Dutch Elm Disease and the Vegetation Composition

of Manitoba's Bottomland Forests.

by

Carol B. Essenburg

A Thesis Submitted to the Faculty of Graduate Studies

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ABSTRACT

In Manitoba's bottomland forests, elms infected with Dutch elm disease are either left standing or removed. Removal creates gaps of various sizes in the canopy whereas dead trees left standing create smaller openings. In order to determine the impact of Dutch elm disease on the forest, 31 5-year old removal gaps, 43 openings beneath dead elms (openings were <15 years old) and a 15 ha clearing (13 years old) were located along the Red River near Winnipeg, MB. In each of these areas and the adjacent undisturbed forest, vegetation was sampled using 5x5m plots and the point-quarter technique for trees, and 2x2m quadrats for shrubs and herbs. Woody species taller than 10cm and a diameter at breast height of less than 5cm were considered shrubs, and separated into three height classes (<1m, 1-2m, >2m). The herb stratum included all non-woody and woody plants less than 10cm tall. The 82 vascular understorey species with total cover values greater than 5% and bare ground were subjected to correspondence analysis. The closed forest consisted primarily of *Ulmus americana*, *Acer negundo* and *Fraxinus pennsylvanica*. Saplings of these species (<1m tall) made up 70% of the shrub stratum in both disturbed and undisturbed areas. *Fraxinus pennsylvanica* saplings dominated all areas except the clearing, where a few young *A. negundo* occurred. All areas had approximately 50 vascular herb stratum species. Native taxa such as *Laportea canadensis* and *Smilacina stellata* predominated everywhere except in the clearing. The clearing was colonized by non-native weedy species such as *Arctium lappa* and *Sonchus arvensis*. It was clearly separated from closed forest plots in correspondence analysis, but the gap and dead elm forest plots were not. Gap and closed forest plots clustered by location,

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possibly reflecting the patchy nature of the forest or its past history.

Dutch elm disease may cause the current *Ulmus-Acer* dominated forest to become dominated by *F. pennsylvanica* and *A. negundo* with *U. americana* present as only small, short-lived individuals. The impact of the loss of mature *U. americana* trees is dependent on its importance in the stand. Canopy openings created by the removal or death of a small number of *U. americana* have an understorey composition similar to the undisturbed forest. Tree regeneration is not occurring in the large clearing created by elm removal. "Weedy" herbs and *Matteuccia struthiopteris* are dominating the clearing.

ACKNOWLEDGEMENTS

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1. INTRODUCTION

1.1 BOTTOMLAND FORESTS

Many naturally forested areas in south central Manitoba are along rivers and streams. These forests are a characteristic component of the bottomland vegetation associated with fluvial landforms. Fluvial processes result in the landscape having four components, the channel bed, channel shelf, floodplain and terrace (Figure 1). Although these landforms have characteristic vegetation, there are rarely discrete boundaries between them.

Since part or all of the channel bed is inundated by water at all times, aquatic plants inhabit this lowest segment. The channel shelf, a horizontal to gently sloping surface that extends from the shoreline of the steep bank to the lower limit of persistent vegetation is dominated by forest pioneers, mainly *Salix* spp. and small *Populus deltoides*[1]. Streamflow reaches the channel shelf 5% to 25% of the time (Hupp and Osterkamp 1985). Floodplains are relatively flat surfaces underlain by unconsolidated sediment and they occupy much of the valley bottom. *Ulmus americana*, *Fraxinus pennsylvanica* and *Acer negundo* dominate the floodplain. Their relatively closed canopy may limit shrub growth but characteristic species such as *Rosa woodsii*, *Prunus virginiana*, *Cornus stolonifera* and *Viburnum lentago* may be present. Arboreal lianas such as *Vitis riparia*, *Amphicarpa bracteata*, *Parthenocissus inserta* and *Menispermum canadense* occur in many stands. Common herbs may include *Laportea canadensis*, *Actium lappa* and *Smilax herbacea*. Rare herbs such as

[1]Vascular plant nomenclature follows Scoggan (1957). Authorities and varieties of species reported in this research are given in Appendix A. Others are noted when the taxon occurs.
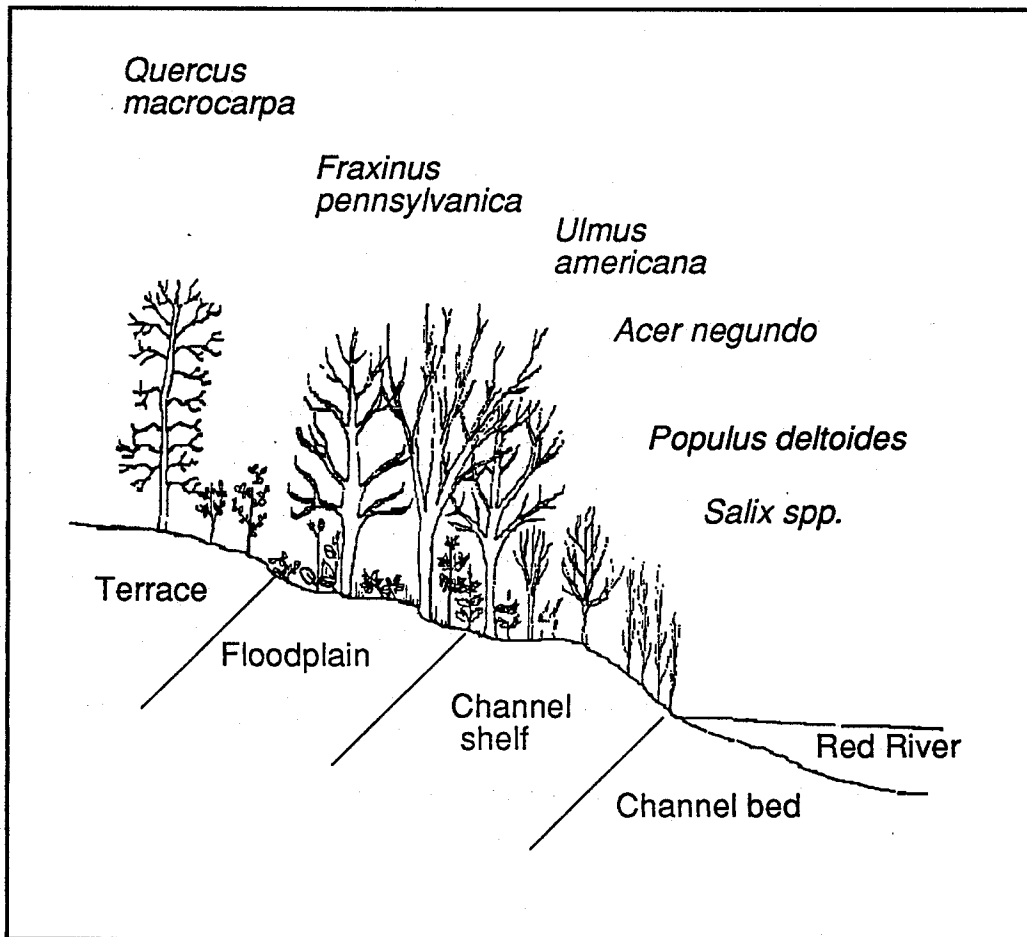
Figure 1. Profile of a representative bottomland forest along the Red
River.- Understorey species include: *Cornus stolonifera,*
Viburnum lentago, Parthenocissus inserta, Laportea canadensis
and *Smilax herbacea.*

Phryma lepostachya L. and *Corallorhiza striata* Lindl. may also be found (Hildermann et al. 1975). Terraces are abandoned floodplains, less prone to flooding. Their species composition is similar to that of the floodplains, with the addition of *Quercus macrocarpa* in the canopy. Generally, species diversity, richness and evenness increase with increasing distance from the river, then decrease slightly in the unflooded areas (Bell 1980).

Many of the bottomland forests have been felled in the northern United States and south-western Canada. In some cases, it was removed to utilize the fertile land for agriculture (eg. in Manitoba, Wanek 1967; Dorber 1979, in North Dakota, Johnson et al. 1976 and in Illinois, Dunn and Stearns 1987). In others, such as in North Dakota (Johnson et al. 1976) and South Dakota (Wilson 1970), forests were destroyed for hydro reservoirs.

The remaining areas of bottomland vegetation are a natural oasis in a sea of agriculture. They provide homes for mammals such as the thirteen-lined ground squirrel (*Spermophlus tridecelineatus* (Mitchell))[1], the eastern grey squirrel (*Sciurus carolinensis* Gmelin), the eastern chipmunk (*Tamias striatus* (Linnaeus)), raccoons (*Procyon lotor* (Linneaus)) and white tailed deer (*Odocoileus virginianus* (Zimmermann)). Some of the more abundant song birds nesting in the forests include the least flycatcher (*Empidonax minimus* (Baird & Baird))[2], red-eyed vireo (*Vireo olivaceus* (Linnaeus)), American robin (*Turdus migrantorius* Linnaeus) and

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[1] Nomenclature follows Banfield, A.W.F. 1974. Mammals of Canada. University of Toronto Press, Toronto

[2] Nomenclature follows Godfrey, W.E. 1966. Birds of Canada. Queens Printer, Ottawa.

rose-breasted grosbeak (*Pheucticus ludovicianus (Linnaeus)*). Large birds such as the great horned owl (*Bubo virginianus* Gmelin), great grey owl (*Strix nebulosa* Forster), sharp-shinned hawk (*Accipiter striatus* Vieillot) and red-tailed hawk (*Buteo jamaicensis* (Gmelin)) also make bottomland forests their home. A variety of migrating birds utilize the forest network for food and shelter.

The importance of all forests was emphasized by Saarin (1984) who acclaimed the opportunity they provide for aesthetic relief, outdoor activities and viewing wildlife. Nebel (1981) commented on the ability of bottomland forests to stabilize streambanks against normal and overflow erosion.

1.2 DUTCH ELM DISEASE

1.2.1 DUTCH ELM DISEASE CYCLE

Dutch elm disease, so-called because it was first identified in the Netherlands and is unique to elms, is a lethal wilt disease caused by the ascomycete fungus *Ceratocytis ulmi* (Buism.) C. Moreau. The fungus damages trees by interfering with the xylem vessels conduction mechanism (Strobel and Lanier 1981). This causes characteristic symptoms of the disease such as leaf yellowing and drop, and eventual tree mortality in most cases.

There are three transmission vectors of *C. ulmi*: unsterilized pruning equipment, natural root grafting and elm bark beetles (Figure 2). Pruning a diseased elm and then trimming a healthy elm without sterilizing the equipment may introduce fungal spores to the healthy tree. Root grafts of elms less than 13m apart may serve as a pathway for hyphae to enter healthy elms from infected elms.

In Manitoba, the major vector of *C. ulmi* is the native elm bark

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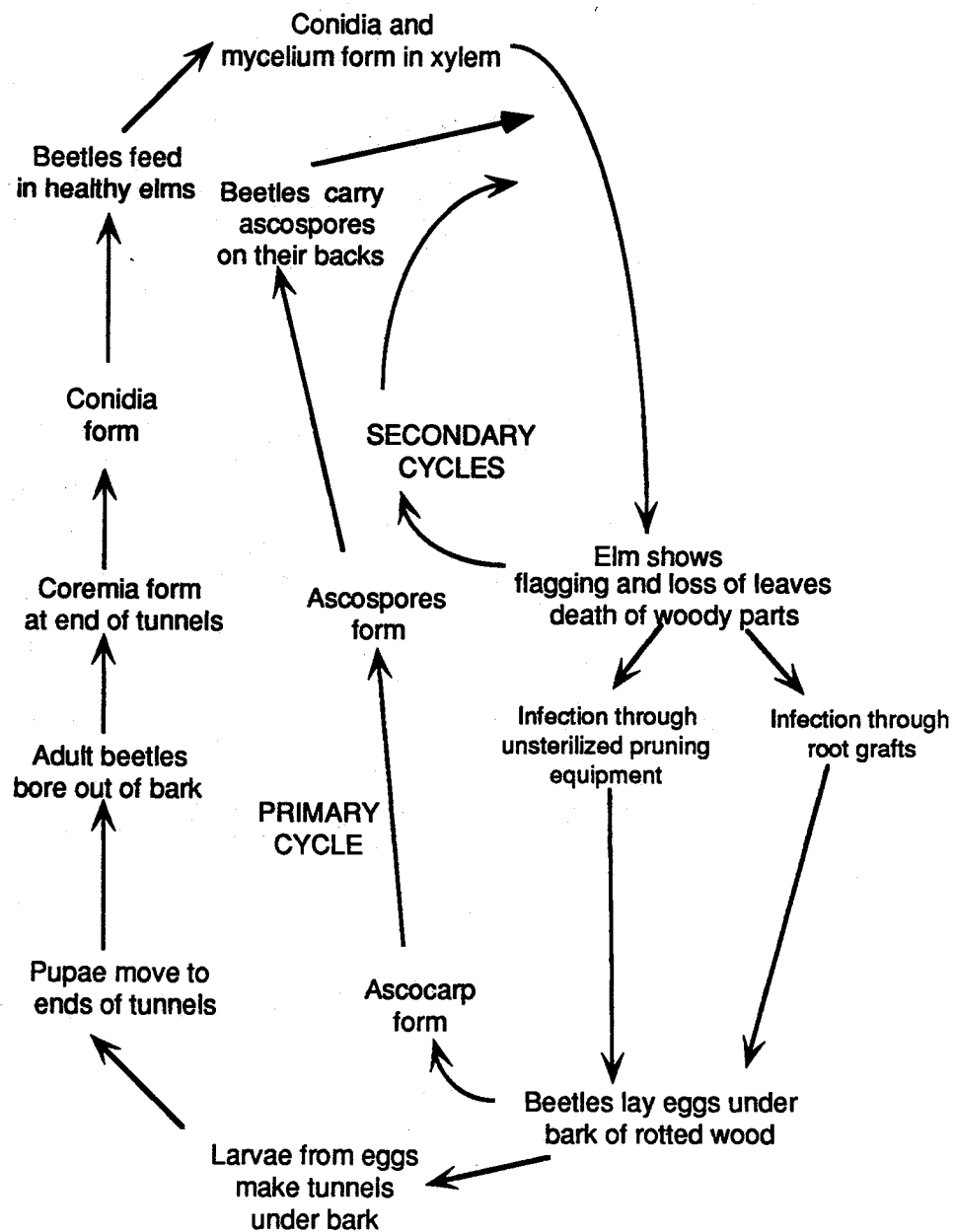
Figure 2. Life cycle of Dutch elm disease. Conidia are asexual reproductive stuctures which produce conidia. An ascocarp is a sexual fruiting body which produces ascospores. (modified from Roberts and Boothryod. 1984)

beetle, *Hylurgopinus rufipes* (Eichoff). The European elm bark beetle, *Scolytus multistriatus* Marsh. is a less numerous vector. Adults of both beetles breed under the bark of stressed, dying or dead elms. If a brood tree has Dutch elm disease, the brood and larval galleries become infested with the fungus. New adult beetles emerge with sticky *C. ulmi* spores on their backs. The disease is introduced to healthy elms when these infected beetles feed.

The timing of the infection varies. Some beetles overwinter as adults, emerging to feed from mid-April to mid-May. This feeding stage causes the highest incidence of infections of Dutch elm disease in Manitoba. It is also thought that another group of beetles may overwinter as larvae, emerging and feeding from late June to late July, causing late season infections.

According to Strobel and Lanier (1981) there are five possible strategies to control Dutch elm disease: 1) to protect valuable trees with fungicides and/or insecticides, 2) to replace elms with less susceptible species, 3) to control fungus or beetle reproduction, 4) to quarantine certain areas and, 5) to remove diseased elms or dead wood.

1.2.2 MANITOBA DUTCH ELM DISEASE PROGRAMME

Dutch elm disease was confirmed in Manitoba in 1975 simultaneously in Winnipeg, Selkirk and Brandon. In an effort to prevent the spread of the disease, the province initiated four of Strobel and Lanier's strategies, namely use of fungicides and insecticides, elm replacement and elm removal. Current policy is to spray the lower part of the trunk of elms in parks with the insecticide Dursban for tree protection and for suppression of the beetle population. Trees considered to be valuable,

eg. trees on the Legislative Building grounds, are injected with the fungicide Lignasan BLD or Arbotect. These methods may not always be completely effective and are very costly. In cities or towns, elms are slowly being replaced by a polyculture of trees such as *Tilia americana* and *F. pennsylvanica*. They are planted in new development areas and in areas where elms have been removed.

A significant component of the integrated management programme is removal of dead and dying elms to destroy beetle breeding sites. This facet of the control programme was started in 1976 in Winnipeg (including a two mile "buffer zone'), Brandon, Portage la Prairie and some rural communities (Dept. Nat. Resources 1979). When the programme began, heavy equipment was used to remove numerous diseased elms and, inadvertently, some other tree species were damaged or removed. On occasion this caused much habitat damage and created large clearings. In subsequent years, techniques have changed and today a minimum of heavy machinery is used. Nevertheless elm removal creates gaps in the forest canopy. Although elm removal has been a practice for more than 15 years, the effect on Manitoba's bottomland forests has not been studied.

1.3 OBJECTIVES

The primary objective of this research was to describe the impact of Dutch elm disease on bottomland forest in the vicinity of Winnipeg. There were available gaps approximately five years old created by the removal of diseased elms, openings beneath dead standing elms and a large 13-year old clearing created by elm removal. These were compared with undisturbed areas of the bottomland forest. Preliminary studies were also conducted on the extent of Dutch elm disease in elm saplings and the vegetation

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composition of areas where felled elms were burned. This research should expand the understanding of forest gap ecology.

2. LITERATURE REVIEW

2.1 TREE SPECIES CHARACTERISTICS

Bottomland trees have evolved specialized life history characteristics and tolerances to withstand the environmental features (flooding, scouring, etc.) associated with their habitat. Many researchers such as Wilson (1970), Bell (1974a; b) and Barnes (1985) have documented these characteristics for bottomland trees. This chapter will concentrate on the important bottomland trees in Manitoba: *Ulmus americana*, *Acer negundo*, *Fraxinus pennsylvanica*, *Populus deltoides*, *Tilia americana* and *Quercus macrocarpa*.

2.1.1 REPRODUCTION

The tree species of concern all can reproduce vegetatively, especially as young saplings, roots and old stumps (Hosie 1973; Barnes 1985). However, Barnes (1985) reported that *U. americana* sprouts only in response to damage. Canham and Marks (1985) reported *P. deltoides* relies heavily on vegetative reproduction for propagation. On a Wisconsin island, 55% of the *P. deltoides* stems originated from sprouts (Barnes 1985). Of the 69 *A. negundo* shoots on the same island, 20% were sprouts, but few hardwoods surpass the capacity of *T. americana* to reproduce by stump sprouts (Fowells 1965).

Ulmus americana produces its first viable seeds at the relatively early age of 15 years (Table 1) and attains maximum production at 40 years (Fowells 1965). *Acer negundo* forms viable seed at approximately 20 years while *Q. macrocarpa* does not seed until it is 35 years old, with a good seed crop every two to three years (Fowells 1965). *Fraxinus pennsylvanica* usually starts flowering when trees are 7-8cm in diameter and 6m tall

Table 1. Characteristics of major bottomland trees in Manitoba.

	Acer negundo	Fraxinus pennsylvanica	Populus deltoides	Quercus macrocarpa	Tilia americana	Ulmus americana
Age when 1st seed produced [1]	20 years	20 years	10 years (max 30-40 years)	35 years (max 75-150 years)	15 years	15 years (max 40+ years)
Fruit type	samara [2]	samara [1,2]	samara [2]	nut [2]	nut like [1]	samara [2]
Seeds ripen	fall [3]	fall [1,2]	summer [1]	fall [1]	fall [1]	spring [1]
Soil conditions needed for germination	--	--	moist mineral soil [1] alluvium [4]	litter layer removed [1]	mineral soil [1]	moist litter decayed wood [1]
Germination success (%)	--	--	88% [1]	30% [1]	--	97% [5]
Germination after soaking in water	--	30% in 5cm after soaking for 30 days [6]	100% in 1.1L after 4 days [8]	--	--	76% in 5cm after 30 days [6]
Seedling shade tolerance	yes [7]	yes [7]	no [1]	--	--	prefers 1/3 light [1]
Flood effect on saplings	66% died in 16 days [9]	all died in 32 days [9]	all died in 16 days [9]	killed by floods [2]	--	withstand if in dormant season
Height growth 1st yr.	15-30cm. [3]	30cm [1]	50cm [10]	--	--	16cm in 1st 5yrs [11]
Avg. height growth/year [1]	--	30cm	1.2-1.5m for 1st 25-30 years	0.1-0.25cm	39-40cm	--

References:
1. Fowells (1965)
2. Looman & Best (1979)
3. Hosie (1973)
4. Keammerer (1972)
5. Jones el al. (1989)
6. DuBarry (1963)
7. Hosner & Minckler (1963)
8. Hosner (1957)
9. Hosner (1958)
10. Barnes (1985)
11. Streng el al. (1989)

(Fowells 1965). *Populus deltoides* begins to flower at ten years of age and produces a good seed crop every ten years (Fowells 1965), although Barnes (1985) reported good crops most years for *P. deltoides*. These species are all wind pollinated, promoting pollination by flowering before, or with leaf emergence (Hosie 1973). In contrast, *T. americana* produces fragrant insect pollinated blossoms in July from 15 years old onward (Fowells 1965).

