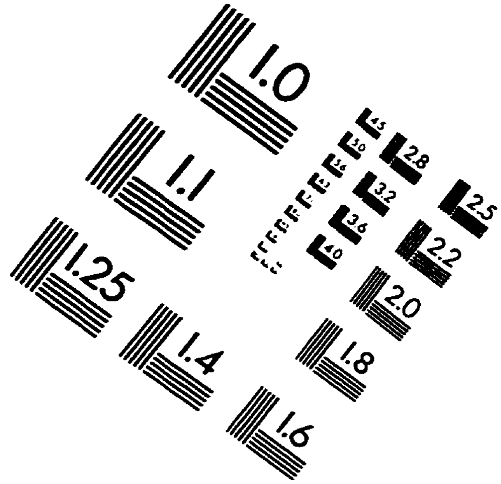
APPENDIX I: SUNSET TIMES FOR 1992 AND 1993

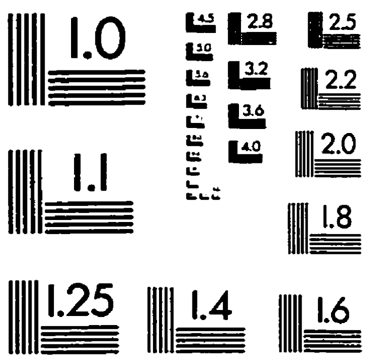
Time of Sunset in 1992							
Date	**Sunset**		**Date**	**Sunset**		**Date**	**Sunset**
May 1	1944		July 1	2039		Sept. 1	1906
2	1945		2	2039		2	1904
3	1947		3	2038		3	1901
4	1949		4	2038		4	1859
5	1950		5	2037		5	1857
6	1952		6	2037		6	1855
7	1953		7	2036		7	1853
8	1955		8	2035		8	1850
9	1956		9	2035		9	1848
10	1958		10	2034		10	1846
11	1959		11	2033		11	1844
12	2001		12	2032		12	1841
13	2002		13	2031		13	1839
14	2004		14	2030		14	1837
15	2005		15	2029		15	1834
16	2007		16	2028		16	1832
17	2008		17	2027		17	1830
18	2010		18	2026		18	1828
19	2011		19	2025		19	1825
20	2013		20	2024		20	1823
21	2014		21	2023		21	1821
22	2015		22	2021		22	1819
23	2017		23	2020		23	1816
24	2018		24	2019		24	1814
25	2019		25	2017		25	1812
26	2020		26	2016		26	1810
27	2022		27	2014		27	1807
28	2023		28	2013		28	1805
29	2024		29	2011		29	1803
30	2025		30	2010		30	1801
31	2026		31	2008		Oct. 1	1758
June 1	2027		August 1	2007		2	1756
2	2028		2	2005		3	1754
3	2029		3	2003		4	1752
4	2030		4	2002		5	1749
5	2031		5	2000		6	1747
6	2032		6	1958		7	1745
7	2033		7	1957		8	1743
8	2034		8	1955		9	1741
9	2034		9	1953		10	1738
10	2035		10	1951		11	1736
11	2036		11	1949		12	1734
12	2036		12	1947		13	1732
13	2037		13	1945		14	1730
14	2037		14	1943		15	1728
15	2038		15	1941		16	1726
16	2038		16	1940		17	1724
17	2039		17	1938		18	1722
18	2039		18	1936		19	1720
19	2039		19	1933		20	1718
20	2040		20	1931		21	1715
21	2040		21	1929		22	1714
22	2040		22	1927		23	1712
23	2040		23	1925		24	1710
24	2040		24	1923		25	1708
25	2040		25	1921		26	1706
26	2040		26	1919		27	1704
27	2040		27	1917		28	1702
28	2040		28	1915		29	1700
29	2039		29	1912		30	1658
30	2039		30	1910		31	1657
			31	1908			

Time of Sunset in 1993							
Date	Sunset		Date	Sunset		Date	Sunset
May 1	1943		July 1	2039		Sept. 1	1906
2	1945		2	2039		2	1904
3	1947		3	2039		3	1902
4	1948		4	2038		4	1900
5	1950		5	2038		5	1857
6	1951		6	2037		6	1855
7	1953		7	2036		7	1853
8	1955		8	2036		8	1851
9	1956		9	2035		9	1848
10	1958		10	2034		10	1846
11	1959		11	2034		11	1844
12	2001		12	2033		12	1841
13	2002		13	2032		13	1839
14	2004		14	2031		14	1837
15	2005		15	2030		15	1835
16	2007		16	2029		16	1832
17	2009		17	2028		17	1830
18	2010		18	2027		18	1828
19	2011		19	2026		19	1825
20	2012		20	2024		20	1823
21	2014		21	2023		21	1821
22	2015		22	2022		22	1819
23	2016		23	2021		23	1816
24	2018		24	2019		24	1814
25	2019		25	2018		25	1812
26	2020		26	2016		26	1810
27	2021		27	2015		27	1807
28	2023		28	2013		28	1805
29	2024		29	2012		29	1803
30	2025		30	2010		30	1800
31	2026		31	2009			
June 1	2027		August 1	2007			
2	2028		2	2006			
3	2029		3	2004			
4	2030		4	2002			
5	2031		5	2000			
6	2032		6	1959			
7	2033		7	1957			
8	2034		8	1955			
9	2034		9	1953			
10	2035		10	1951			
11	2036		11	1950			
12	2036		12	1948			
13	2037		13	1946			
14	2038		14	1944			
15	2038		15	1942			
16	2039		16	1940			
17	2039		17	1938			
18	2039		18	1936			
19	2040		19	1934			
20	2040		20	1932			
21	2040		21	1930			
22	2040		22	1928			
23	2040		23	1926			
24	2040		24	1923			
25	2040		25	1921			
26	2040		26	1919			
27	2040		27	1917			
28	2040		28	1915			
29	2040		29	1913			
30	2040		30	1911			
			31	1908			

IMAGE EVALUATION TEST TARGET (QA-3)

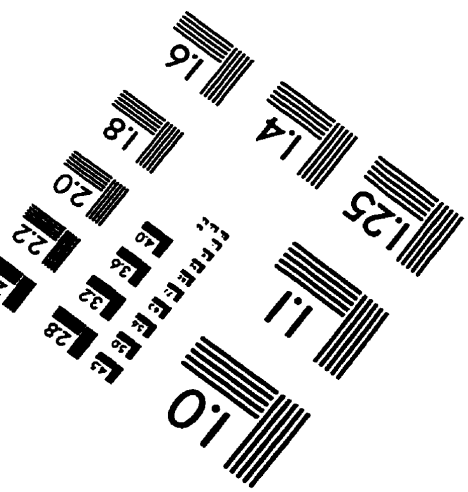






150mm

6"



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