With the exception of *Q. macrocarpa*, Manitoba's bottomland trees produce numerous, light winged fruits adapted for wind and water dispersal (Fowells 1965; Barnes 1985). A 12m tall *P. deltoides* may produce 28 million seeds (Bessey 1904). *Ulmus americana* is a prolific seed producer whose seeds may be carried up to 92m (Fowells 1965). The continued survival of *Ulmus*, despite the occurrence of Dutch elm disease, has been attributed to its effective seed dispersal and prolific seed production (McBride 1973; Richardson and Cares 1976; Parker and Leopold 1983; Dunn 1986). Streng et al. (1989) found *U. americana* survivorship increases with distance from a conspecific adult. *Quercus macrocarpa* produces heavy animal dispersed acorns.

2.1.2 GERMINATION

Although all the bottomland trees flower in spring, only *U. americana* and *P. deltoides* seed germinates soon after the seed is set (Fowells 1965; Barnes 1985). In the others, the fruit ripens on the trees and falls in autumn or early winter, and the seeds germinate the following spring. This strategy may increase survivorship since survival is highest for seedlings that emerge earliest in the season (Streng et al. 1989). The date of seed dispersal in *P. deltoides* is quite variable, even among

adjacent trees, providing for long term seed dispersal (Noble 1979).

Preferred germination conditions vary among the species (Table 1) (Fowells 1965). For *P. deltoides,* an 88% success in germination may be achieved in moist, flooded mineral soil. In a study of other *Populus* species, Moss (1938) found seeds would germinate only if the substrate was moist for one week. While *U. americana* more frequently germinated on moist litter or decaying logs and stumps, *T. americana* preferred drier mineral soil. Maximum germination levels (33%) for *Q. macrocarpa* were noted when the litter layer was removed (Fowells 1965).

Researchers have studied the ability of some bottomland species to germinate in inundated soil (Table 1). DuBarry (1963) investigated the germination of, among other species, *U. americana* and *F. pennsylvanica* while seeds were immersed in water for up to 30 days. Laboratory experiments indicated that *U. americana* had higher germination in 5cm of water than on a wet sponge, while *F. pennsylvanica* germinated only in water. Hosner (1957) found that after up to 32 days of soaking in 1.1L of water, soaked seeds of *U. americana* had consistently higher germination than un-soaked seeds for all treatment periods. All *P. deltoides* seeds germinated after four days of soaking with no additional germination when the seeds were removed from the water. Wilson (1970) noted *P. deltoides* needed constant moisture for 14 days prior to germination. It appears that short term inundation of the six bottomland hardwood species discussed has a positive effect on their germination. As the studies were all conducted in the laboratory, it is not possible to apply these results directly to the effect of natural flooding on germination.

2.1.3 SEEDLINGS

Hosner (1958) examined the effects of complete inundation on six bottomland tree seedlings, including *P. deltoides, F. pennsylvanica* and *A. negundo*. Seedlings (7.5cm tall) of each species were placed in tanks filled with water 30cm deep for 2, 4, 8, 16 and 32 days. All survived 8 days of complete inundation. Following 16 days of inundation, all *P. deltoides* and 66% of the *A. negundo* died soon after removal from the water. All individuals of all species died after 32 days of inundation (Table 1). It was concluded that *F. pennsylvanica* was the most flood tolerant, *P. deltoides* the least and *A. negundo* intermediate. Fowells (1965) noted that *F. pennsylvanica* becomes less flood tolerant as it matures.

The response of first year *U. americana* seedlings to waterlogging and inundation was investigated by Jones et al. (1989). They found 38% survival after 3-4 days of inundation while 97% survived without flooding. Waterlogging caused a significant reduction in seedling total biomass, leaf area, height and diameter. It was postulated that later life stages in *U. americana* are more tolerant of flooding than are current year seedlings. The results of a study of Texas floodplain trees, including *U. americana*, confirmed that seedling mortality due to flooding is highest in the first year and declines in succeeding years (Streng et al. 1989). Seedlings can withstand flooding in the dormant season, but will die if the flooding is prolonged into the growing season (Fowells 1965).

Although flooding causes woody seedlings many indirect hardships such as siltation, litter build-up and scouring, it may be less important to seedling survival than emergence time, distance from a cospecific adult

and available light (Streng et al. 1989).

The majority of bottomland trees are shade tolerant (Table 1). Although *U. americana* seedlings tolerate full light, they flourished in one third (1/3) light (Fowells 1965). They were able to persist under a closed canopy and grew well when released (Hosner and Minckler 1963). *Ulmus americana* and *F. pennsylvanica* survived and tolerated shade better than *A. negundo* (Hosner and Minckler 1963), but *A. negundo* is still considered to be shade tolerant (Horn 1981). *Ulmus americana, F. pennsylvanica* and *A. negundo* could germinate and establish in closed stands (Johnson et al. 1976). *Fraxinus pennsylvanica* seedlings were able to withstand competition (Curtis 1959) but flourished in the open (Horn 1981). In contrast, *P. deltoides* seedlings are shade intolerant (Hosner and Minckler 1963; Fowells 1965) and cannot reproduce under a dense canopy. They require fully exposed alluvium to survive (Keammerer 1972).

The seedlings of *U. americana, A. negundo, T. americana, F. pennsylvanica* and *P. deltoides* are all relatively fast growing with *P. deltoides* being the fastest (Table 1). Under optimal conditions, its seedlings may grown to 0.5m tall by the end of the first year (Barnes 1985), while an *A. negundo* may grow only 15-30cm (Hosie 1973). This difference in growth rates persists through maturity (Table 1). A 50-55cm diameter at breast height (dbh) *P. deltoides* may be the same age as a 7.5-10cm dbh *A. negundo* (Hosner and Minckler 1963). *Ulmus americana* may grow to 16cm tall in the first five years after emergence, with the majority of the growth being in the first year (Streng et al. 1989). In Iowa, *Q. macrocarpa* grew only 0.25-0.63cm/year (Fowells 1965).

2.1.4 FLOOD TOLERANCE

The tolerance of mature trees to flooding regimes is often very different from their tolerance in early stages of development (Bell 1974a). Trees may grow effectively into their juvenile stage on sites to which mature individuals are not well adapted (Hosner and Minckler 1963). However, research indicates that bottomland trees are dependent on flooding (Johnson et al. 1976; Reily and Johnson 1982). Decreased growth rates of *U. americana*, *F. pennsylvanica*, *A. negundo* and *Q. macrocarpa* have been attributed to the near elimination of over-bank flooding and apparent lowering of the water-table associated with the Garrison Dam (Reily and Johnson 1982). The altered flood regime was also implicated in the decline of establishment of *U. americana* and *A. negundo* stems (Johnson et al. 1976).

2.2 BOTTOMLAND FOREST SUCCESSION

Successional changes in floodplain vegetation can be postulated by examining changes in plant communities with elevation. Several authors (Johnson 1950; Noble 1979; Bell 1974a; Barnes 1985) have examined succession along rivers and streams in the northern United States and Canada. The youngest community is on the low, recently deposited sand and alluvium, while the oldest is on high terraces. Despite a change in vertical elevation of less than 4m, there are significant changes in the canopy species (Bell 1974a). Although these communities are often examined as distinct zones, most integrate continuously along the elevation gradient (Wikum and Wali 1974; Bell 1980).

2.2.1 TREES

The pioneer woody colonizers of exposed sand bars are species of *Salix*. *Salix interior* was the most abundant woody species on a frequently flooded island in Wisconsin (Barnes 1985). *Salix* spp. dominated elevations up to 2m along the Mississippi and Missouri Rivers (Johnson 1950; Shelford 1963) for approximately 15 years (Johnson 1950). After the *Salix* stabilized the sand bar, *P. deltoides* invaded. The *Salix/Populus* sere may persist for 150 years, accumulating organic matter (Johnson 1950; Wilson 1970). As *P. deltoides* is able to achieve greater height and is more shade tolerant than *Salix* (Noble 1979) it soon dominates. After 20 to 25 years, the *Salix* spp. are totally eliminated and *P. deltoides* ceases to produce root-sprouts (Wilson 1970; Noble 1979). Beneath the *P. deltoides* canopy, *Acer* (*A. negundo* and/or *A. saccharinum* L.), *F. pennsylvanica*, *Ulmus* (*U. americana* and/or *U. rubrum*) and *Quercus* spp. begin to establish. Along the Missouri River, *A. negundo* and *F. pennsylvanica* were the first non-pioneers to reach tree size followed by *U. americana* and finally *Q. macrocarpa* (Johnson et al. 1976). Hosner and Minckler (1963) predicted *F. pennsylvanica* and *U. americana* would survive and grow better than *A. negundo* in the shade of *P. deltoides*. Johnson (1950) observed that these species became dominant about 2m above the river. The climax sere, in the flood-free terrace, consists primarily of *Quercus* spp. and some secondary *A. negundo*, *F. pennsylvanica* and *U. americana*. Giant relic *P. deltoides* may be found throughout the last two seres.

According to Johnson (1950), it would take 40 years for bottomland succession to reach the climax sere. Along the Missouri River in North

Dakota, the oldest *U. americana* and *Q. macrocarpa* trees were 300 to 350 years old, although the surrounding forest was probably 200 to 250 years old (Johnson et al. 1976).

Gradient trends in an Illinois streamside forest were studied by Bell (1974a; 1980). He calculated the cumulative percentage of time that the river exceeded flood levels (190.9m) from 55 years of flow data. Mature *U. americana* tolerated flooding frequencies of 15%, but was not an important forest component until flood frequency fell below 2% (Bell 1974a). It dominated in the 0.5% to 1% flood level (Bell 1980). Areas that flooded 25% of the time were dominated by *A. saccharinum* with *F. pennsylvanica* and *Platanus occidentalis* L.. Maximum numbers of *F. pennsylvanica* were found in areas with a 15% flood frequency.

Trends in species diversity, richness and dominance become evident with elevational and/or successional changes in vegetation composition. Early seres where *Salix* spp. and *P. deltoides* dominated, had numerous tree stems, but a relatively open canopy (Keammerer et al. 1975; Johnson et al. 1976). Noble (1979) attributed the dense shrub stratum, composed of species such as *Ribes* spp. and *Rosa* spp. in early seres to high levels of light penetration. Later seres with *U. americana*, *A. negundo*, *F. pennsylvanica*, and *Q. macrocarpa* had fewer trees/ha than early ones, but their canopy was denser and the undergrowth was sparse. Although many researchers (Curtis 1959; Keammerer et al. 1975; Noble 1979) noted this trend, none gave density figures.

Tree diversity and richness increase with an increase in age and decrease in flood frequency (Johnson et al. 1976; Bell 1980). Wikum and Wali (1974) showed a strong negative correlation between tree basal area

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and elevation, with maximum diversity in mid-coenocline. Bell (1980) reported tree species richness, diversity and evenness increased from a minimum at the stream bank to a maximum at mid-coenocline areas and then regressed slightly in the unflooded areas. These results supported the hypothesis that a normal curve best describes woody species distribution along a gradient.

2.2.2 UNDERSTOREY

Successional changes are also evident in the understorey of bottom-land forests. Menges (1986) tested environmental correlates of herbs with elevation, light, soil properties (particle analysis and moisture content) and found elevation had the greatest influence on herb composition. Generally, as elevation increased and flood frequency decreased, species richness increased (Bell 1974b; Menges 1986), although correlation analysis by Bell (1980) revealed that the number and cover of herbs was highest on lowest elevations. Above the flood zone, there was little difference in understorey with changes in elevation (Bell 1974b). In one study area, 80% of the understorey species were present in the flood-free portion of the elevation gradient, while only 17% were restricted to flood prone areas (Bell 1974b). Two species, *Rhus radicans* and *Smilax hispida* L., were present in every elevation increment.

In a North Dakota forest, arboreal lianas such as *Vitis vulpina* L., *Parthenocissus inserta* and *Celastrus scandens* L. grew in stands dominated by intermediate aged *P. deltoides* (Johnson et al. 1976). Menges (1986) found *Urtica dioica* and *Laportea canadensis* characterized higher, less frequently flooded sites.

Rhus radicans was the most common woody understorey species in

frequently flooded areas in an Illinois streamside forest (Bell 1974b). *Ranunculus* spp., *L. canadensis*, *Aster simplex* and *Ambrosia trifida* were the most frequently occurring species in areas flooded up to 20% of the time. They dominated throughout the growing season. In the higher areas, *Parthenocissus quinquefolia* (L.) Planch. was the most frequently occurring woody species. *Symphoricarpos* sp. and *Ribes missouriense* Nutt. had frequencies greater than 25% throughout the unflooded zone.

Other species showed seasonal dominance. Perennials which quickly break dormancy, develop rapidly and flower early were the most common herbs in late April. By late May, *Menispermum canadensis*, *Smilax herbacea* and *Smilax ecirrhata* (Engelm.) Wats. were visible. When the canopy closed in June, *Impatiens pallida* Nutt. was the most frequently occurring herb in the upper zone. The mid-zone did not have unique herbs, but consisted of an association of outliers from both upper and lower elevations (Bell 1974a).

2.3 DUTCH ELM DISEASE RESEARCH

Although pathologists generally agree that the fungus *Ceratocytis ulmi* interferes with elms's vascular system, the exact mechanism of the interference is unclear. When the vascular system of a higher plant is invaded by a pathogen, the host normally responds by sealing off infected vessels (Backman 1981). Research suggests that in susceptible elms, *C. ulmi* secretes a toxin which disrupts or delays this response (MacHardy and Backman 1973). The fungus is then able to invade the entire vascular system unchecked. Strobel and Lanier (1981) isolated the toxin peptidorhamnomannan from *C. ulmi* cultures, but it is unclear if this is the toxin to which MacHardy and Backmann (1973) referred. Another

possible mechanism of interference is that the fungus produces enzymes to break down vessel walls and pit membranes (Elgersman 1981). Partially degraded cell wall chemicals are released in the vessel lumina which then impede water transport. These enzymes and other products of the fungus would induce tylose formation. The combined effect of these factors is proposed to influence Dutch elm disease symptom expression (Elgersman 1981).

Although many species of *Ulmus* are susceptible to Dutch elm disease, *U. americana* is particularly vulnerable (Stipes and Campana 1981). When a young, vigorously growing tree is infected, it may succumb to the disease in less than one year (Strobel and Lanier 1981). Older, slower growing individuals may survive two or more years.

Scientists have investigated the results of inoculation with *C. ulmi* and the timing of infections. Caroselli and Feldman (1951) studied the effects of mechanical wound inoculation in *U. americana* seedlings. They found 2-year old seedlings were not so readily infected as 6-year old trees. Seedlings developed typical symptoms only if they were subjected to total darkness for 5 days, inoculated and then placed in daylight. This is not a regime likely to be encountered in a natural setting. No studies were found which tested insect inoculation on young seedlings or saplings.

In order to determine the period when *U. americana* is most susceptible to *C. ulmi* infection, Takai and Kondo (1979) and Takai et al. (1979) conducted field experiments in Ontario. Their results suggested that the most susceptible period for artificial inoculation and inoculation through beetle (*Hyluropinus rufipes*) feeding is early June to

early July, with slower development continuing until mid-August. These dates correspond with the time of maximum beetle feeding, initial leaf expansion and large spring wood vessel development. As the outermost growth ring of a healthy *U. americana* is responsible for 90% of the xylem transport (Ellmore and Ewers 1986), *C. ulmi* infection has little effect until these new vessels develop each spring. The exact dates of disease development were found to be highly dependent on host morphological and physiological condition (Takai and Kondo 1979).

2.4 GAP DYNAMICS

Canopy gaps may be formed by the death of a single tree (as in Barden 1980) or by the death of many trees (as in Ehrenfeld 1980). They may be caused by a number of factors, including disease, eg. chestnut blight, (Keever 1953) or Dutch elm disease, (Parker and Leopold 1983), windthrow (Brewer and Merritt 1978) and fire (Thompson and Willson 1978). In some cases, the dead bole remains standing (Richardson and Cares 1976), in others it falls (Thompson 1980). Gaps range in size from $1m^2$ to over $1490m^2$ (Runkle and Yetter 1987).

There are two general patterns of closure. The first is a response through reorganization of existing vegetation and the second is through vegetation established after the disturbance (Marks 1974; Runkle 1985; Connell 1989). Reorganization includes the release and growth of seedlings and saplings, lateral growth of the adjacent canopy, and production of stump sprouts or root suckers. New establishment may be by recent seed influx or germination of the existing seed bank.

2.4.1 GAP CHARACTERISTICS

Gaps in the forest canopy may have abiotic characteristics that

differ from the closed forest. They may have greater light intensities, different soil characteristics and different microclimates (Runkle 1985). The extent of these differences depends on characteristics of the gap such as size, shape and orientation. Canopy height and density and the severity of disturbance also influence the abiotic factors and in turn the colonizers. A brief discussion of gap light regimens, soil properties, microclimate and gap structure follows.

Changes in light intensity are the most obvious effects of canopy gaps. Light levels below canopies are often as low as 1-2% of full sun (Canham 1988). Canopy gaps can increase this level significantly. Even without leaves, deciduous canopies have less light than gaps (Collins et al. 1985) thus differences between gaps and closed forest may persist through the growing season. The enhanced light from gaps can cover a much larger area than the projected outline of the gap on the forest floor (Canham 1988). A hypothetical $78m^2$ gap in a 25m canopy at $44N^o$ latitude could potentially enhance an area greater than $500m^2$ by 1% of full sun over a growing season (Canham 1988). This indirect increase in light could trigger the release of shade tolerant plants in the vicinity of the gap.

An increase in gap size results in an increase in direct and indirect light until the ratio of D:H (gap diameter to canopy height) reaches two, after which the light level remains fairly constant (Runkle, 1985). Considering a whole growing season, photosynthetically active radiation at a height of 1m was higher in young gaps than the same size old gaps (because of canopy closure) or under an intact canopy (Moore and Vankat 1986). Similar results were noted for mid-day insolation on clear days (Collins and Pickett 1988a).

The death of a canopy tree and resultant canopy opening not only means the removal of a major consumer, but also the release of nutrients from organic matter (Marks 1974; Franklin et al. 1987). This should improve the soil nutrient levels. There should also be changes in soil moisture and temperature associated with gaps. Runkle (1985) speculated that large gaps would have higher maximum and lower minimum soil temperatures than surrounding areas. In Pennsylvania, Collins and Pickett (1988b) found there was no significant difference between gaps and closed forests in soil temperature, moisture or inorganic nitrogen. Significantly higher soil moisture in gaps after canopy closure was observed by Moore and Vankat (1986). However, few other studies were found which have investigated the effect of gaps on soil properties.

Runkle (1985) predicted that air temperatures would increase in gaps until the D:H ratio was 1.5-2. Above two, the wind would cool the gap (Collins et al. 1985). Field measurements by Collins and Pickett (1988a; b) showed gaps and closed forest had the same minimum daily temperatures, but gaps had higher maximum daily temperatures which supports the findings of Runkle (1985).

Many factors may influence gap characteristics (Collins et al. 1985). Small gaps in either open or tall canopies have little effect. Long narrow gaps will have much less influence than will isodiametric ones. A gap orientated east-west should receive more light than one orientated north-south. Prevailing wind direction, gap orientation and size affect wind velocity in the gap.

Gap orientation was found to have little influence on herb layer composition in a northern hardwood forest (Collins and Pickett 1988b).

For six colonizing annuals, the probability of reaching reproductive maturity increased with increasing gap size (McConnaughay and Bazzaz 1987), but few publications on gap dynamics include details of gap size and shape.

The severity of the disturbance influences the type of colonizing species. A mild disturbance should promote growth of suppressed seedlings, a more severe disturbance should allow progeny from the seed bank to prevail (new establishment response) (Collins et al. 1985). Gaps formed by severe disturbances that destroyed the seed bank usually relied on wind or animal dispersed seeds for colonization (Canham and Marks 1985). No studies were found which investigated these ideas.

2.4.2 GAP CLOSURE - TREES, GENERAL

Trees may be classified as either shade intolerant (pioneers) or shade tolerant (climax) (Barden 1980; Ehrenfeld 1980; Brokaw 1985; Whitmore 1989; Canham 1985; 1989; 1990). To become established, shade intolerant species (eg. *P. deltoides*) rely on large gaps or openings where direct sunlight reaches the ground at least part of the day. They close the canopy by invasion. Shade tolerant species (eg. *U. americana*) can survive under a closed canopy but respond positively to gaps. They close the canopy when they are released from suppression.

There may be a gradient of shade intolerances to light (Canham 1985). At one extreme, saplings persist only in deep shade, growing slowly in shade and are released by very little increase in light, even from an adjacent gap. *Ulmus americana* showed this response (Hosner and Minckler 1963). At the other extreme there are species whose saplings persist only under low levels of shade and are released by substantial

increases in light. *Fagus grandifolia* Ehrh. reacted in this manner (Canham 1988). Canham (1990) defined three modes of shade intolerant canopy recruitment: 1) slow growth to canopy size without any intervening growth stoppage due to lack of light, 2) an initial, single period of suppression as a sapling due to lack of light, followed by release that allows continuous growth into the canopy and 3) multiple periods of suppression and release when light levels change.

Suppression and release of shade intolerant species was studied by Canham (1985), Canham and Marks (1985) and Runkle and Yetter (1987) in an *Acer saccharum-F. grandifolia* forest in the New York and the southern Appalachian Mountains. Their studies indicated that shade intolerant species rarely reach the canopy in one gap episode, lending support to one of Canham's (1990) intolerance modes. Frequency of disturbance was more important than gap size and light regime in determining eventual dominants of small ($<205m^2$) gaps.

There may be mechanical and physiological constraints for shade tolerant trees. The ability to tolerate shade may decrease as the individual grows (Canham 1989). Low light results in reduced resource levels, increasing chances of saplings succumbing to drought, pathogens or defoliation (Waring 1987). Susceptibility to windthrow and fire may also increase as a result of the increased stress (Waring 1987). If light levels increase, shade tolerant trees are poor competitors and their growth may plateau or decline well below full light levels (Canham and Marks 1985). Should a shade tolerant species reach the canopy in a closed forest, further growth may be physically prevented by canopy tree branches (Canham 1989), although it seems unlikely that a shade tolerant tree would

reach the canopy while there were neighbouring trees close enough to physically restrain it.

Martinez-Ramos et al. (1989) have criticized the classification of species as shade tolerant or intolerant. They argued that it de-emphasizes the latter part of the life cycle. Successful colonization may be followed by different survivorship, growth and/or reproduction. Although they considered the model too simplistic, no alternative was suggested.

It has been proposed that in undisturbed old growth forests the dominant, shade tolerant species should replace themselves and other species in small gaps (Connell 1978). Past investigations lend some support to this idea. One worker found an increase in shade tolerance characterized a forest, regardless of the presence or absence of gaps (Ehrenfeld 1980). A shift towards more shade tolerant species beneath dead elms gaps was noted by McBride (1973). In contrast, shade tolerant trees were replaced by less shade tolerant trees in an Appalachian *Tsuga canadensis* (L.) Carr. forest (Barden 1979) and in a Wisconsin climax forest (Curtis 1959).

2.4.3 GAP CLOSURE - TREES, *ULMUS*

Several authors (McBride 1973; Huenneke 1983; Dunn 1986) have studied the effect of *Ulmus* mortality on forest canopy and shrub composition. Their studies showed that forests become shrubby (i.e dominated by shrub stratum species such as *Ribes* and *Rubus*) beneath dead elms, possibly preventing tree regeneration. This phenomena occurred when dead *U. americana* were clustered (Huenneke 1983) and when their density exceeded a few stems hectare (Dunn 1986). McBride (1973) also reported

shrubbiness associated with dead *U. americana*, but he did not comment on elm density.

Variations were noted in *U. americana* regeneration after the arrival of Dutch elm disease. Less than 20 years after the introduction of Dutch elm disease, New York forests did not have a significant number of *U. americana* seedlings or saplings in any gaps (Huenneke 1983). Other canopy dominants were replacing them. Conversely, 16 years after the arrival of Dutch elm disease in Iowa, *U. americana* seedlings were an important component of canopy openings and *U. americana* was still an important species in regeneration (McBride 1973).

Twenty-four years after the initial Dutch elm disease infection, *U. americana* still dominated a Michigan forest and *U. americana* seedlings and saplings made up a high percent of the understorey (Richardson and Cares 1976). As long as only partial elimination of elms continues, future forests are predicted to have approximately the same composition. If the elms are completely eliminated in Michigan forests, a red maple/ash community is expected to be established (Richardson and Cares 1976).

In Indianna, 50 years after the introduction of Dutch elm disease, relative density and basal area of *U. americana* had increased from the values in 1926 (Parker and Leopold 1983). It's density-diameter distribution had truncated to smaller size classes, but saplings were still reproducing. However, unless there is a heavy seed crop, the existence of *U. americana* in future stands is questionable.

Dutch elm disease arrived in Wisconsin in the mid 1950's (Dunn 1986). It appears that the remaining *U. americana* will be replaced by other canopy dominants and *U. americana* will persist as short lived

individuals.

These differences in elm survival may be due to differences in elm stem density and/or drainage conditions. Richardson and Cares (1976) noted that mortality was highest in poorly drained lowland pockets with *U. americana* densities greater than 50%. As drainage improved and *U. americana* density declined, mortality decreased (Richardson and Cares 1976).

2.4.4 GAP CLOSURE - HERBS

The herb layer also responds to canopy gaps, usually by new establishment. However, species may also respond with changes in their phenology. Collins et al. (1985) delimitated three broad categories of herb responses to environmental factors - sun herbs, light-flexible herbs and shade herbs. They postulated that since these categories reflect genetic capabilities of the plants, possible responses of each group to a canopy gap could be predicted. As sun herbs mature and senesce before the canopy closes, they were expected to emerge, flower and seed earlier in gaps than under a closed canopy. Light-flexible herbs show a characteristic shift from shade to light photosynthesis spatially or temporally. The authors predicted they would also emerge, flower and seed earlier in gaps than under a closed canopy. Shade herbs mature and senesce beneath a closed canopy. Increased light associated with gaps was expected to be detrimental to shade herbs. They would likely be absent from all but small gaps or grow beneath taller herbs.

Generally, observations by other researchers indicated herbs did not respond to gaps as predicted by Collins et al. (1985). Herb response to gaps in a mature Ohio *Fagus/Acer* forest was studied by Moore and Vankat

(1986). In general, temporally light-flexible and summer herbs increased their cover with gap formation, while spring herbs were either unaffected by gaps or decreased their cover. However, another study on Ohio (Dahlem and Boerner 1987) showed *Geranium maculatum* L., a light-flexible herb, emerged earlier in gaps than under a closed canopy, allowing exploitation of high light levels prior to gap closure. The system is not useful to most researchers because the parameters of the classifications are poorly defined.

In summary, the effect of gaps on vegetation depends on the size of the gap and the severity of the disturbance. Small gaps and gaps formed by mild disturbances close by growth of species already present. Larger gaps and gaps formed by severe disturbances are colonized by invading plants or germination of the seed bank. Different species have different responses to gaps.

2.5 VEGETATION DATA ANALYSIS

2.5.1 ORDINATIONS

The vegetation data collected in field studies are often multivariate - i.e. a variable (eg. cover) is measured for a number of individuals (eg. species) in a number of samples (eg. plots). One method to reveal the structure of such data matrices is to utilize an ordination method. Ordination is an exploratory data analysis technique which attempts to reveal a pattern in data or analyze responses to a gradient (Pielou 1984). This is accomplished by displaying the data points in fewer dimensions than they actually occupy while retaining as much as possible of the information they contain (Pielou 1984). Similar entities are close to each other and dissimilar entities are far apart (Gauch

1982). There are many ordination methods available, including principal component analysis, polar ordination, correspondence analysis and detrended correspondence analysis. Plant ecologists have used these techniques to reveal structure in a variety of data. No one method has been favoured for all types of data analysis. Bray and Curtis (1957) used polar ordination to examine trends in Wisconsin forest communities, while Carleton and Taylor (1982) used detrended correspondence analysis to examine trends in an Ontario urban ravine system. Principal component analysis has been used to study vegetation in relation to soil and topographic gradients (Wikum and Wali 1974) and to determine the response of the herb layer to canopy gaps (Collins and Pickett 1988a).

Numerous studies, such as Kenkel and Orloci (1986), Del Moral (1980), Feoli and Feoli-Chiapella (1980) and Gauch et al. (1977) have been conducted to compare ordination methods. Their findings (and those of other authors) suggested that correspondence analysis was the most appropriate ordination technique for this study.

2.5.2 CORRESPONDENCE ANALYSIS

Correspondence analysis is a more robust technique than principal component analysis (Fashman 1977, Gauch et al. 1977; Pielou 1984) or polar ordination (Gauch et al. 1977) when non-linearity is involved. It is also less susceptible to sample errors, outliers and disjunction (Hill 1973). Although detrended correspondence analysis is said to improve upon correspondence analysis (Hill and Gauch 1980; Pielou 1984), its statistical accuracy has been questioned (Kenkel and Orloci 1986; Wartenberg et al. 1987). Non-metric methods such as non-metric multidimensional scaling do not assume linearity, but they have the disadvantages of being

computationally demanding and may not extract correct configurations (Hill and Gauch 1980).

In correspondence analysis, the sample and species scores are ordinated simultaneously (Pielou 1984). Scores are assigned to each sample and to each species in such a way as to maximize the correlation between sample and species scores. Correspondence analysis can be derived in two ways, by an iterative approach or by eigenanalysis.

In the iterative approach, species are arbitrarily weighted by their positions along a rough initial gradient. These weights are used to calculate the first set of sample scores. The first set of sample scores are then used to calculate the second set of species scores, which in turn are used to calculate the third set of sample scores. These iterations continue until a stable, optimal solution is found. This solution accounts for the most variation in the data and does not depend on the initial species arrangement (Hill 1973). The process is repeated to find solutions that account for the second most variation and so on. At every stage, each sample score is a weighted average of the last derived species score and each species score is a weighted average of the last derived sample score (Pielou 1984). The interdependence of sample scores and species scores is why correspondence analysis is also called "reciprocal averaging".

When correspondence analysis is considered as an eigenvector technique, the algorithm is more complex. The data are not centred or standardized. Each element in the data matrix is divided by the square root of its row total and by the square root of its column total (Pielou 1984). The resulting matrix is subjected to eigenanalysis - a matrix

algebra method to rigidly rotate data to account for linear trends. First, the variances are repartitioned to maximize linear variation on the first axis. Subsequent axes each maximize the remaining variation. Eigenvalues indicate the amount of variance accounted for by each ordination axis. Species and sample scores are ordinated simultaneously, in such a way as to maximize the correlation between the two types of scores.

In summary, correspondence analysis is an ordination method to reduce data to fewer dimensions while retaining as much information as possible. The first axis accounts for the greatest linear variance, which is reported as an eigenvalue. The second axis accounts for the second most variance, etc. When resulting species or sample (plot) scores are plotted on two consecutive axes, similar entities are close together, dissimilar ones are far apart.

3. METHODS & MATERIALS

3.1 SITE DESCRIPTION

Potential study sites were located by examining 1974 and 1987 air photos for forested areas along the Red and Seine rivers and through discussions with members of the provincial government Dutch elm disease programme. With permission of the property owners, site suitability was determined by personal reconnaissance to ensure that it fulfilled the following requirements: 1) it was relatively undisturbed except by elm removal, 2) it was at least 100m wide to reduce the edge effect, 3) it was dominated by an *Ulmus americana*, *Fraxinus pennsylvanica* and *Acer negundo* community and 4) it contained suitable gaps created by the provincial government Dutch elm disease programme or by the death of an elm or elms.

In order to describe the impact of Dutch elm disease on bottomland forests in Manitoba, relatively undisturbed closed forest was compared with gaps, with openings beneath dead elms and with a large clearing. Gaps were also compared with openings beneath dead elms to determine whether there was a difference in their vegetation composition.

Terms were defined as follows:

closed forest: undisturbed bottomland forest where elms were not stricken by Dutch elm disease

gaps: openings created in bottomland forest by the removal of one or more elms

openings beneath dead elms: openings below dead elms in areas where dead elms were not removed. These occur in areas referred to as dead elm forest

clearing: 15ha area in Selkirk Park where the provincial Dutch elm

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disease programme removed the majority of the trees

openings: gaps and openings beneath dead elms

The majority of the study sites were located along the Red River in the Ritchot municipality (49°38'N, 97°07'W) near Winnipeg, although one site was beside the Seine river, near Vermette (49°48'N, 97°04'W) (Table 2). The clearing was along the Red River, in Selkirk (50°08'N, 97°49'W).

The relief is generally flat, but local topography is gently sloping due to river terraces (Michalyna et al. 1975). Elevation above sea level ranges from 225m to 234m (Environment Canada n.d.).

Southern Manitoba has a subhumid, cool continental climate (Environment Canada n.d.). Although the mean annual temperature is 1.9°C, mean seasonal temperatures range from -19°C in January to 19°C in July (Environment Canada n.d.) with a mean of 118 frost free days (Michalyna et al. 1975). The majority of the annual 528cm of precipitation falls as rain between April and September. Mean precipitation in January is 25.6cm and in July is 73.9cm (Environment Canada n.d.).

The bedrock formation underlying the study sites is of the Red River Formation (Ordovician Period) consisting of calcareous dolomitic limestone and dolomite. Unconsolidated glacial outwash covers the bedrock to depths of approximately 18m (Michalyna et al. 1975). Alluvial deposits of silt, clay and some sand fill the valley floor. As the soil is relatively young and subject to periodic flooding, no horizon development has occurred and the surface layers are described as belonging to the cumulic regosol Great Soil group. On a local scale, the soil is classified as a Riverdale silty clay (Michalyna et al. 1975).

Much of the original forest along the Red River was felled in the

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Table 2. Study site information. Distance refers to the number of kilometers cross-country from the site to the mouth of the Red River. Orientation is river bank on which the site is located. Site names are abbreviations of property owner names. Plots in closed forest are in transects ("T") or adjacent to openings ("A").

Site	Type	# Plots	# Openings	Distance (km)	Orientation
Selk	clearing	20	1	25.9	West
F *	gap	1	1	68.0	West
	closed forest	1 A	--		
R	gaps	7	4	72.8	West
	closed forest	7 A	--		
	closed forest	10 T	--		
RE	gaps	17	13	73.7	East
	closed forest	5 A	--		
	closed forest	10 T	--		
S	gaps	6	5	75.6	West
	closed forest	6 A	--		
	closed forest	10 T	--		
Y	closed forest	20 T	--	73.7	West
C	dead elm forest	9	4	83.3	West
G	dead elm forest	12	9	84.2	West
	closed forest	1 A	--		
M	dead elm forest	13	**	74.7	East
	closed forest	1 A	--		
P	dead elm forest	4	4	85.2	East
	closed forest	4 A	--		
V	dead elm forest	5	3	79.5	West

* located on the Seine River
** no boundaries could be delineated

1880's, to provide building material for the settlers and to provide fuel for the steam boats that travelled along the rivers (Macoun 1882). Still more of the wooded land was cleared in the early 1900's for farmland. In many areas, only a narrow band of second growth forest remains along the rivers.

Descriptions of the early forest are similar to those of the present - a tree stratum of *U. americana*, *A. negundo*, *Populus deltoides* and *Quercus macrocarpa* with an understorey of shrubs such as *Ribes* spp., *Prunus virginiana*, *Cornus stolonifera* and *Corylus* spp., vines including *Parthenocissus inserta*, *Vitis riparia* and herbs such as *Echinocystis lobata*, *Fragaria virginiana* and *Amphicarpa bracteata*.

The study sites are subject to periodic flooding as river flows above the bank-full stage can be expected once every ten years (Senjem and Freshwater 1981). The gentle slope of the land, both beside the river (avg. slope of 0.47m/km for 16km on either side) and down the river (0.095m/km, Graham 1984) tends to slow the rate at which the flood water rises and recedes. Major floods, with water levels at least 9m above normal occurred in all sites as recently as 1950, 1974 and 1979 (Senjem and Freshwater 1981) and as far back as 1826, 1852 and 1861 (Anonymous 1958).

In the spring of 1989, the Red River exceeded bankflow stage at some sites and did not subside until early May. Water marks on trees indicated that there was approximately 25cm of standing water, while debris on tree trunks and branches showed the river may have reached the 1m mark.

3.2 VEGETATION SAMPLING

Vegetative sampling began at the end of May, as soon as buds on woody vegetation had opened and the herb layer had emerged through the recently deposited silt. Voucher specimens are in the University of Manitoba herbarium.

The majority of vegetation sampling took place in 5x5m plots. This size was selected so that plots could fit within the smaller gaps. Within these plots, all trees were counted and their diameter at breast height (dbh) measured. Three 2x2m quadrats were placed in a random block design within each plot. The density and cover of all woody vegetation with a dbh ≤5cm and >10cm tall was recorded. In mid-growth season (July and August), these 2x2m quadrats were also used to assess the cover of herbs, woody species less than 10cm tall and bare ground. Cover data were recorded using the Braun-Blanquet scale (Braun-Blanquet 1932), and mid-points (Appendix B) were used in all calculations.

Plots were placed in the centre of gaps created by elm removal and beneath dead standing elms. If the gaps were large enough, more than one plot was used. In the closed forest surrounding each gap, another plot was sampled in the same manner. The large clearing at Selkirk was sampled using 20 plots randomly placed along 2 transects parallel with the river.

In some cases disturbances in the surrounding forest precluded the use of a plot. Therefore in order to secure a larger sample of undisturbed forest, four sites (R, RE, S, Y) were sampled with 10 5x5m plots randomly selected in transects 15m from the channel shelf and parallel with the river. At one site (Y) an additional 10 plots were sampled along a transect 25m from the channel shelf. Preliminary analysis

indicated that the 5x5m plots were too small to give an accurate representation of the tree composition. The point quarter technique (Cottam and Curtis 1956) was therefore used to sample 95 points in the closed forest (in R, RE, F, S) and 64 in the dead elm forest (in C, G, M, V). For all trees sampled, a forked trunk was considered as two or more individuals unless the fork was above breast height.

Thirty-one plots in 23 gaps were sampled in 1989 and resampled in 1990. Forty-three dead elm plots in 20 openings were sampled 1990. In 1989, 50 closed forest plots and 19 plots adjacent to gaps were sampled. In 1990 only 9 could be re-sampled because of disturbance to the forest. Six additional closed forest plots were sampled in 1990. The 1989 closed forest plots (19 adjacent to gaps and 50 in transects) were grouped with the 6 additional 1990 plots for analysis.

Elm shrubs and small trees (5-10cm dbh) were sampled in late July and August, 1990 to test for *Ceratocystis ulmi* fungus infection. A maximum of 10 elms within 1m of a transect across 2 gap sites and 2 dead elm forest sites and the large clearing were collected for a total of 55 samples. Sterilized pruning shears were used to cut at least three 10cm pieces from each elm. The pieces were wrapped in wax paper to prevent desiccation and stored in numbered paper bags. Sapling size, site location and indication of Dutch elm disease symptoms were recorded. The Department of Forestry cultured the elm samples on potato dextrose agar to determine incidence of infection with *C. ulmi*.

Sites where felled elms had been burned were sampled in 1989 by recording the percent cover of each species and the density of shrub species. Thirty-four burn sites were sampled in this manner. The length

and width of the burned area was also noted.

3.3 ABIOTIC SAMPLING

Records were not available regarding the exact age and initial size of the gaps created by elm removal, i.e. when the first elm was removed and the size of the resulting gap. Although a gap may have reached its current size after a number of removal episodes, the vertical projection of the present canopy was considered to represent the actual gap size. For all gaps, the length along the longest axis and breadth at right angles to this were measured from the vertical projection at the time of first sampling. A Gentian digitizing table at the Manitoba Air Photo library was used to determine the forested areas in aerial photos of Selkirk Park taken in 1974 (before elm removal) and 1984 (after elm removal). Changes in the other sites were too small for detection on aerial photos.

In the spring and fall of 1990, the elevation of all plots was surveyed using a transit and stadia rod. Elevations were recorded relative to the river (summer level) or to another plot. Due to the flat topography of the clearing plots, only the elevation of the end and central plots was determined.

In 1989, soil samples at 2 depths, 0-15cm and 15-30cm were taken from all closed forest plots and randomly selected gap plots. Initially, soil was taken from two quadrats per plot. However, preliminary analysis of soils from 40 plots indicated little within plot variation. Thereafter, only one quadrat was sampled in the remaining plots.

Samples were placed in numbered plastic bags and placed in a cold room on return to the laboratory. They were dried at 40°C. When dry, 146

samples (106 from closed forest, 32 gaps and 8 from the dead elm forest) from each depth were made into saturated pastes using the method described in Hesse (1971). Conductivity of the saturated pastes was determined using an Analytical Instrument Science Conductance/TDS meter, pH was determined using a Canlab pH meter (model 607).

Particle size analysis was conducted on 12 randomly selected soil samples (5 closed forest plots, 4 from gap plots, 3 from clearing) from each depth. A modified version of the sedimentation method based on Stoke's law (McKeague 1978) was used. Percent sand, silt and clay were calculated. Organic matter was removed using the peroxide method. The pipette method and calculations are outlined in Appendix C.

During August, 1990, temperature and light readings were taken in 7 gaps and openings beneath dead elms and in 8 points in the closed forest. Readings were taken between 1130hrs and 1300hrs on sunny days using mercury centigrade thermometers and a Licor model Quantum/Radiometer/ Photometer. Several readings were taken from each plot; in the closed forest - in sunspots and the shade and in disturbed areas - above understorey vegetation and at ground level.

3.4 ANALYSES

3.4.1 VEGETATION DATA

All plot vegetation data were entered in a spreadsheet (using the P.C. programme Quattro). To allow comparison of species' importance in the four areas (closed forest, gaps, openings beneath dead elms and the clearing), a number of calculations were undertaken. Mean herb and shrub cover was calculated for each species, but these values had high variances. Relative cover values were calculated instead.

Relative cover is the cover of a particular herb or shrub species as a percentage of total herb or shrub cover.

In addition, the mean of 1989 and 1990 shrub stem densities were used for analysis. Shrub stem density per hectare and relative density for the three height classes in each area were determined.

Relative density is the number of stems of a particular shrub species as a percentage of the total number of shrub stems.

For trees, plot and point quarter values were used to calculate the relative dominance of cover, frequency and density for each tree species in the closed forest and the dead elm forest. Tree values obtained by plot and point quarter calculations were combined.

Relative dominance is the basal area of a particular tree species as a percentage of the total basal area of all trees.

Relative frequency is the number of plots or points with a particular tree species as a percentage of the number of plots or points with all tree species.

Relative density is the number of individuals of a particular tree species as a percentage of the total number of individuals of all tree species.

Total tree density per hectare for the two areas was also determined.

The correspondence analysis option in the P.C. programme CANOCO was used to analyze understorey species cover values. Four pairs of areas, i.e. closed forest and gaps, closed forest and openings beneath dead elms, closed forest and the clearing, and gaps and openings beneath dead elms were ordinated. The purpose was to determine whether there was more variation within or between areas. Closed forest understorey data were

analyzed to expose any within forest variation. From each ordination, plot and species scores of the first and second axes were plotted in scattergrams to aid in interpretation. Gap size, dead elm opening size and plot elevation data were overlaid on the scattergrams to determine whether there was any correlation between plot distributions and these variables. Authors such as Bell (1980), Ehrenfeld (1980) and Collins et al. (1985) have noted that these factors influence species composition.

Two steps were taken to condense the data before ordination. Rare species were removed and only bare ground and 82 understorey species with total cover values greater than 5% were included (see Appendix A). To obtain a species cover for each herb and shrub species in each plot, the mean cover value of the three quadrats in each plot was calculated. These means were used in the ordinations.

For the clearing and gap plots, 1989 and 1990 correspondence analysis scattergrams were very similar therefore only the 1990 data are presented.

3.4.2 SOIL AND ENVIRONMENTAL DATA

The means for soil particle analysis, pH and conductivity results were calculated to obtain average values for each depth. The mainframe SAS package was used to conduct t-tests on the temperature and light data.
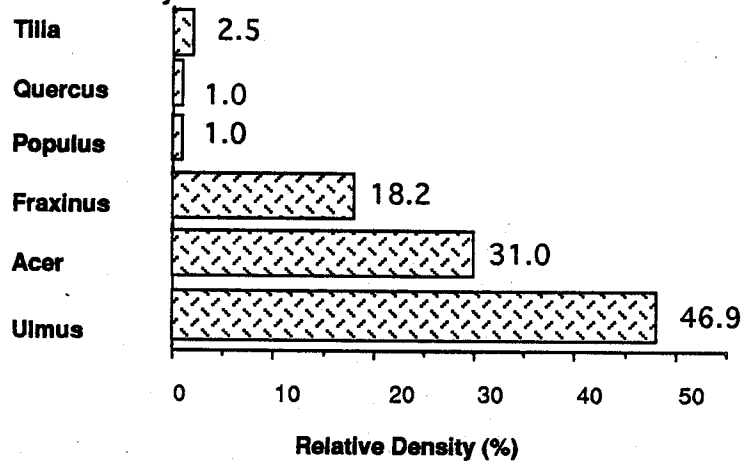
4. RESULTS

4.1 TREES

4.1.1 CLOSED FOREST TREES

Based on relative density, dominance and frequency, the closed forest was composed of, in order of importance, *Ulmus americana*, *Acer negundo* and *Fraxinus pennsylvanica*, with small numbers of *Populus deltoides*, *Quercus macrocarpa* and *Tilia americana* (Figure 3a, b, c). On the basis of 165 5x5m plots and 95 points, the mean tree density was 905 ± 297/ha. *Ulmus americana* had the highest relative density (47%) with 418 trees/ha and a total basal area of 940m^2/ha. Individuals elms ranged in size from 5cm diameter at breast height (dbh) to 95cm dbh, with a mean size of 16 ± 13cm.

Acer negundo and *F. pennsylvanica* were lower in all parameters (Figure 3a, b, c) in the closed forest. *Acer negundo* had a relative density of 31%, representing 272 trees/ha and a relative frequency of 31%. The relative density of *F. pennsylvanica* was 18% and its relative frequency was 22%. *Fraxinus pennsylvanica* had a mean dbh of 24 ± 13cm and *A. negundo* had a mean dbh of 22 ± 11cm. *Acer negundo* contributed 26% of the tree stratum basal area and *F. pennsylvanica* contributed 17%.

Quercus macrocarpa and *P. deltoides* were minor components in the closed forest. A representative hectare of forest would contain four *Q. macrocarpa*. Despite the few individuals (22/ha), the large size of *P. deltoides* (mean dbh 31 ± 29cm) caused it to have a relative dominance of 13%. *Tilia americana* was found only in one site, where the 15 individuals ranged in size from 6cm dbh to 53cm dbh.

(a) Relative density

Tilia 2.5
Quercus 1.0
Populus 1.0
Fraxinus 18.2
Acer 31.0
Ulmus 46.9

0 10 20 30 40 50

Relative Density (%)

(b) Relative dominance

Tilia 2.3
Quercus 1.4
Populus 13.1
Fraxinus 17.1
Acer 26.5
Ulmus 39.5

0 10 20 30 40

Relative Dominace (%)

(c) Relative frequency

Tilia 3.0
Quercus 2.0
Populus 2.0
Fraxinus 21.5
Acer 30.8
Ulmus 40.7

0 10 20 30 40
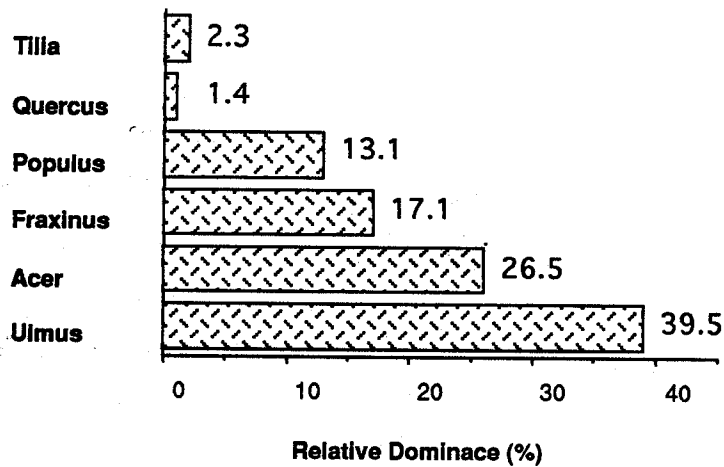
Relative Frequency (%)

Figure 3. Closed forest tree stratum.   n=260 (165 5x5m plots and 95 points)

4.1.2 DEAD ELM FOREST TREES

The dead elm forest had a tree species composition similar to the closed forest, but forty percent of the forest's elms were dead. Of its 1253 trees/ha (n=84 points), 327/ha wer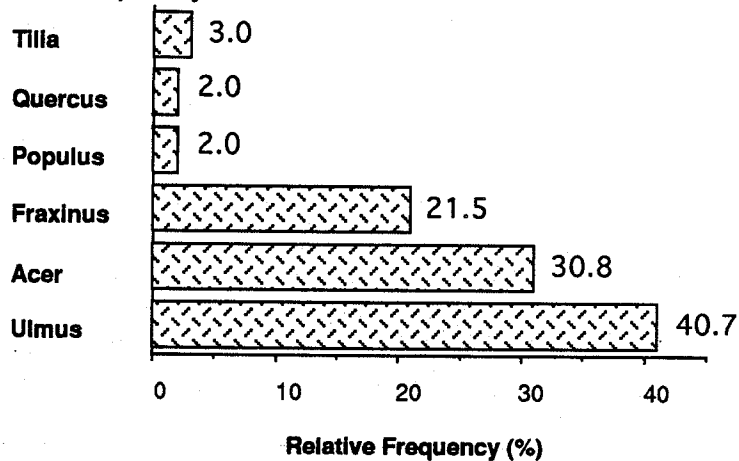e dead *U. americana*. *Ulmus americana*, *A. negundo*, *F. pennsylvanica*, *T. americana* and *Q. macrocarpa* were present, but *P. deltoides* was not. One *Viburnum lentago* and *Prunus virginiana* also reached tree size (dbh >5cm) in this forest.

4.1.3 CLEARING TREES

According to forest inventory records, before elm removal, over half the trees in Selkirk Park were *U. americana*, 33% were *F. pennsylvanica* and 10% were *A. negundo* (Dept. Forestry 1977). After elm removal, two *A. negundo* (37cm and 22cm dbh), two *F. pennsylvanica* (8cm and 6cm dbh) and one *U. americana* (10cm dbh) were recorded in a 400m^2 sample of the clearing.

4.2 SHRUB STRATUM

Seventeen species were observed in the shrub layer, the most common being the saplings of *U. americana*, *A. negundo* and *F. pennsylvanica* which made up 70% of the shrub stratum in both undisturbed and disturbed areas. Most shrubs in all plots were less than a meter tall (Figure 4). The closed forest had the highest density of such individuals (38078 stems/ha) but the dead elm forest had the greatest number of shrubs in the taller than 2m class (2771 stems/ha). The clearing had 2562 stems/ha, a mere 6% of the total number recorded in the closed forest. *Fraxinus pennsylvanica* had the highest relative density in all areas except the clearing (Figure 5). *Acer negundo* was most abundant in the clearing, but its density was considerably lower (1667stems/ha) than shrubs in other areas. The
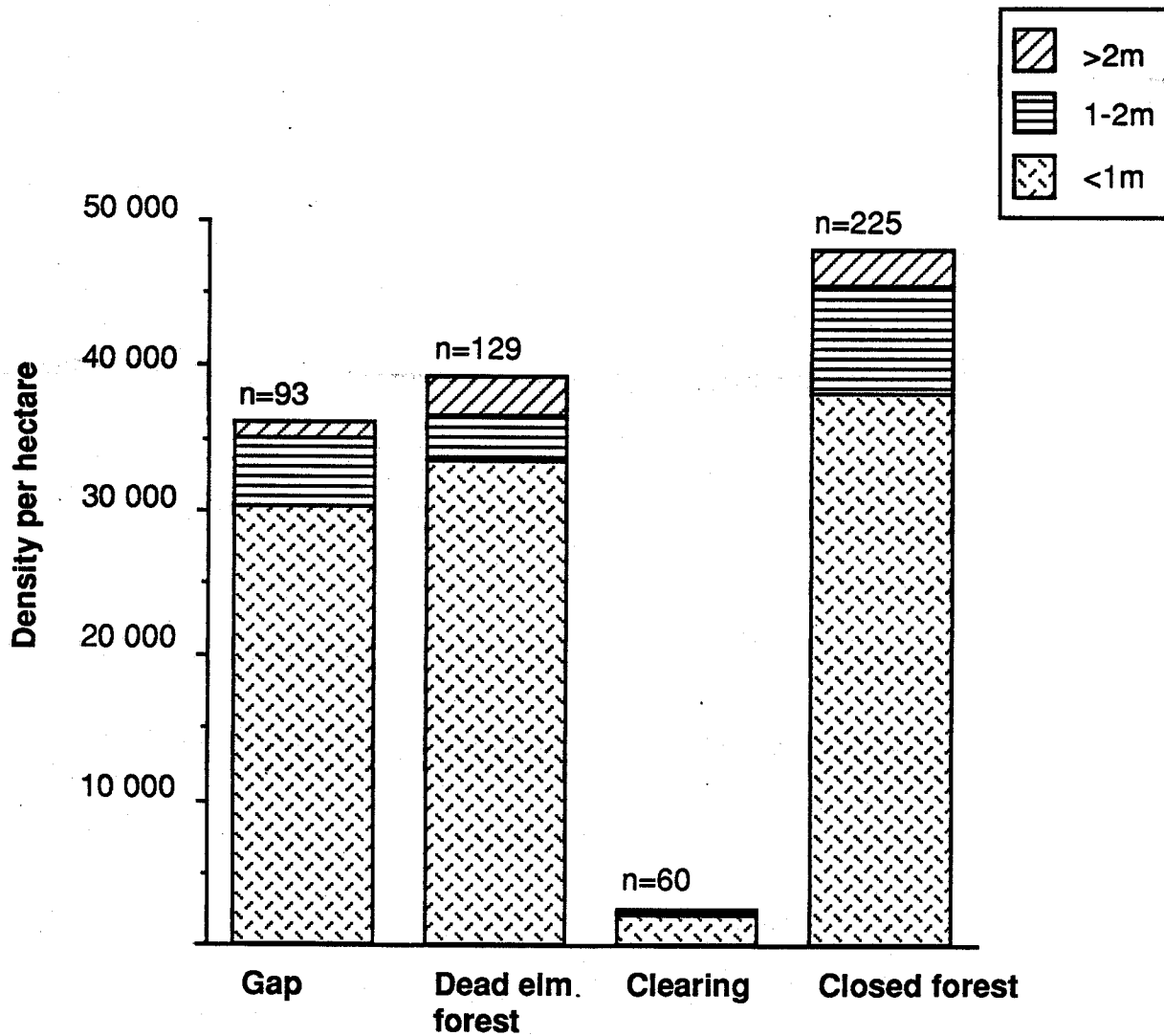
Figure 4. Shrub stratum density per hectare for each area. Data are given for three height classes. n=number of 2x2m quadrats sampled.

(a) Gap saplings

Relative density (%)

n=93

Fraxinus pennsylvanica — Ulmus americana — Acer negundo
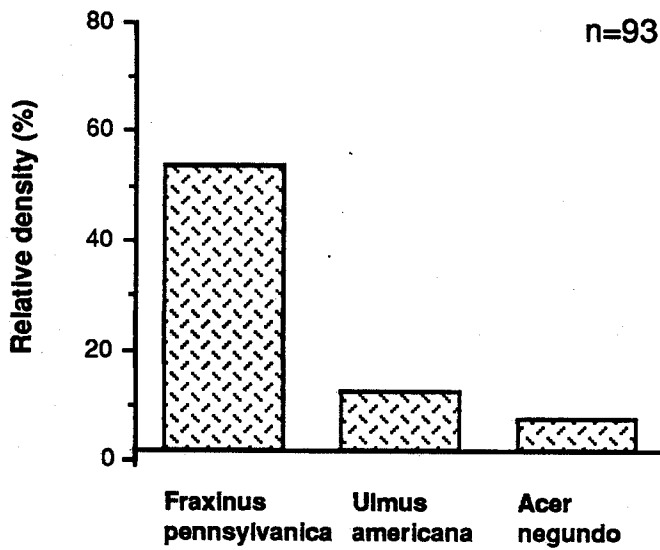
(b) Dead elm forest saplings

n=129

Fraxinus pennsylvanica — Ulmus americana — Acer negundo

(c) Clearing saplings

Relative density (%)

n=60

Fraxinus pennsylvanica — Ulmus americana — Acer negundo

(d) Closed forest saplings

n=225

Fraxinus pennsylvanica — Ulmus americana — Acer negundo
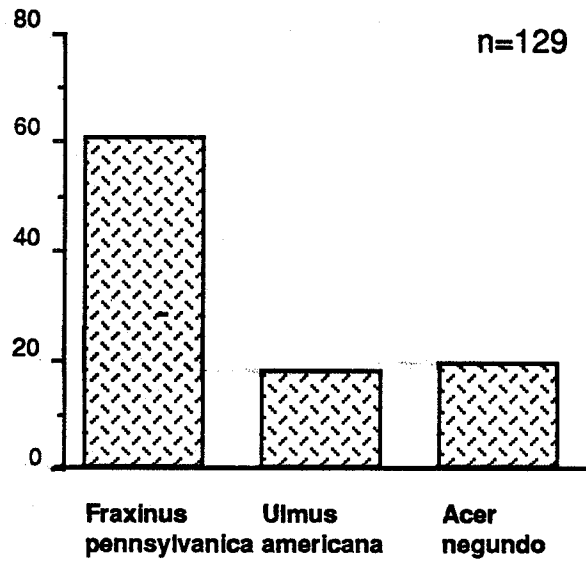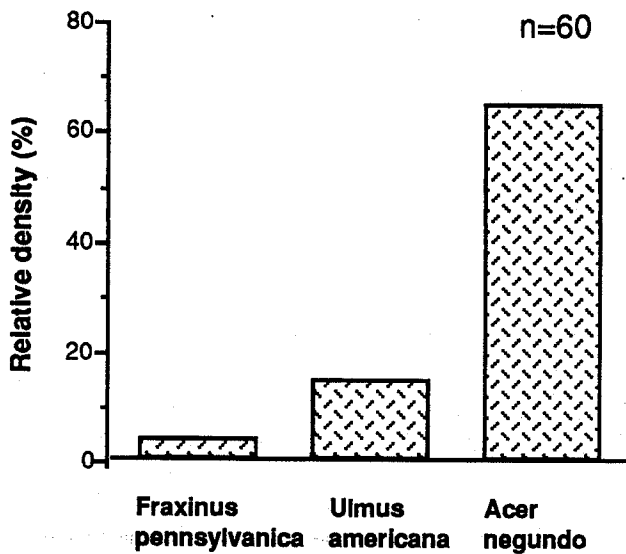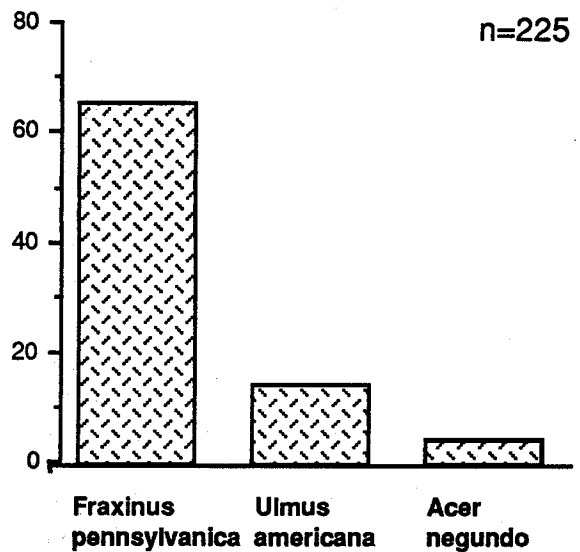
Figure 5. Relative density of saplings in shrub stratum.
n=number of 2x2m quadrats sampled.

relative density of *U. americana* was the highest in the dead elm forest (18%) and varied slightly among the closed forest, gaps and clearing.

Other shrubs recorded were *Cornus stolonifera, Ribes hudsonianum, Prunus virginiana* and *Viburnum lentago* (Table 3). *Symphoricarpos occidentalis* was found only in the dead elm forest, while *Amelanchier alnifolia, Crataegus chrysocarpa* and *Corylus cornuta* were found only in the closed forest. Saplings of *Q. macrocarpa* and *T. americana* were recorded in a few plots in the closed forest and openings but no *P. deltoides* was observed in any areas.

Of the 55 small elm trees and saplings tested for *Ceratocystis ulmi* infection, only two were positive. One was a small tree (5-10cm dbh), in the dead elm forest, and one was a sapling taller than 2m, in gaps. Both showed symptoms typical of Dutch elm disease - yellow and flagging leaves. No other individuals showed any disease symptoms.

4.3 HERB STRATUM

The number of herb species present in disturbed and undisturbed areas was similar. There were 47 in the closed forest, 53 in the gaps, 47 in the dead elm forest and 50 in the clearing (Appendix A). Each type of area had some unique species (Table 4), but they contributed little cover (<1% relative cover each).

Of the six species found only in the gaps, all are found in thickets and woods, except *Amaranthus retroflexus*, which is common in waste places (Scoggan 1957). *Symphoricarpos occidentalis* was the only herb stratum species unique to the dead elm forest.

Almost 20% of the species found in the clearing occurred nowhere else. These nine species are primarily weeds, common in road-sides and

Table 3. Species present in the shrub stratum of disturbed and undisturbed areas. "X" indicates presence. n=number of 2x2m quadrats sampled.

Species	Gaps n=93	Dead elm forest n=129	Clearing n=60	Closed forest n=225
Acer negundo	X	X	X	X
Cornus stolonifera	X	X	X	X
Corylus americana	X	X	X	X
Fraxinus pennsylvanica	X	X	X	X
Prunus virginiana	X	X	X	X
Viburnum lentago	X	X	X	X
Ulmus americana	X	X	X	X
Lonicera dioica	X	X		X
Quercus macrocarpa	X	X		X
Ribes americanum	X	X		X
Rosa woodsii	X	X		X
Tilia americana	X	X		X
Amelanchier alnifolia	X			X
Corylus cornuta	X			X
Rubus idaeus	X			X
Crataegus chrysocarpa				X
Symphoricarpos occidentalis		X		

Table 4. Herb stratum species unique to disturbed and undisturbed areas.
        n=number of 2x2m quadrats sampled.

Gaps n=93	Dead elm forest n=129	Clearing n=60	Closed forest n=225

Amaranthus
  retroflexus
Botrychium
  virginianum
Fragaria
  virginiana
Rosa woodsii
Trillium cernuum
Viola pubescens
	Symphoricarpos
	  occidentalis
		Arenaria
		  lateriflora
		Lepidium
		  densiflorum
		Pastinaca
		  sativa
		Poa pratensis
		Potentilla
		  anserina
		Ribes hudsonian
		Thlaspi arvense
		Trifolium hybridum
		Vicia cracca
			Hesperis
			  matronalis
			Lonicera
			  dioica
			Quercus
			  macrocarpa
			Sterionema
			  ciliatum

Table 5. Herb stratum species common to disturbed and undisturbed areas
        and their relative cover values (%). Trace values are <0.5%.
        n=number of 2x2m quadrats sampled.

Species	Gaps n=93	Dead elm forest n=129	Clearing n=60	Closed forest n=225
Acer negundo	1.3	0.1	3.9	2.2
Amphicarpa bracteata	15.7	1.2	0.3	7.9
Arctium lappa	1.7	5.2	18.7	0.6
Aster simplex	0.4	2.0	1.0	1.0
Cirsium arvense	1.7	0.5	11.2	1.0
Echinocystis lobata	0.1	0.6	trace	0.6
Elymus canadensis	5.3	1.9	0.2	3.0
Fraxinus pennsylvanica	2.9	1.1	trace	1.3
Galium triflorum	1.4	0.8	0.1	0.5
Laportea canadensis	9.7	18.4	5.8	23.5
Phalaris arundinacea	0.1	0.9	1.3	0.2
Smilacina stellata	5.5	2.2	2.5	3.7
Solidago spp.	1.7	0.1	1.6	0.2
Sonchus arvensis	2.0	0.1	5.9	0.4
Stachys palustris	4.8	3.3	2.6	0.9
Thalictrum venulosum	5.2	3.7	0.4	4.9
Ulmus americana	4.7	4.2	0.4	4.2

waste places and/or escaped cultivars (Scoggan 1957). Four species were found only in the closed forest. One of them, *Hesperis matronalis* is an ornamental (Scoggan 1957) which probably escaped from a nearby garden. The others are considered common in woods and thickets (Scoggan 1957).

The herb layer taxa which were found in both disturbed and undisturbed areas (Table 5) are well documented as floodplain species, adapted to occasional scouring and flooding (Keammerer et al. 1975; Menges 1990). *Acer negundo*, *Aster simplex*, *Echinocystus lobata*, *Galium triflorum*, *Phalaris arundacia* and *Solidago* spp. had low relative cover in all areas. *Laportea canadensis* was the only species with a relative cover value greater than 5% in all areas (Table 5, Figure 6). *Menispermum canadense* contributed more than 5% to the cover in the closed forest, gaps and dead elm forest (Figure 6). *Amphicarpa bracteata* had a relative cover of 16% in gaps and 8% in the closed forest. *Thalictrum venulosum* had relative cover of 5% in gaps and the closed forest. *Arctium lappa* had a relative cover of 19% in the clearing and 5% in the dead elm forest. *Matteuccia struthiopteris* was an important component of the clearing (relative cover of 15%). The relative cover values of the remaining common plants varied between disturbed and undisturbed areas, but the difference was greatest in the clearing. For example, *Thalictrum venulosum* had 5% cover in the closed forest and gaps, but less than 1% in the clearing (Appendix A). Conversely, *A. lappa* and *Cirsium arvense* had low relative cover values in the closed forest and gaps (<6% and <2% respectively) but had covers of 19% and 11% respectively in the clearing. Bare ground was present in all areas. It contributed 9% to the cover in the gaps, 22% in the dead elm forest, 2% in the clearing and 21% in the

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(a) Gap herbs

n=93

(b) Dead elm forest herbs

n=129

(c) Clearing herbs
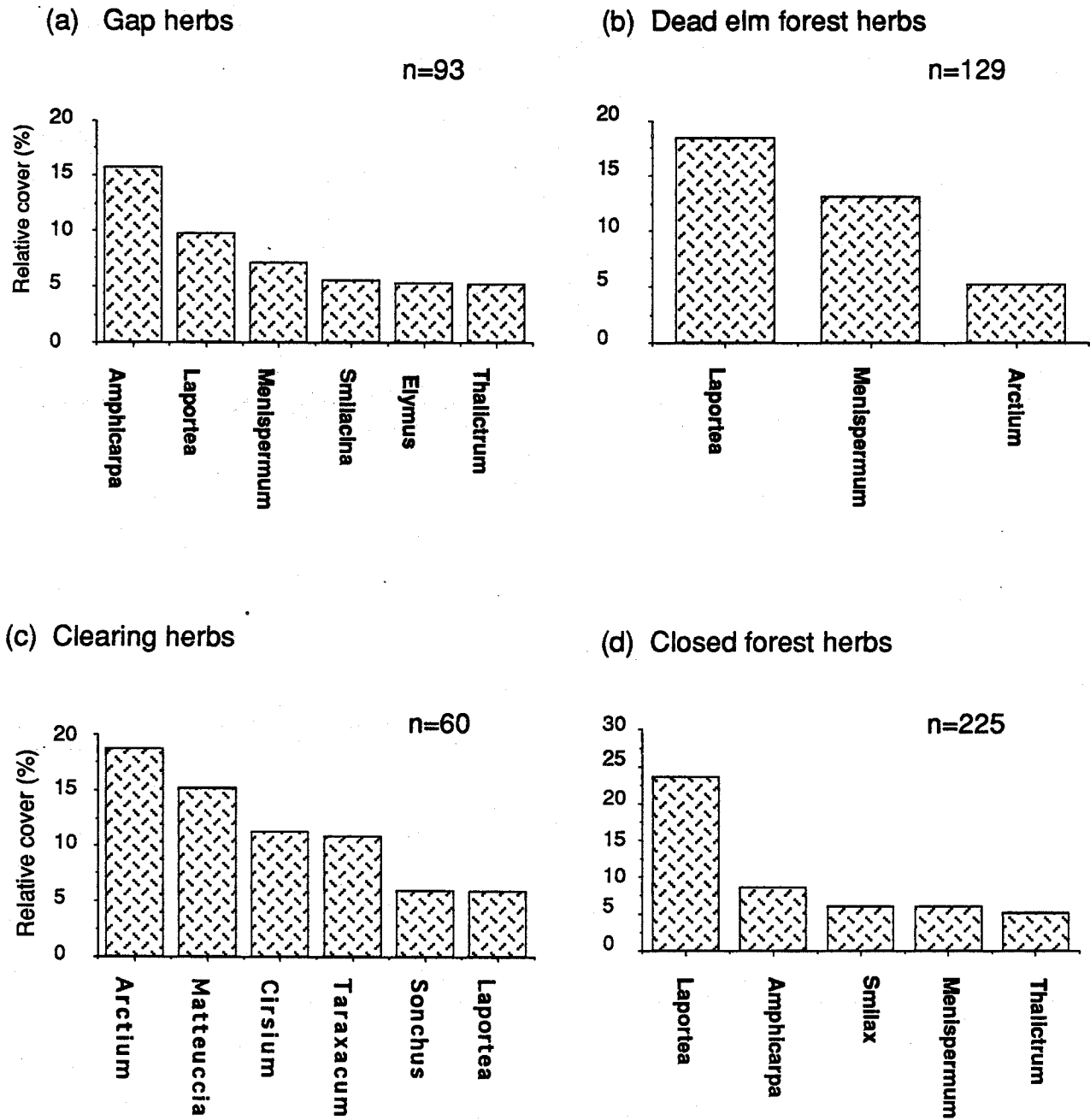
n=60

(d) Closed forest herbs

n=225

Figure 6. Herb stratum species with relative cover values greater than 5%.
See Appendix A for full names of species. n=number of 2x2m quadrats.

closed forest.

4.4 GAP ELEVATION AND SIZE

The sites were between 0.6m and 8.0m above the river (at mid-summer level) and had an average elevation of 3.8 ± 1.8m (Figure 7). The clearing had the lowest mean elevation of 1.7 ± 0.9m and the dead elm forest had the highest mean elevation, 5 ± 1.87m.

The majority of gaps and dead elm forest openings were less than 100m^2. Gaps ranged in size from 25m^2 to 731m^2 (Figure 8a) while openings in the dead elm forest ranged from 25m^2 to 307m^2 (Figure 8b). The elm death in one site (M) was so extensive that no gap boundaries could be delineated. Therefore, gap sizes were not measured in this site.

In 1972, the Selkirk site had 26.9 ha of trees. After elm removal, only 11.1 ha remained, primarily along the river. That is a 41% reduction in tree cover. The area became a 15.8ha clearing.

4.5 CORRESPONDENCE ANALYSIS

Correspondence analysis clearly separated the closed forest plots from the clearing plots (Figure 9a). The clearing plots were tightly clustered along axis I between 20 and 40. The closed forest plots were primarily clustered between 10 and 20 on axis I, but were more vertically dispersed along the positive side of axis I. Figure 9b showed that the species scores group in the same manner as the plot scores. Most shrub species were found on the negative side of axis I (closed forest plots).

A slight clumping by property owner was evident in the correspondence analysis scattergrams of plot scores of the closed forest (Figure 10a), clearly indicating intersite differences. The "S" plots were primarily on the upper left side of the scattergram, the "R'" plots
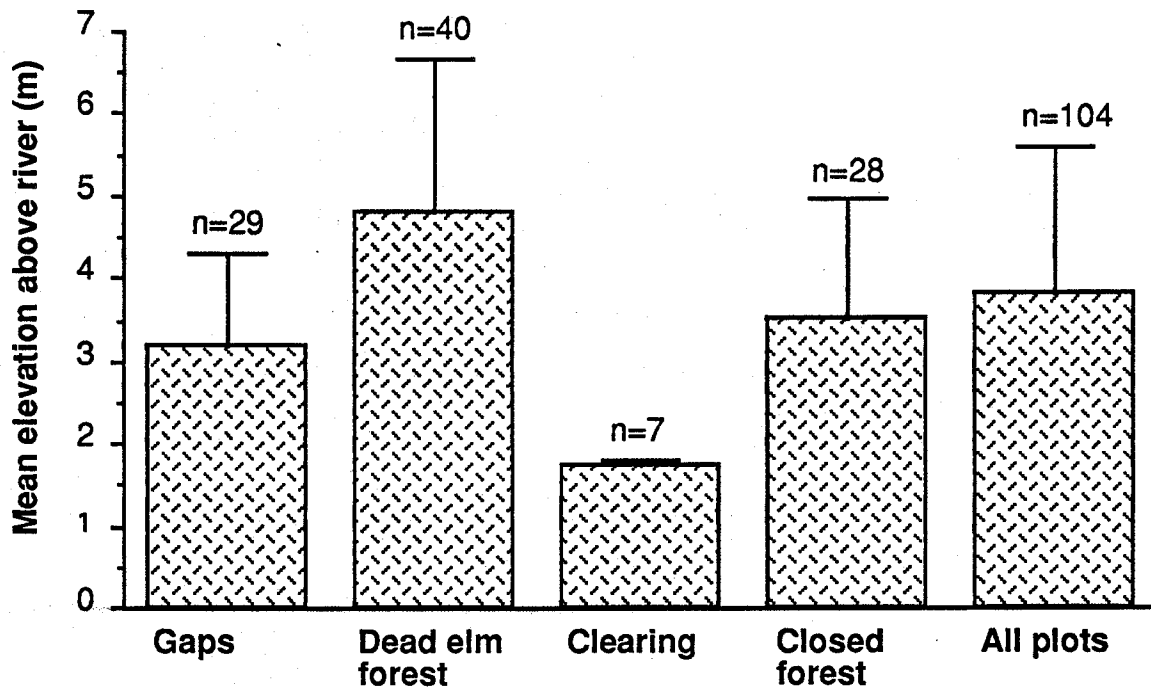
Figure 7. Mean plot elevations above river for disturbed and undisturbed areas
and all plots combined. Bars are standard deviations.
n=number of 5x5m plots sampled.

(a) Plot scores

o Closed Forest n = 75
□ Clearing n = 20
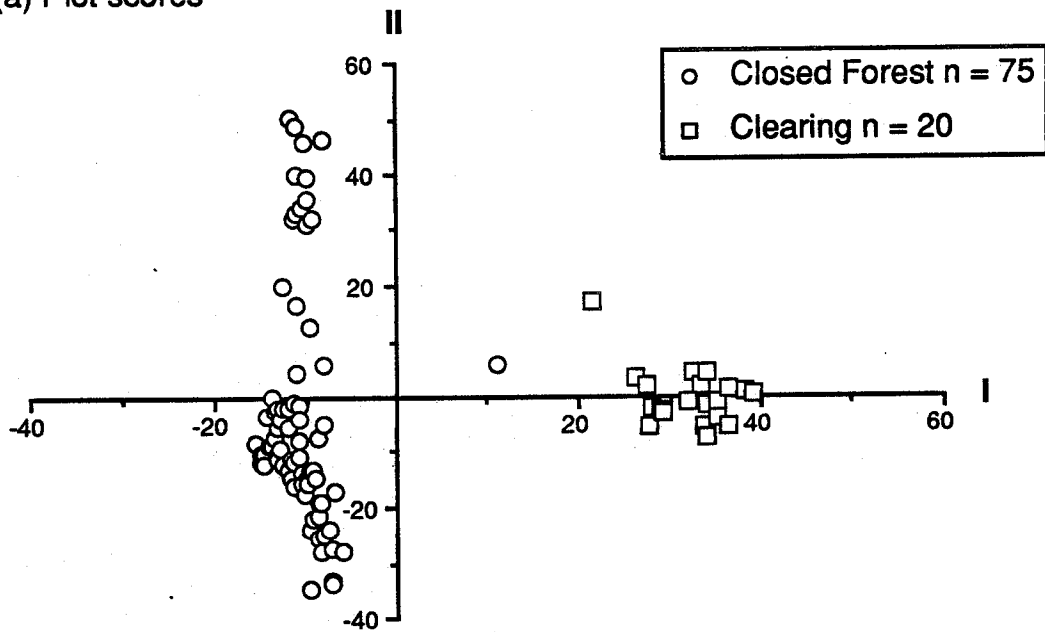
(b) Species scores

o Herbs
□ Shrubs
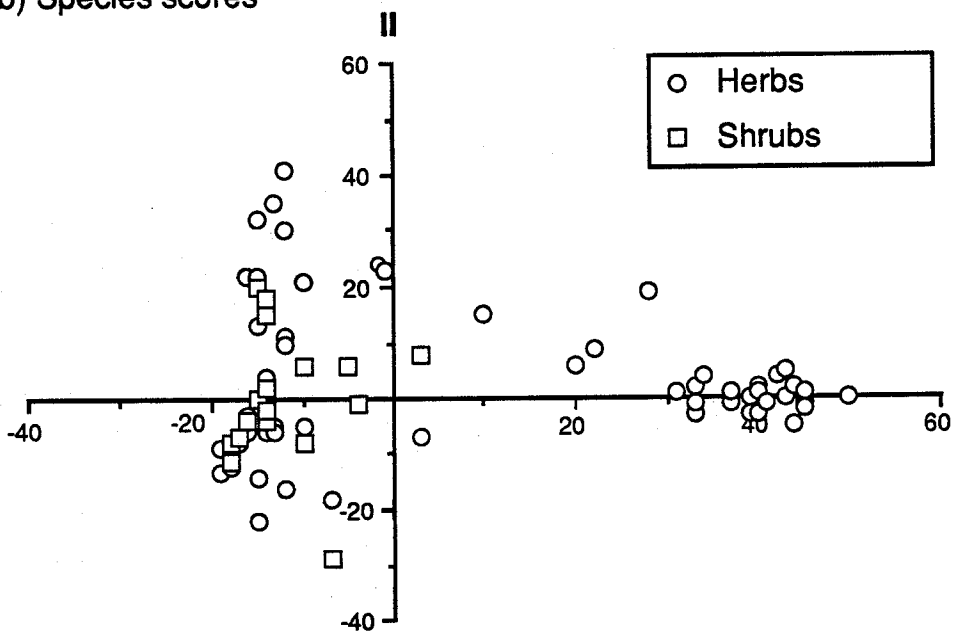
Figure 9. Correspondence analysis scattergram of the first and second
axes of closed forest and clearing data.
Eigenvalues: I = 0.78, II = 0.46.

(a) Plot scores
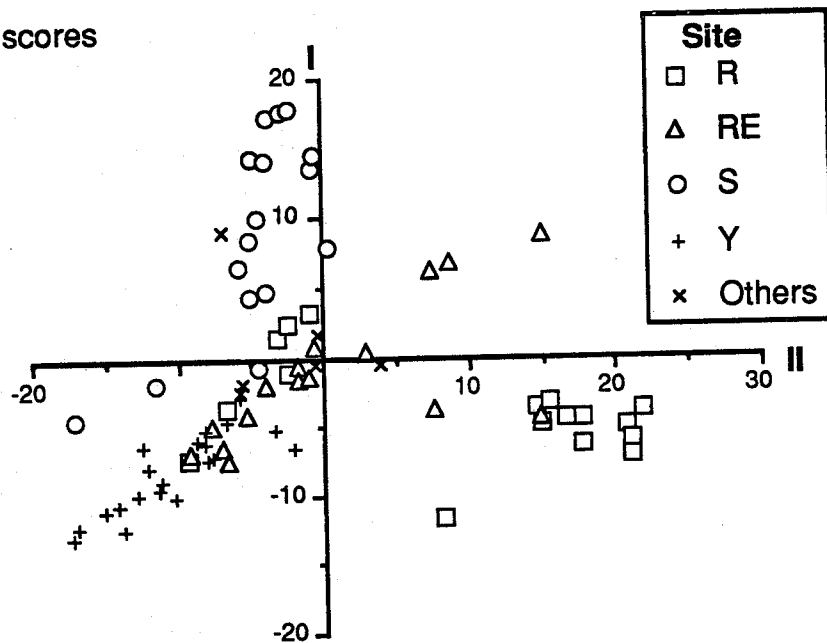
(b) Species scores

Figure 10. Correspondence analysis scattergram of the first second axes of closed forest data. Sites are property owners, see Table 2. Others are sites with <10 plots. n=75 closed forest plots. Eigenvalues: I = 0.47, II = 0.35.

were in the lower right and the "Y" plots were in the lower left. "RE" plots were central but dispersed. There was little separation in the closed forest species scores (Figure 10b). Only one shrub, *C. cornuta* was found in the extreme lower left ("Y" plots). Few species occurred in "Y" plots.

Gap plots and closed forest plots did not form separate groups when analyzed with correspondence analysis (Figure 11a). Instead, the gaps grouped with adjacent closed forest plots. Most "S" gap and closed forest plots grouped on the middle right side of the scattergram, while "RE" plots were concentrated in the middle left area scattergram's lower side. A diffuse group of "R" gap and closed forest plots occurred across the lower half of the scattergram. The scattergram of the gap and closed forest species scores (Figure 11b) showed no separation. Shrubs appear slightly concentrated along axis I. Species did not trend together.

There was considerable overlap in the distribution of closed and dead elm forest plots (Figure 12a). The species scores revealed little separation or pattern (Figure 12b).

The correspondence analysis scattergram of gap and dead elm forest plot scores revealed some separation in the two types of disturbance (Figure 13a). A group of dead elm forest plots formed in the upper half of the scattergram, a group of gap plots formed in the lower left. Plots from both types of disturbance intermix at the lower right. The species scattergram is rather diffuse (Figure 13b).

4.6 BURN AREAS

The areas where removed elms were burned ranged in size from $0.5m^2$ to $32.4m^2$, with the majority being between $5m^2$ and $10m^2$ (Figure 14) The

(a) Plot scores

Site
- □ R, Closed
- ■ R, Gaps
- △ RE, Closed
- ▲ RE, Gaps
- ○ S, Closed
- ● S , Gaps
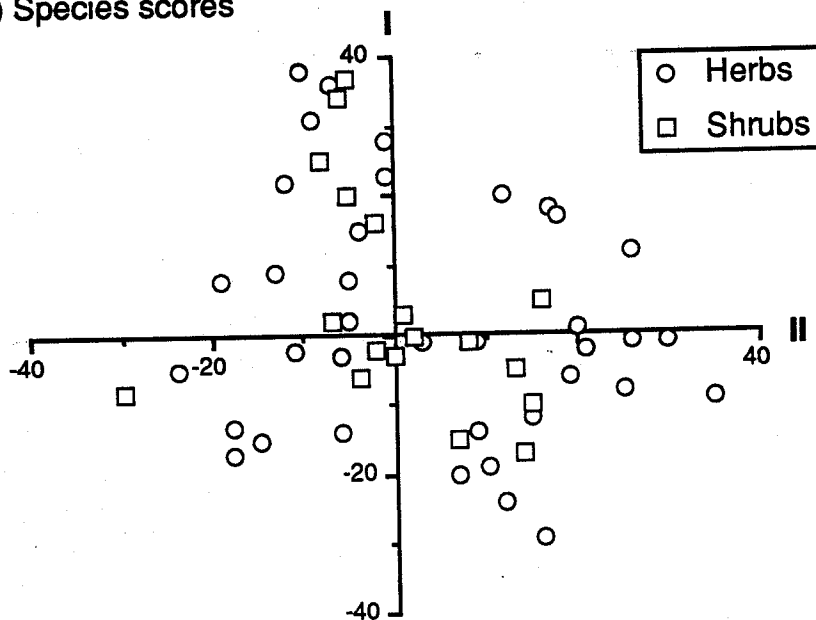- + Others, Closed
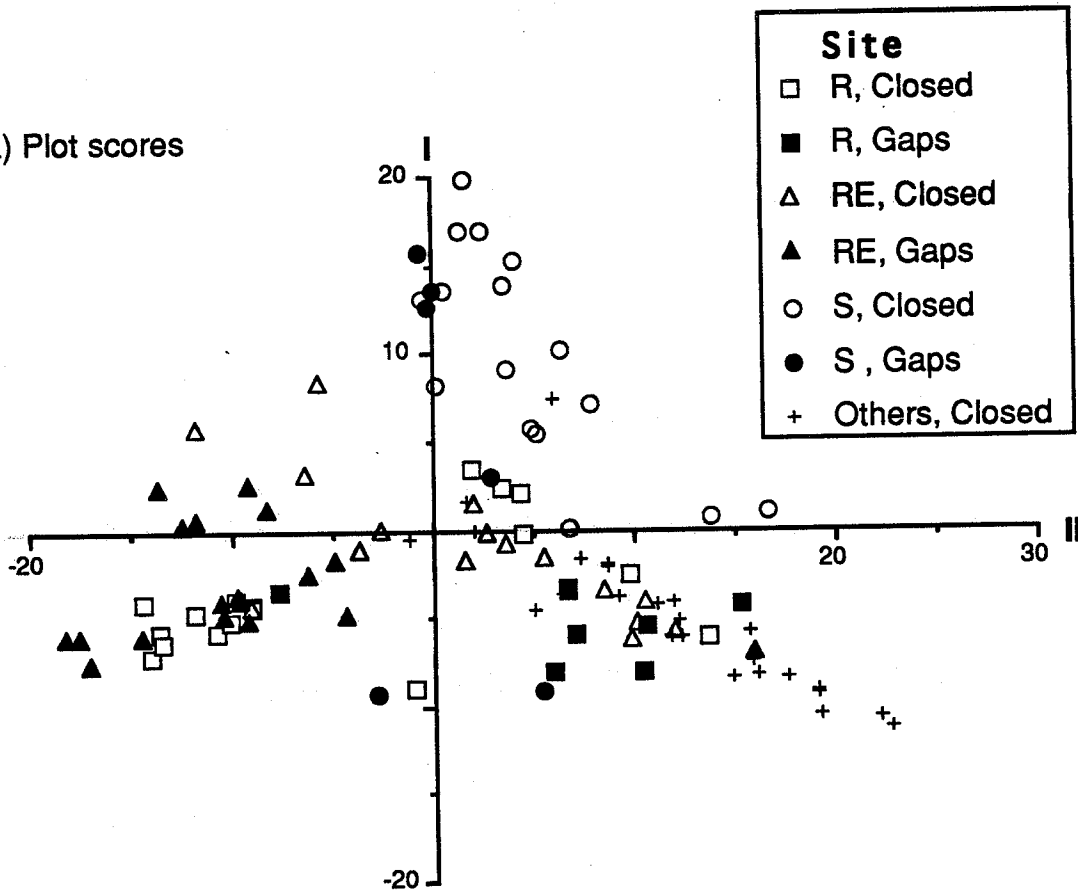
(b) Species scores

- ○ Herbs
- □ Shrubs
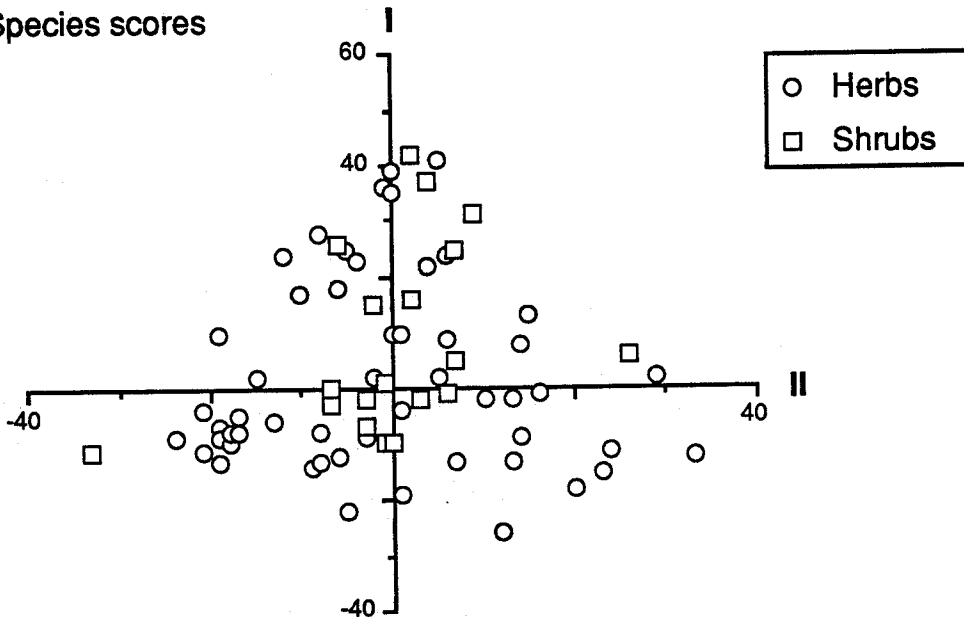
Figure 11. Correspondence analysis scattergram of the first second axes of closed forest and gap data. Sites are property owners, see Table 2. Open symbols are closed forest sites, others are closed forest sites with <10 plots. n=75 closed forest plots and 31 gap plot plots. Eigenvalues: I = 0.47, II = 0.35.
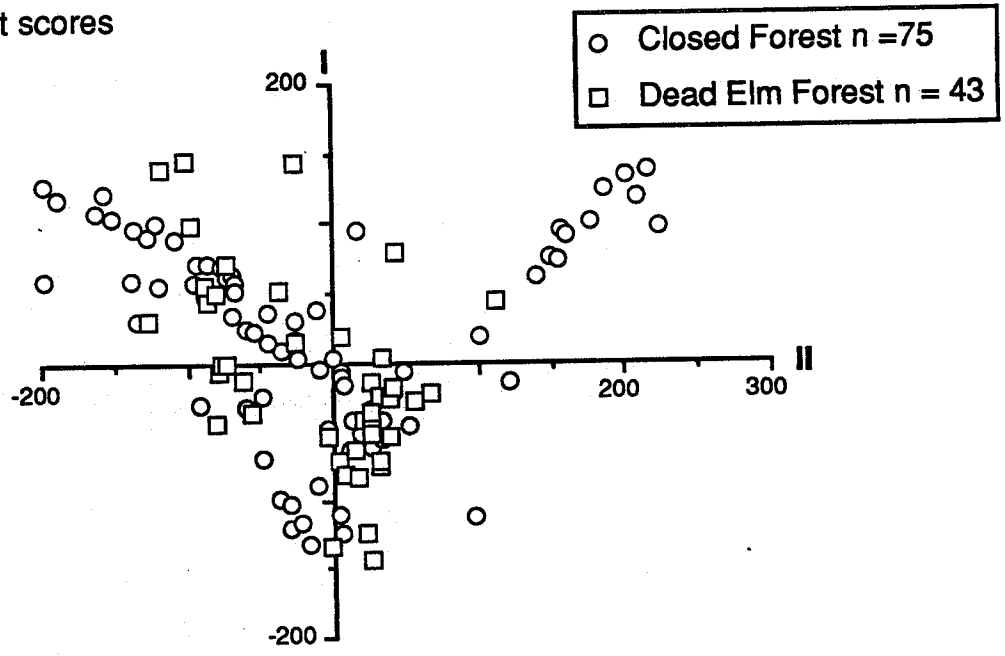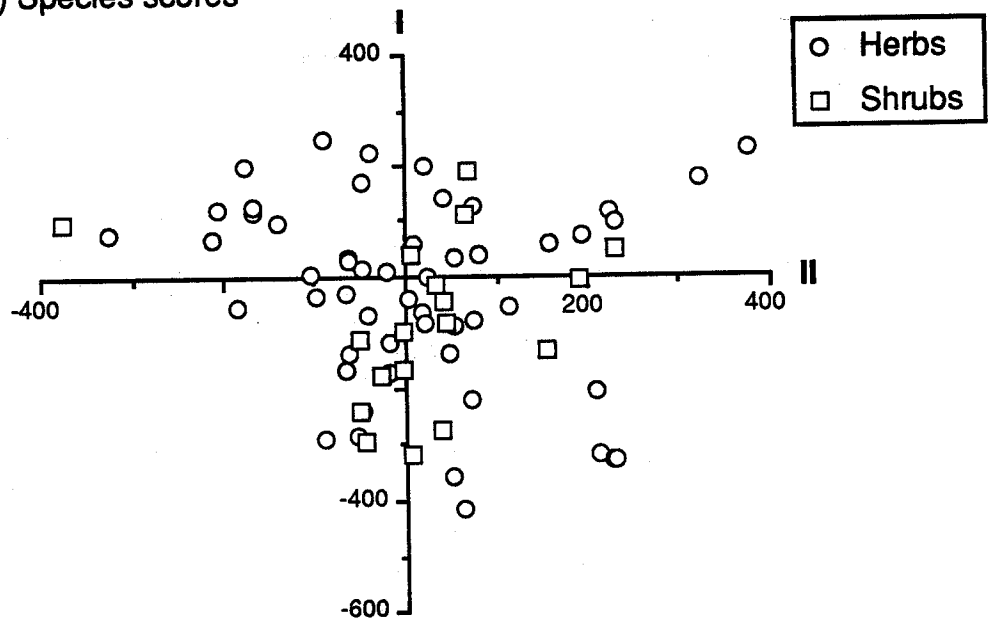
Figure 12. Correspondence analysis scattergram of the first and
second axes of closed forest and dead elm forest data.
Eigenvalues: I = 0.42, II = 0.35.

(a) Plot scores
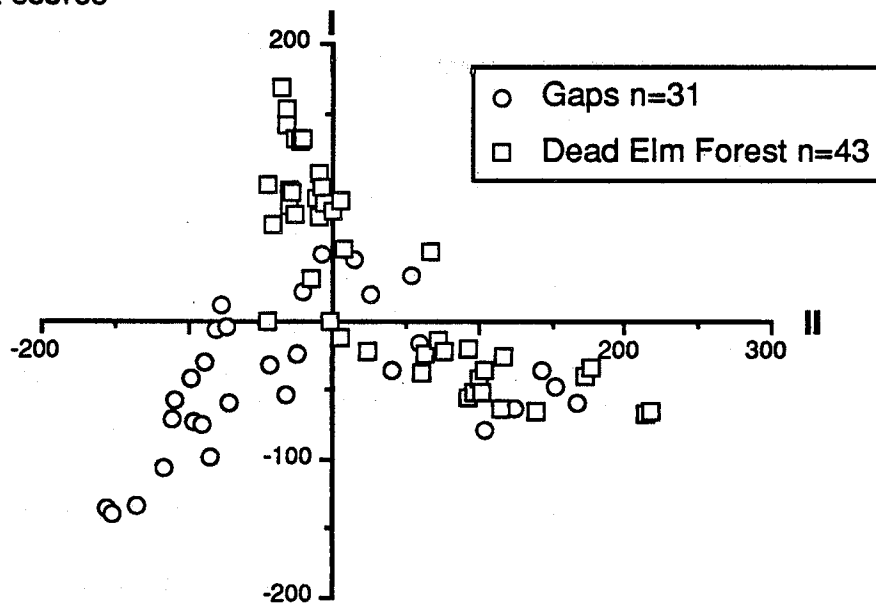
(b) Species scores
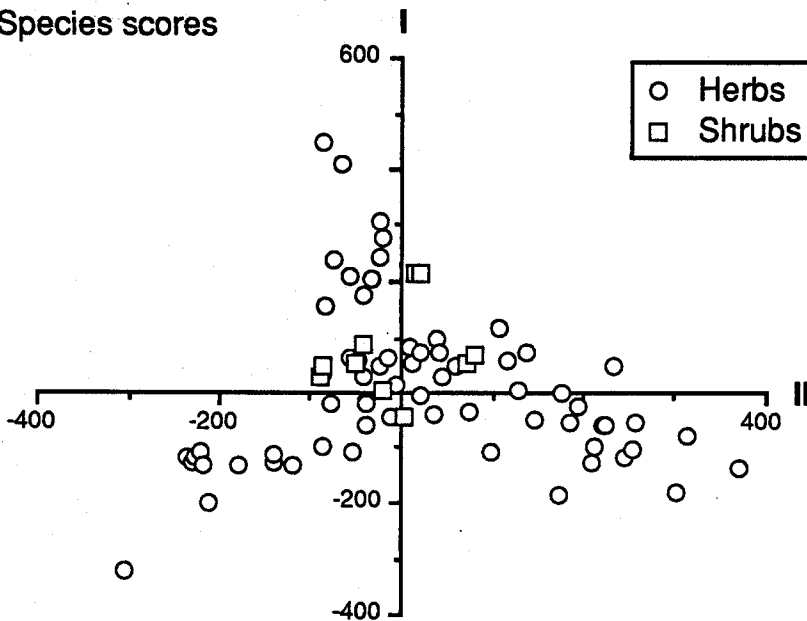
Figure 13. Correspondence analysis scattergram of the first
and second axes of gap and dead elm forest data.
Eigenvalues: I = 0.42, II = 0.35.

61
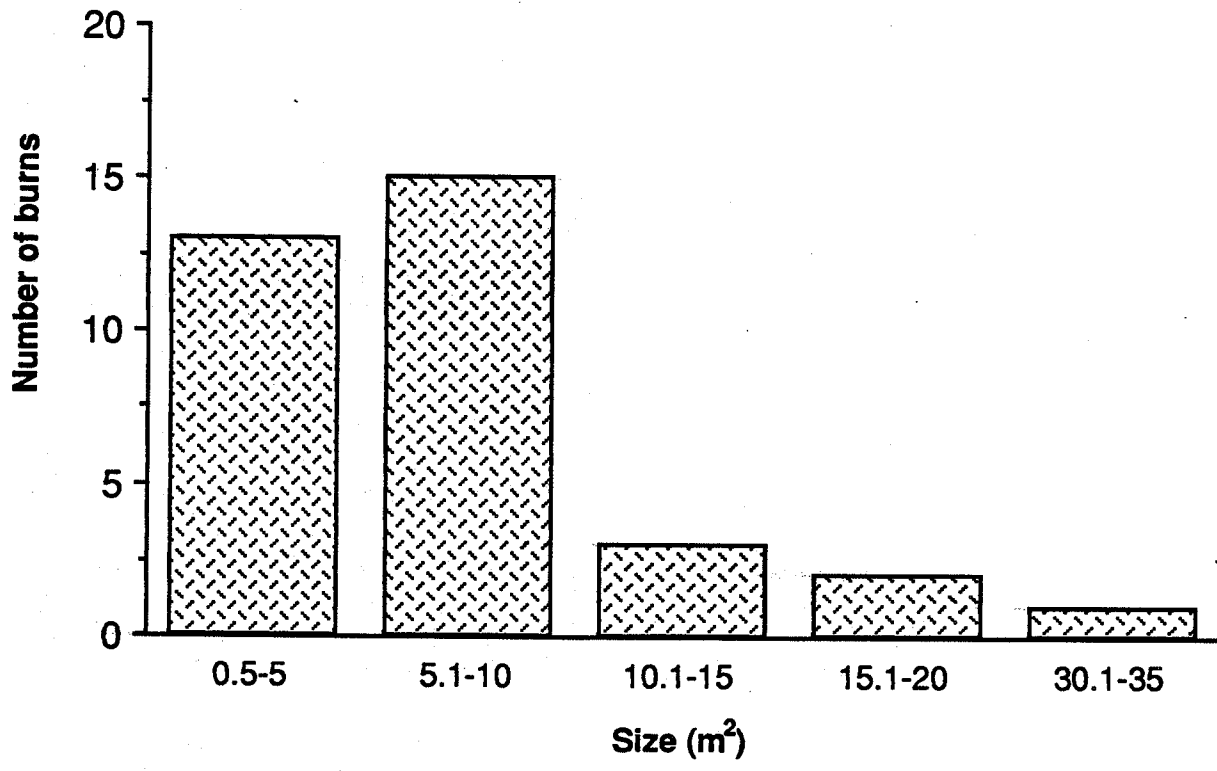
Figure 14. Size of areas where felled elms were burned. n=34 burn areas.

mean size was 7.4 ± 5.9m^2. They were all created between 1984 and 1986.

Six species from the shrub stratum, all less than a meter tall, were recorded (Table 6). *Fraxinus pennsylvanica* had the highest frequency (21%) and density in the total burn area was 22 stems/253m^2, i.e. 869/ha). The other plants occurred in less than 10% of the burns and had densities of less than 10 stems/253m^2 (395/ha).

There were 27 herbs stratum species in the burn areas (Table 7). Most of these were present in the closed forest. *Fraxinus pennsylvanica* seedlings occurred in 88% of the burns and *U. americana* in 85%. These two species also had the highest relative cover values, 24% and 23% respectively. *Sonchus arvensis* had a frequency of 44% and a relative cover of 11%. All other species had frequencies of less than 30% and cover values of less than 10%. *Atriplex* sp. and *Plantago major* were the only species found in the burns but not in the closed forest.

4.7 ABIOTIC DATA

The soil was found to be primarily silt (approximately 70%), with 21% clay at 0-15cm and 15-30cm (Figure 15a, b). The upper layer had slightly less sand than the lower layer (5% vs 8%). There was little variation between the areas, with the exception of the clearing (Figure 15c, d). At both depths, the clearing had more silt (approximately 80%) and sand (approximately 9%), but less clay. However, this difference may be due to the small sample size from the clearing (mean of 3 samples).

The average pH of the soil samples from both depths was 7.6 ± 1.2 (Table 8). According to Michalyna et al. (1975) the average pH of the Winnipeg area surface soil is 6-7.8. Sub-soils have an average pH between 7.4 and 8.2. The surface layer of matted layer of leaves and silt had a

Table 6. Shrub stratum species recorded in 34 burned areas. Frequency and total density values are given. All shrubs were less than a meter tall.

Species	Frequency %	Stems/253m^2
Fraxinus pennsylvanica	21	22
Lonicera dioica	6	4
Rosa woodsii	3	8
Rubus idaeus	3	3
Quercus macrocarpa	9	4
Viburnum lentago	3	3

Table 7. Herb stratum species frequency and relative cover in 34 burned areas. Trace values are <0.05%.

Species	Frequency %	Relative cover %
Acer negundo	14.7	1.4
Ambrosia trifida	5.9	0.6
Amphicarpa bracteata	14.7	4.2
Arctium lappa	8.8	0.6
Artemisia absinthium	23.5	3.0
Aster simplex	17.6	6.4
Atriplex sp.	2.9	0.3
Bromus inermis	8.8	0.1
Cirsium arvense	14.7	2.7
Elymus canadensis	8.8	0.1
Fraxinus pennsylvanica	88.2	24.3
Grass spp.	11.8	1.1
Menispermum canadense	8.8	1.6
Parthenocissus inserta	2.9	0.5
Phalaris arundinacea	8.8	1.1
Plantago major	5.9	trace
Potentilla anserina	2.9	trace
Rorripa islandica	17.6	1.2
Rumex maritimus var. *fueginus*	29.4	5.2
Smilax herbacea	5.9	1.0
Sonchus arvensis	44.1	10.6
S.asper	17.6	4.3
Stachys palustris	17.6	2.9
Sterionema ciliatum	2.9	trace
Thalictrum venulosum	11.8	1.1
Ulmus americana	85.2	23.1
Moss	5.9	2.6
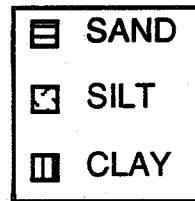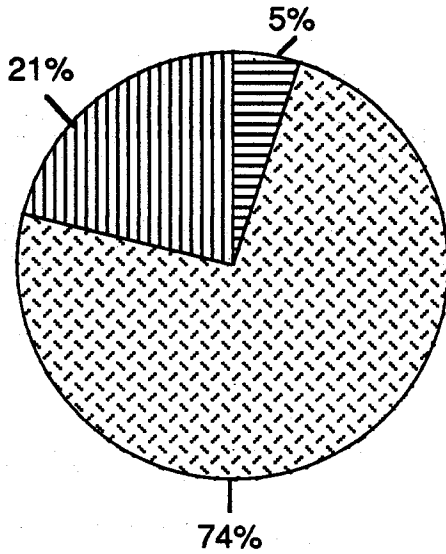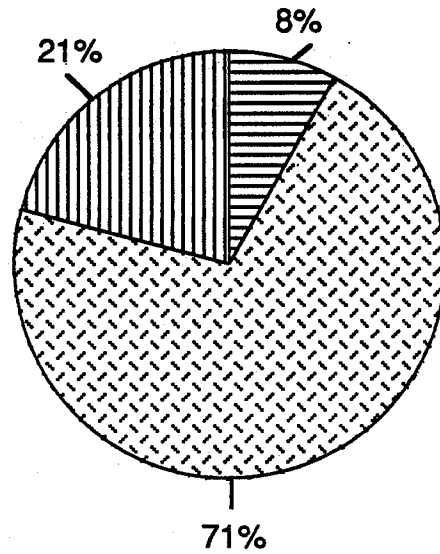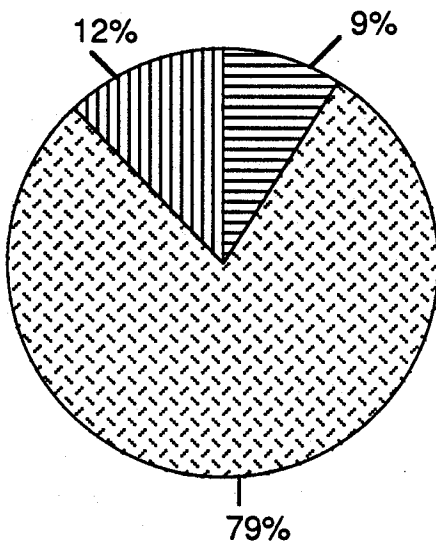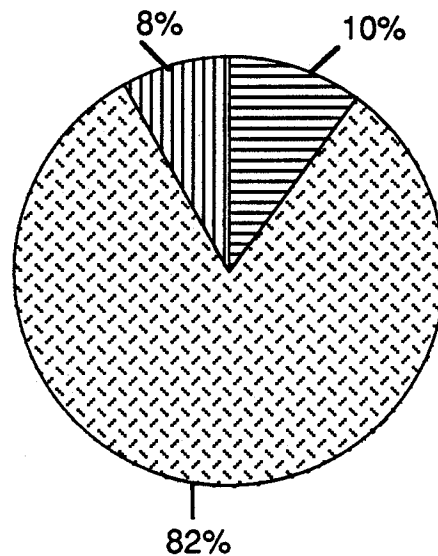
Figure 15. Soil particle composition. n=mean of 12 samples per depth for all samples, n=mean of 3 samples per depth for Clearing.

Table 8. Soil pH and conductivity. Values are means with standard
deviation values values.

Depth (cm)	n	pH	Conductivity (mS)	Conductivity range (mS)
Surface	4	8 ± 0.2	724 ± 13.8	705 to 738
0-15	136	7.6 ± 0.2	697 ± 91.9	430 to 888
15-30	140	7.6 ± 0.2	673 ± 91.7	416 to 872

Table 9 t-test values for environmental data. "n" is the number
of readings, " var" is the variance, an "*" indicates statistical
significance at the 90% confidences level, "me/m^2/s" is
microeinsteins per square meter per second. n=8 for closed
forest. For disturbed areas - temperature, n=7, light levels, n=6.

Temperature (°C)

	mean	var.		mean	var.	t
Disturbed, above vegetation	27.5	1.9	with closed forest shade	23.8	1.4	6.5*
			with closed forest sunspot	24.1	1.8	5.9*
			with disturbed ground level	25.0	1.7	6.1*
Disturbed, ground level	25.0	1.7	with closed forest shade	23.8	1.4	2.1*
			with closed forest sunspot	24.1	1.8	1.7*
Closed forest shade	24.1	1.8	with closed forest sunspot	24.1	1.8	2.7*

Light (me/m^2/s)

	mean	var.		mean	var.	t
Disturbed, above vegetation	0.71	0.11	with closed forest shade	0.06	0.01	3.6*
			with closed forest sunspot	0.24	0.17	7.7*
			with disturbed ground level	0.20	0.10	1.3
Disturbed, ground level	0.21	0.13	with closed forest shade	0.06	0.01	2.0*
			with closed forest sunspot	0.24	0.17	0.3
Closed forest shade	0.06	0.01	with closed forest sunspot	0.24	0.17	2.7*

pH of 8.0. Mean conductivity values were approximately 700mS (Table 8). The 0-15cm and 15-30cm samples had similar variations (ranges of 458mS and 456mS respectively) while the surface layer showed little variation (705mS to 738mS).

The differences in temperature between disturbed and closed forest sites were all statistically significant at the 90% confidence level (Table 9). Differences were larger when readings were taken above the understorey vegetation in the disturbed area. There were also statistically significant temperature differences in the closed forest, between the shade and a sunspot and in the disturbed area, between above vegetation and at ground level.

Light readings in the closed forest at ground level were significantly lower than readings taken in disturbed areas (Table 9). However, the difference between readings from the disturbed area at ground level and the closed forest in a sunspot were not significant.

5. DISCUSSION

The results of this research show that the closed forest is composed, in order of importance, of *Ulmus americana*, *Acer negundo* and *Fraxinus pennsylvanica* and that these species are fairly uniformly distributed in the tree and shrub strata. *Fraxinus pennsylvanica* saplings dominate the less than the less than one meter size class in the shrub stratum and few saplings are taller than the 1m class. There is little difference in the understorey composition of the closed forest, gaps and openings beneath dead elms. Plots from the same sites have a similar composition which does not seem to be affected by the elevation or the opening size. Vegetation has only partially covered the burn areas. The herb stratum composition of the forest appears patchy. Vegetation has only partially covered the burn areas. The clearing has very few trees and shrubs and its herb composition differs from that of the closed forest. Elm saplings have a low incidence of Dutch elm disease.

5.1 CLOSED FOREST

The closed forest sites are grouped by property owner (Figure 10a). As each plot contains a number of species, this indicates that plots in the same site have similar herb and shrub strata compositions. The property boundaries, which were ecologically arbitrary, include patchiness in the forest floor vegetation. Five possible causes for this patchiness are the growth habit of understorey plants, site past history, seed dispersal mechanisms, variations in flooding regimes and differences in soil composition.

The growth habits of understorey plants may contribute to the patchiness found in the herb stratum of the bottomland forests. The

majority of the dominant understorey herbs and vines reproduce vegetatively and/or spread horizontally. For example, vines such as *Parthenocissus inserta*, *Vitis riparia*, *Menispermum canadense* and *Amphicarpa bracteata* have rapid horizontal growth. Herbs such as *Laportea canadensis*, *Smilacina stellata*, *Thalictrum venulosum* and *Elymus canadensis* spread by rhizomes. Once established, their horizontal spread allows them to form patches of local dominance if they can out-compete their neighbours. Most of the groups of plots in Figure 10a can be explained by the local dominance of such species.

Past history of the site may also promote patchiness. Different sites may have been subjected to events such as fire, grazing and local disturbances such as blow downs in the past. They would then be at different stages of development and have different colonizing species.

Seed dispersal mechanisms may also influence the local species composition. The arrival of initial colonizers is a chance event, determined by wind and water currents and animal dispersion (Harper 1977). The range of species to arrive first at various sites may have differed. They were then able to establish and dominate for the reasons outlined previously.

As plots with similar elevations are generally subject to similar flooding regimes and species have different tolerances to flooding (Bell 1974b; Johnson et al. 1976; Menges 1986), it was expected that elevation would have a bearing on the understorey composition of plots. Flood tolerant plants such as *F. pennsylvanica* seedlings were expected to dominate lower areas than less tolerant plants such as *Populus deltoides* seedlings (Hosner 1958). However, when elevation data were visually

compared with the arrangement of plots in the Figure 10a, there was no correlation, indicating that the understorey composition of the plots was probably not determined by elevation.

Since the arrival of Dutch elm disease in Manitoba, the Red River water level has been considered high only once, in 1979 (Warkentin, pers. comm.), but personal observation indicates that all areas except the clearing have been flooded recently. In 1989 at some sites the author observed standing water, while at others, 2-4cm layers of alluvium and lack of litter layer suggested recent scouring and siltation by flooding. Flood conditions may have occurred in all plots despite the range in their elevations (Appendix D) because of local topography. In most cases, the higher sites were in a position where water would drain into them from above or where standing water would accumulate. Their flood conditions would therefore be similar to other sites at lower elevations. In addition, the objectives of the study required sampling to be restricted to sites dominated by *U. americana*, *F. pennsylvanica* and *A. negundo* which generally occur in flood prone areas.

Differences in soil parameters are not likely to be responsible for the variations in plot vegetation. The ranges in particle size were small (less than 10% per particle size category), and there was no correlation between these differences and plant composition. These results do not agree with those of Menges (1986) who found soil texture was significantly correlated with axes of several site ordinations. The pH and conductivity values had a small range (Table 8), their small within plot variation and lack of correlation with vegetation composition indicate that these variables are not likely the cause of the patchiness. The soil in all

plots is alluvium, the parent material is approximately the same age and is subject to similar weathering processes. It is therefore improbable that nutrient status is the influencing factor.

Patchiness is a universal phenomena, caused and influenced by infrequent events such as hurricanes and fires, but also fine-scale events like the death of an individual plant (White and Pickett 1985). Local environmental characteristics such as soil micronutrient content, predation and seasonality affect species patches (Harper 1977). Characteristics of species also influence spatial heterogeneity. Some plants form dense mats, others form a sparse, spreading vegetative body. Factors such as fecundity, pollen dispersal, dormancy and competitive ability further influence patch dynamics (Harper 1977). Detailed discussion of such events and factors is beyond the scope of this thesis.

Figure 10b indicates that there is no strong pattern of species association in the herbs and shrubs. No particular species were found to frequently occur together.

5.2 OPENINGS AND CLOSED FOREST

There was little difference between the understorey vegetation of the closed forest and either type of opening (Table 5, Figure 11, Figure 12). Reasons for this similarity include the age of the openings, the size of the openings and the severity of the disturbance. If there is a lag time between a disturbance and its effect on vegetation, the openings may be too young to show changes in their vegetation. The dead elm openings were a maximum of 15 years old and the removal gaps were approximately five years old. While Collins and Pickett (1988a) attribute lag time to the lack of difference between three-year old gaps and closed

forest, other authors (Brokaw 1985; Moore and Vankat 1986; Collins and Pickett 1988b; Runkle 1990), studying temperate and tropic vegetation have noted species changes in gaps less than six years old. It is therefore unlikely that the similarity between the closed forest and openings in this study is due to lack of time for response.

Perhaps most likely is the fact that the openings may be too small to cause changes in the understorey composition of the forest vegetation. They range from $25m^2$-$731m^2$, with most being less than $100m^2$ (Figure 8). The range in opening size does not appear to cause variations in plot's species composition. All openings were similar to the closed forest, whether considered in groups (i.e. gaps and dead elm forest - Table 5), or separately (Figure 11 and Figure 12). When sizes were compared with the plot distributions in the distribution of the points (Figure 11, Figure 12), they did not correspond with the groupings.

Light and temperature levels were higher in gaps than in the surrounding forest, but the extent of these differences is determined by opening size among other factors (Runkle 1985). Although there was a significant difference between light and temperature readings in the disturbed and undisturbed areas (Table 9), the size of openings and the height of the surrounding trees (approximately 22m) may cause these differences to occur for a short time, only when the sun is at or near its zenith. As readings were taken between 1130 and 1300, this possibility was not tested.

Researchers have reached different conclusions regarding the effects of gap size. Sapling response in $130m^2$ temperate gaps (Barden 1979) and $20m^2$ to $705m^2$ tropical gaps (Brokaw 1985) have been noted by some authors,

but Collins and Pickett (1988b) found no herb response in temperate gaps from $33m^2$ to $151m^2$. The lack of variation in the herb stratum among the wide range of openings sizes and the similarity of the openings to the closed forest in this study, suggest that the openings were too small to have an impact on the vegetation. This observation agrees with Canham and Marks (1985) and Runkle and Yetter (1987) who found the frequency of the disturbance was more important than gap size in determining eventual dominants.

Elm removal and death may not have been severe enough disturbances to promote changes in the vegetation. As the sampled gaps were not created by heavy machinery, soil and understorey vegetation was not severely disturbed and favourable areas for weed[1] species were not created. Seeds in the seed bank were able to germinate and bottomland species were able to colonize the openings.

The small size of the openings created by elm removal or death and the small impact of these disturbances has permitted the openings to closed primarily by re-organization processes involving lateral growth of the adjacent canopy, release of saplings and/or encroachment by surrounding understorey species. Although crown expansion was not measured in the current study, results of other researchers (Huenneke 1983; Runkle and Yetter 1987; Runkle 1990) suggest this process is probably important in closing the openings.

The release of suppressed saplings and seedlings is promoted in openings. As the openings are small, there is not enough light for the

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[1]weeds - defined as non-native species capable of vigorous seed production and dispersal and/or rapid vegetative propagation (Harper 1977).

germination of shade intolerant species (eg. *P. deltoides*), but shade tolerant species are released (eg. *U. americana* and *F. pennsylvanica*). The presence of numerous individuals of shade tolerant species in the gaps and the dead elm forest (Figure 5) support this suggestion. Although Barden (1979) reported that minor disturbances maintain low and mid-shade tolerant species, other authors (Connell 1978; Ehrenfeld 1980; Canham 1985, 1990; Whitmore 1989; Runkle 1990) found shade tolerant plants are released in small gaps.

Another re-organization response that is occurring in the openings in this study is encroachment of surrounding understorey species. Rapid vegetative reproduction or horizontal spread by vines such as *M. canadensis*, *P. inserta* and herbs like *L. canadensis* can quickly cover the ground in the openings. All these re-organization responses – crown expansion, release of shade tolerant saplings and encroachment by surrounding species – result in little change in the understorey species composition.

The species composition of the gaps was more similar to the adjacent closed forest plots than to other gap plots when grouped by site (Figure 11). This is to be expected because the natural distribution of herbs in the closed forest is patchy and the species in these patches fill in the gaps. In each site, locally dominant herbs and vines have colonized the gaps.

Dead elm forest plots were similar to the closed forest plots (Figure 12), but they did not form groups by location with closed forest sites. This is probably because there were no dead elm forest plots in closed forest sites. However, as a result of the patchy nature of the

understorey and the past history of the forest, dead elm forest plots were aggregated by the site where they occurred.

The dominant understorey species were different in the gaps and dead elm forest (Figure 6, Figure 13). These differences may be due solely to the pre-disturbance vegetation of the areas. The Dutch elm disease programme was designed to remove diseased trees within the circumscribed area around Winnipeg and other Manitoba towns and cities. Beyond this, dead trees are only removed when private landowners undertake this responsibility. It is therefore unusual to find gaps and dead standing elms in the same site. The species around openings probably play an important role in determining the plant composition in openings.

Although the understorey composition of gaps and the dead elm forest were similar, it is possible that disturbance have changed the performance of species rather than the composition of species. Collins et al. (1985) predicted that light, shade and light flexible (photosynthetically plastic over spatial or temporal ranges) herbs would have different responses to canopy openings. Menges (1986) predicted that species which grow in both the shade and the open will be more vigorous and larger in gaps. Species specific responses to canopy openings have also been reported. *Smilacina stellata* produces larger fruit displays in gaps (Piper 1986) and *L. canadensis* grew smaller, thicker leaves (Menges 1987). *Erythronium americanum* in gaps had greater leaf area than beneath closed forest (Collins and Pickett 1988a).

The results of this research indicate that Manitoba's bottomland forests are not becoming dominated by shrubs (eg. *Rubus acaulis, Ribes americanum*) as a result of elm removal or death. In fact, the undisturbed

Manitoba forest has a higher shrub density than the disturbed areas (Figure 4) and a greater range of shrub species (Table 3). The primary shrub stratum species in all areas are saplings (Figure 5). This lack of shrub dominance after tree removal is contrary to the results of McBride (1973), Niering and Goodwin (1974) and Huenneke (1983). However, their study sites were not in floodplains and had more diverse species compositions than the Red river sites. The flooding regime of the plots in this research may be too harsh for many shrub species but may favour growth of tree saplings, eg. *F. pennsylvanica* whose leaves emerge after flood and ice have passed.

The canopy of the closed forest is dominated by *U. americana*, with decreasing amounts of *F. pennsylvanica* and *A. negundo* (Figure 3). However, the shrub stratum in all areas is dominated by *F. pennsylvanica*, with fewer *U. americana* and *A. negundo* (Figure 5). This shift in dominance is due to Dutch elm disease and the ability of *F. pennsylvanica* saplings to out-compete *A. negundo* saplings (Curtis 1959).

Dutch elm disease has reduced the number of *U. americana* saplings. Although elms begin to set viable seed at 15 years of age, they do not have maximum seed set until they are about 40 years old (Fowells 1965). Thus, as more mature elms succumb to the disease, the seed source continually declines. *Ulmus americana* saplings are persisting despite the occurrence of Dutch elm disease in the adult population. Several authors (McBride 1973, Richardson and Cares 1976; Parker and Leopold 1983; Dunn 1986) also noted elms survived in stands infected with the disease. There are a number of possible reasons for elms' persistence, including low infection rate, early seeding and shade tolerance.

My preliminary study of *U. americana* saplings showed low infection levels of *Ceratocysitis ulmi*. These levels may reflect the feeding behaviour of elm bark beetles. Beetles feed primarily in upper elm tree branches (Stipes and Campana 1981). Therefore as long as mature, large trees are available, beetles will favour them and not feed on saplings. Even when feeding on saplings, beetles rarely inoculate these trees with the fungus (Caroselli and Feldman 1951). Inoculation experiments by Banfield (1968) indicated that young elms were able to recover from vascular incursion by the fungus. Low infection levels in saplings contribute to the survival of elms.

Ulmus americana individuals begin to set viable seed at an early age (Fowells 1965) and are thus likely to produce seed before succumbing to Dutch elm disease. Spring germination allows the seedlings to gain a competitive advantage by becoming established before other bottomland trees. Additionally, *U. americana* saplings are able to persist because of their ability to tolerate shade. They can grow under a closed canopy but respond positively to very small increases in light (Hosner and Minckler 1963).

Fraxinus pennsylvanica is replacing *U. americana* in the understorey rather than *A. negundo* because of life history characteristics and tolerances of *F. pennsylvanica* saplings. *Fraxinus pennsylvanica* is able to withstand competition of other tree species (Curtis 1959), is more shade tolerant (Hosner and Minckler 1963) and is more flood tolerant (Hosner 1958) than *A. negundo*.

The abundance of tree saplings in the gaps, dead elm forest and closed forest confirm that regeneration is occurring. As the majority of

individuals are less than a meter tall, it is not yet possible to determine which species will eventually dominate. However, if Connell's observation (1978) holds true that the abundance of offspring foretells abundance in the next generation of adult trees, the future forests will probably be dominated by *F. pennsylvanica*. As adult elms will be prone to death by Dutch elm disease, *A. negundo* will probably be the second most important tree. *Ulmus americana* will persist as small, short lived individuals.

5.3 BURN AREAS

Removed elms were burned on site in several places. Although many bottomland species are present around the 34 burns (Table 6 and Table 7), they have not grown or spread to cover the burns. Most plants remain on the periphery. Tree seedlings have germinated, but few have grown to the smallest shrub class (>10cm tall, Table 6). The burns are at least four years old and saplings such as *F. pennsylvanica* could have grown to a minimum of 60cm tall (based on growth rate of 15cm/yr, half the optimal rate presented in Fowells 1965), but no individuals are taller than 30cm. *Ulmus americana* is growing poorly, all individuals are less than 10cm tall.

Flooding regime, burn size and local conditions could be influencing the burn area vegetation. As all the burns are within the same elevation range as the sample plots, flooding is not likely to be preventing establishment and growth. The size of burn also seems unimportant to the colonization process as there was no trend in number of species, dominance or cover over the $31m^2$ size range (Figure 14). The poor growth in burns probably is the result of the harsh local environment. The fires released

nutrients but destroyed all the organic matter, which is vital for the growth of most species (Brady 1974). The ashes have a poor water holding capacity, causing species to experience frequent water shortages. When organic matter builds up, conditions will become less harsh and peripheral bottomland species will probable recolonize the areas.

5.4 SELKIRK CLEARING

The clearing had a different understorey species composition (Table 4) and correspondence analysis clearly separated the two types of plots (Figure 9). These differences may be due to differences in the flooding regimes of the clearing and the closed forest and/or the severity and extent of disturbance in Selkirk Park. Unlike other areas, the clearing showed no indication of flooding. There was a dense litter layer and no alluvial deposits. The regulation of downstream water by the Winnipeg floodway and the river gates have protected the clearing from recent floods, despite its elevation (mean of 1.7m above the river). However, this reduced flood frequency has occurred since the controls were built in 1968 and records indicate that the forest composition prior to elm removal in 1977 was similar to the closed forest (Dept. Forestry 1977). It is therefore unlikely that elevation differences between the closed forest and clearing can account for the observed differences in vegetation.

At Selkirk Park, the occurrence of Dutch elm disease caused the removal of up to 40% of the trees, creating a 15.8ha clearing. Disturbance was obviously severe and damaged or destroyed most of the understorey vegetation and perhaps the seed bank. Such a clearing is an ideal site for invasion of weeds and germination of species present in the seed bank. There are a number of ways by which these plants inhibit

native bottomland species, including rapid reproduction, early growth, shading and litter accumulation. Many plants common to the clearing such as *Cirsium arvense*, *Taraxacum officinale* and *Sonchus arvensis* seed prolifically. Once established, they spread rapidly vegetatively. These perennials, and biennials such as *Arctium lappa*, begin growth early in the season, competing for space and light with later emerging native species. Finally, litter accumulation beneath established plants prevents the roots of bottomland tree seedlings, vines and herbs from reaching the mineral soil and seedlings beneath litter from emerging (Bergelson 1990). Bottom-land species are generally adapted to germinate and grow on exposed mineral soil or alluvium, not on dense litter.

Matteuccia struthiopteris, a herb found in damp woods (Scoggan 1957), was present in small quantities in the closed forest (0.1% relative cover) but was important in the clearing (15% relative cover). This fern was probably present as a suppressed shade tolerant herb in the Selkirk forest prior to elm removal. Being rhizomatous, it was able to emerge rapidly after the clearing was created. The increased light and decreased competition from taller bottomland species allowed *M. struthiopteris* to flourish, growing tall enough (1m) to overshadow invading weeds. The increased height and resulting increased photosynthetic ability permitted further spread. *Matteuccia struthiopteris* likely prevents the invasion of other native species by using the same mechanisms as the weedy species – rapid reproduction, early growth, shading and litter accumulation.

Tree regeneration is not occurring in the clearing and there are only 2562 shrubs/ha (Figure 4). Weedy species and *M. struthiopteris* appear to be preventing sapling establishment.

5.5 CONCLUSIONS

5.5.1 MANITOBA DUTCH ELM DISEASE PROGRAMME

The provincial government Dutch elm disease removal programme has been effective in slowing the loss of *U. americana* to Dutch elm disease. Mature, healthy elms still dominate Manitoba bottomland forests 15 years after the disease arrived in the province. Wallner and Hart, quoted in Richardson and Cares (1976) indicate that in approximately 15 years, mortality in many areas without control programmes has reached 95% of all elms with a diameter at breast height greater than 10.2cm. Ecologically, the removal of elms appears to cause no more harm than if the trees were left standing. Presently, both options seem to cause negligible effects on the understorey composition of the bottomland forest. Leaving the elms standing not only does not require removal expenses, but also provides nesting sites and song posts for birds (Osborne 1982; 1983). However, it has the disadvantage of causing more rapid loss of the elms by leaving large reserves of infected trees which act as breeding sites for elm bark beetles. In addition, the dead elm boles are safety hazards, as limbs are prone to break off in strong winds.

Lack of adequate records of Manitoba's Dutch elm disease programme created some difficulties in undertaking this research. Although property owners and forestry personnel could, in some cases provide information on the number of elms removed and mechanisms of removal, this was not always the case. Information such as the number of elms removed in a specific area each year, the size of the openings created and the season of removal was not always available. If such information were available, a more thorough study of the ecological impacts of the programme would be

possible.

Two recommendations emerge for agencies embarking on a Dutch elm disease programme. The first is to adequately describe the forest where trees are to be removed prior to the commencement of the programme. Such a description should include an inventory of tree, shrub and herb species, and details about the forest composition. If possible, a control area with similar vegetation where elm removal will not occur should also be described. Removal and control area should be monitored throughout the programme to permit the assessment of the impact and effectiveness of programme.

Secondly, detailed records should be kept throughout the programme. Data should include the year of removal, the method of removal, the method of tree disposal and details of any other impacts (such as removal of a neighbouring tree as a safety precaution). This information is essential for subsequent impact assessment.

Additionally, the present study clearly showed that there is a need for more research. Methods to re-establish bottomland vegetation, including trees, in Selkirk Park should be examined. A possible method would be a controlled burn. More research is also needed on the Dutch elm disease cycle, including use by beetles of young saplings for feeding and breeding and incidence and toxicity of *C. ulmi* in elm saplings.

5.5.2 SUMMARY

The main findings of this research are that:

- very little original bottomland forest remains in south western Manitoba along the Red River

- Dutch elm disease may cause the current *Ulmus-Acer* dominated forest to

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become a *F. pennsylvanica* and *A. negundo* dominated forest with *U. americana* present only as small, short lived individuals

- the impact of the loss of mature *U. americana* trees in a stand depends on the number of *U. americana* present in the stand

- *U. americana* saplings are present in the understorey of both the closed forest and the canopy openings

- only 2% of the sapling *U. americana* tested were infected with the Dutch elm disease fungus

- numerous *F. pennsylvanica* saplings are present in the understorey of both the closed forest and the canopy openings

- the canopy openings in the bottomland forest created by the removal of one *U. americana* or a small number of *U. americana* have a similar effect on the understorey vegetation as if the dead trees had been left standing

- the canopy openings created by the removal of one *U. americana* or a small number of *U. americana* have a similar understorey composition as the undisturbed forest

- there are approximately 50 vascular species in the herb strata of the undisturbed forest and the canopy openings

- all sites examined have similar soils

- tree regeneration is not occurring in the clearing created in Selkirk Park by the removal of hundreds of *U. americana* trees

- the large clearing in Selkirk Park is dominated by "weedy" herbs and *M. struthiopteris.*

6. APPENDICES

APPENDIX A SPECIES LIST OF VASCULAR PLANTS

"*" indicates species which had total covers ≥5% and were used in correspondence analysis

i Herb Stratum - with relatve cover values (%) for each area, trace values are <0.05%.

	Gaps	Dead elm forest	Clearing	Closed forest
Acer negundo L.*	1.3	0.1	3.9	2.2
Amaranthus retroflexus L.		0.1		
Ambrosia trifida L.		0.1		0.9
Amphicarpa bracteata (L.) Fern. *	15.7	1.2	0.3	7.9
Anemone quinquefolia L. var. interior Fern.		trace		0.3
Arctium lappa L. *	1.7	5.2	18.7	0.6
Arenaria lateriflora L. *			0.6	
Artemisia absinthium L. *	0.1		0.1	
A. biennis Willd.				
Aster simplex Willd. *	0.4	2.0	1.0	1.0
Atriplex sp.				
Bidens frondosa L.	trace	trace	0.1	
Bromus inermis Leyss. *	0.3			trace
Botrychium virginianum (L.) SW *	0.4			
Carex alopecoidea Tuckerm. *			0.1	0.1
C. assiniboinensis Boott *	2.1	0.4		1.3
C. sprengelii Dew.*		0.1	0.9	
Celastrus scandens L.				
Chenopodium sp. *	0.1	0.2	0.7	
Cirsium arvense (L.) Scop. *	1.7	0.5	11.2	1.0
Convolvulus sepium L.			0.1	trace
Cornus canadensis L. *			0.2	0.7
Corylus americana Walt. *			0.1	
Cuscuta gronovii Willd. *	0.3		trace	0.1
Echinocystis lobata (Michx.) T. & G. *	0.1	0.6	trace	0.6
Elymus canadensis L. *	5.3	1.9	0.2	3.0
E. innovatus Beal *	0.2	0.7	4.0	
Erigeron philadelphicus L. *	3.7			
Erysimum cheiranthoides L.				
Fragaria virginiana Dcne. *	0.2			
Fraxinus pennsylvanica Marsh. *	2.9	1.1	trace	1.3
Galium boreale L. *	0.2	0.2		trace
G. triflorum Michx. *	1.4	0.8	0.1	0.5
Grass spp. *		trace		1.1
Heracleum lanatum Michx.				

i Herb stratum - relative cover values

	Gaps	Dead elm forest	Clearing	Closed forest
Hesperis matronalis L.				trace
Impatiens capensis Meerb. *		trace	0.5	
Lactuca scariola L.				
Laportea canadensis (L.) Wedd. *	9.7	18.4	5.8	23.5
Lepidium densiflorum Schrad. *			trace	
Lonicera dioica L. var. glaucescens (Rydb.) Butters				trace
Maianthemum canadense var. interius Fern. *	7.1	13.1		6.3
Matteuccia struthiopteris (L.) Tordaro var. penslvanica (Willd.) Morton *		0.8	15.2	0.1
Melilotus alba Desr. *	trace		4.0	
Menispermum canadense L. *	7.1	13.1		6.3
Menthe arvensis L. var. villosa (Benth. Stewart *	0.1		0.2	trace
Mertensia * paniculata (Ait.) G. Don	0.2		0.9	
Osmorhiza longistylis (Torr.) DC. *	0.9	0.4		0.3
Oxalis stricta L.	0.1	trace		
Parthenocissus inserta (Kerner) K. Fitsch *	3.0	4.5		3.2
Pastinaca sativa L. *			0.6	
Phalaris arundinacea L. *	0.1	0.9	1.3	0.2
Plantago major L.				
Poa pratensis L. *			trace	
Polygonatum canaliculatum (muhl.) Pursh *	0.1	0.1	0.3	
Potentilla anserina L.			0.1	
Quercus macrocarpa Michx.				trace
Ranunculus abortivus L. *	0.1	trace	0.6	
Rhus radicans L. * var. rydbergii (Small) Rehd.	0.7	1.0		0.2
Ribes americanum Mill.				
R. hudsonianum Richards.			0.1	
Rorippa islandica (Oeber) var. fernaldiana Butt. & Abbe *	0.1			trace
Rosa woodsii Lindl.	trace			
Rudbeckia laciniata L.				
Rumex maritimus L. var. fueginus		trace	0.1	trace
Smilax herbacea L. var. lasioneura (Hook.) DC.	3.6	3.8		6.0
Smilacina stellata (L.) Desf. *	5.5	2.2	2.5	3.7

i Herb Stratum - relative cover values

	Gaps	Dead elm forest	Clearing	Closed forest
Solidago spp. *	1.7	0.1	1.6	0.2
Sonchus arvensis L. *	2.0	0.1	5.9	0.4
S. asper (L.) Hill *	0.3		0.6	trace
S. oleraceus L. *		trace	0.6	
Sonchus spp. *	0.3	0.3		trace
Stachys palustris L. var. pilosa (Nutt.) Fern.	4.8	3.3	2.6	0.9
Sterionema ciliatum (L.) Raf				0.2
Symphoricarpos occidentalis Hook. *		trace		
Taraxacum officinale Weber *	0.1	0.1	10.8	
Thalictrum dasycarpum Fisch. & Lall. *		0.3		trace
T. venulosum Trel. *	5.2	3.7	0.4	5.0
Thlaspi arvense L.			0.1	
Tilia americana L. *	trace	trace		
Trifolium hybridum L.			trace	
T. repens L.				
Trillium cernuum L.	0.1			
Ulmus americana L. *	4.7	4.2	0.4	4.2
Urtica dioica L. * var. procera (Muhl.) Wedd.		1.9	0.1	
Vicia americana Muhl. *	0.1		0.2	
V. cracca L.			0.1	
Viola pubescens L. *	0.3			
Viola rugulosa Greene *		trace	0.1	0.1
Vitis riparia Michx. *	0.5	2.3		0.4
Xanthium strumarium L.				
moss *	0.7	1.4		0.6
bare ground *	8.7	21.5	1.6	20.6

ii Shrub stratum - with density/ha

	Gaps	Dead elm forest	Clearing	Closed forest
Acer negundo L. *	2217	6143	1667	1878
Amelanchier alnifolia nutt. *	27			200
Amorpha fruticosa L. var. angustifolia Pursh				
Cornus stolonifera Michx. *	2473	1027	271	1289
Corylus americana Walt. *	202	19	21	233
C. cornuta Marsh. *	86			278
Crataegus chrysocarpa Ashe. *				100
Fraxinus pennsylvanica Marsh.*	19207	19554	83	27844
Lonicera dioica L. * var. glaucescens (Rydb.) Butters		1102	136	1044
Populus deltoides Marsh. *				

APPENDIX A   SPECIES LIST OF VASCULAR PLANTS   (cont'd)

ii Shrub stratum - with density/ha

	Gaps	Dead elm forest	Clearing	Closed forest
Prunus virginiana L. *	672	1008	167	367
Quercus macrocarpa Michx. *	1089	388		1611
Ribes americanum Mill. *	1048	2364		644
Rosa woodsii Lindl. *	833	698		222
Rubus acaulis Michx. *	1371			122
Tilia americana L. *	148	39		578
Symphoricarpa occidentalis Hook. *		2112		
Ulmus americana L. *	3938	5601	333	6055
Viburnum lentago L. *	685	97	21	44

APPENDIX B   BRAUN-BLANQUET SCALE

Cover Value (%)	Braun-Blanquet Number	Midpoint
75-100	5	85.5
50-74	4	62.5
25-49	3	37.5
5-24	2	15
<5	1	1
Trace	T	0.5

(modified from Braun-Blanquet 1932)

APPENDIX C SOIL PARTICLE ANALYSIS TECHNIQUE

Dried samples of a known weight (approximately 10gm) and distilled waster were stirred to a thin paste. Aliquots of 30% H_2O^2 were added to the pastes to digest organic matter. the solutions were placed on a hot plate and H_2O^2 added until effervescence subsided. After allowing a few more minutes of digestion, distilled water was added to bring the solutions to 200ml. Ten ml of dispersing agent (40gm Calgon {hexameta sodium phosphate}/litre distilled water) was stirred into the soil solutions and mixed for 15 minutes. The suspensions were poured through a 200 mesh seive to remove sand particles. The remaining solutions were poured into 1000ml graduated cylinderes and made to volume with distilled water. After resuspending the particles in the solutions, 25ml aquots of silt and clay were drawn off at a 10cm depth. The solutions werre allowed to settle for the appropriate time (determined by Stoke's Law, using the table in McKeaugue 1971) and a second 25ml aliquot removed from a 10cm depth. All fractions were washed into pre-weighed beakers and dried in at 105°C. Percent sand, silt and clay were calculated.

(McKeaugue 1978)

APPENDIX D PLOT ELEVATION DATA

(meters above the Red River)

Gaps	Dead elm forest	Clearing	Closed forest
3.6	8.1	1.8	0.1
3.8	7.9	1.8	5.4
4.1	8.0	1.7	2.9
2.4	4.4	1.7	4.0
3.0	6.5	1.6	3.1
3.4	6.5	1.8	2.7
1.3	6.5	1.8	2.5
2.1	6.4		2.5
2.9	5.7		2.1
5.5	5.2		6.2
5.8	4.8		3.9
5.4	3.9		3.1
3.1	4.6		3.6
3.0	4.0		2.9
2.1	3.6		2.2
2.7	3.6		3.7
2.9	4.6		3.7
3.0	3.8		1.9
2.9	3.5		2.3
2.4	4.7		2.8
2.1	4.0		2.1
2.8	3.0		5.7
4.1	2.4		5.5
3.3	3.0		5.2
2.2	3.2		5.5
3.8	3.1		5.4
3.7	4.2		4.8
4.3	4.5		2.5
0.6	3.3		
	2.8		
	5.4		
	4.6		
	6.7		
	6.4		
	5.1		
	5.2		
	1.8		
	8.6		
	8.6		
	0.4		

APPENDIX E SIZE OF GAPS AND OPENING BENEATH DEAD ELMS (m^2)

Gaps	Openings beneath dead elms
731	25
562	307
494	288
354	239
340	106
273	93
264	84
261	70
288	58
190	53
158	45
127	45
123	35
80	25
72	25
68	25
54	25
51	25
46	25
36	25
25	
25	
25	

APPENDIX F SIZE OF BURN AREAS (m^2)

9.4	6.2	3.2	4.0
10.4	5.2	0.5	8.2
6.0	3.8	5.6	7.8
7.5	1.7	7.7	1.8
4.6	5.1	2.7	5.3
5.8	2.0	3.2	18.2
11.0	10.0	18.0	8.0
4.8	7.2	32.4	8.0
6.8	11.0		

APPENDIX G CLIMATIC DATA

i Temperature (^{0}C)

	Under vegetation	Above vegetation		Shade	Sunspot
Disturbed areas	23	27	Closed forest	23.5	24
	24	24.5		21	20
	22.5	26		23.5	24
	26.5	27.5		25.5	26
	26	27.5		25.5	26
	27	29.5		25	25.5
	26	30.5		24	24
				23	23

ii Light (me/m^2/sec)

	Under vegetation	Above vegetation		Shade	Sunspot
Disturbed areas	0.10	0.71	Closed forest	0.08	0.13
	0.12	0.52		0.08	0.35
	0.18	0.76		0.08	0.20
	0.11	0.78		0.05	0.07
	0.48	0.62		0.05	0.32
	0.25	0.86		0.04	0.62
				0.06	0.10
				0.05	0.13

7. REFERENCES

Anonymous. 1958. Report of the Royal Commission on flood cost benefit. Winnipeg, Manitoba.

Banfield, W.M. 1968. Dutch elm disease recurrence and recovery in American elm. Phytopathol. Z., 62: 21-60.

Barnes, W.J. 1985. Population dynamics of woody plants on a river island. Can. J. Bot., 63: 647-655.

Barden, L.S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. Oecologia, 44: 141-142.

_____ 1980. Tree replacement in a cove hardwood forest in the southern Appalachians. Oikos, 35: 16-19.

Beckman, C.H. 1981. Pathogenesis. *In* Compendium of elm diseases. *Edited by* R.J. Stipes and R.J. Campana. American Phytopathological Society, U.S.A. pg. 16.

Bell, D.T. 1974a. Tree stratum composition and distribution in the streamside forest. Am. Mid. Nat., 92: 35-46.

_____ 1974b. Studies on the ecology of a streamside forest: composition and distribution of vegetation beneath the tree canopy. Bull. Torrey Bot. Club, 101: 14-20.

_____ 1980. Gradient trends in the streamside forest of Central Illinois. Bull. Torrey Bot. Club, 107: 172-180.

Bergelson, J. 1990. Life after death: site pre-emption by the remains of *Poa annua*. Ecol., 71: 2157-2165.

Bessey, C.E. 1904. The number and weight of cottonwood seeds. Science, 20: 118-119.

Brady, N.C. 1974. The nature and properties of soil, 8th edition. MacMillan Publishing Co., New York.

Braun-Blanquet, J. 1932. Plant sociology: the study of plant communities. McGraw-Hill, New York.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr., 27: 325-349.

Brewer, R. and Merritt, P.G. 1978. Wind throw and tree replacement in a climax beech-maple forest. Oikos, 30: 149-152.

Brokaw, N.V. 1985. Gap-phase regeneration in a tropical forest. Ecol., 66: 682-687.

Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. Club, **112**: 134-145.

_____ 1988. An index for understorey light levels in and around canopy gaps. Ecol., **69**: 1634-1638.

_____ 1989. Different responses to gaps among shade-tolerant tree species. Ecol., **70**: 548-550.

_____ 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. Bull. Torrey Bot. Club, **117**: 1-7.

_____ and Marks, P.L. 1985. Responses of woody plants to disturbances: patterns of establishment and growth. *In* The ecology of natural disturbances and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Orlando. pp. 197-216.

Carleton, T.J. and Taylor, S.J. 1984. The structure of a wooded urban ravine system. Can. J. Bot., **61**: 1392-1401.

Caroselli, N.E. and Feldman, A.W. 1951. Dutch elm disease in young elm seedlings. Phytopath. **41**: 46-51.

Collins, B.S., Dunne, K.P. and Pickett, S.T.A. 1985. Responses of forest herbs to canopy gaps. *In* The ecology of natural disturbances and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Orlando. pp. 218-234

Collins, B.S. and Pickett, S.T.A. 1988a. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. J. Ecol., **76**: 437-450.

_____ 1988b. Response of herb layer cover to experimental canopy gaps. Am. Midl. Nat., **119**: 282-290.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science, **199**: 1302-1310.

_____ 1989. Some process affecting the species composition in forest gaps. Ecol., **70**: 560-562.

Cottam, G. and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. Ecol., **37**: 451-460.

Curtis, J.T. 1959. The vegetation of Wisconsin — an ordination of plant communities. University of Wisconsin Press, Madison.

Dahlem, T, S. and Boerner, R.E.J. 1987. Effects of canopy light gap and early emergence on the growth and reproduction of *Geranium maculatum*. Can. J. Bot., **65**: 242-245.

Del Moral, R. 1980. On selecting indirect ordination methods. Vegatatio, 42: 47-58.

Department of Forestry. 1977. Forest inventory report for Township 14, Range 55. Government of Manitoba, Manitoba.

Department of Natural Resources. 1979. Dutch elm disease detection surveillance report summary. Government of Manitoba Forestry publication, Winnipeg.

Dorber, L. 1979. Recommendations for wildlife management in Beaudry Provincial Park, developed from an inventory of its wildlife and natural vegetation. MNRM practicum. University of Manitoba, Manitoba.

DuBarry, A.P. 1963. Germination of botttomland tree seed while immersed in water. Jour. Forestry, 61: 225-226.

Dunn, C.P. 1986. Shrub layer response to death of *Ulmus americana* in southeastern Wisconsin lowland forests. Bull. Torrey Bot. Club., 113: 142-148.

_____ and Stearns, F. 1987. A comparison of vegetation and soils in floodplain and basin forested wetlands of southeastern Wisconsin. Am. Midl. Nat., 118: 375-384.

Ehrenfeld, J.G. 1980. Understorey response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club, 107: 29-41.

Elgersma, D.M. 1981. Host susceptibility and resistance. *In* Compendium of elm diseases. *Edited by* R.J. Stipes and R.J. Campana. American Phytopathological Society, U.S.A. pp. 17-18.

Ellmore, G.S. and Ewers, F.W. 1986. Fluid flow in the outermost xylem increment of a ring-porous tree, *Ulmus americana*. Amer. J. Bot. 73: 1771-1774.

Environment Canada. n.d. Canadian climate normals - temperature and precipitation 1951-1980, prairie provinces. Canadian Climate Program.

Fasham, M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal component and reciprocal averaging for ordination of simulated coenoclines and coenoplanes. Ecol., 58: 551-561.

Feoli, E. and Feoli-Chiapella, L. 1980. Evolution of ordination methods through simulated coenoclines: some comments. Vegatatio 42: 35-41.

Fowells, H.A. 1965. Silvics of forest trees of the United States. Agr. handbook 271, U.S. Dept. of Agr., Washington D.C.

Franklin, J.F., Shugart, H.H. and Harmon, M.E. 1987. Tree death as an ecological process. Bioscience, 37: 550-556.

Gauch, H.G. Jr. 1982. Multivarient analysis in community ecology. Cambridge University Press, Cambridge. pp. 109-172.

_____, Whittaker, R.H. and Wentworth, T.R. 1977. A comparative study of reciprocal averaging and other ordination techniques. J. Ecol., 65: 157-174.

Graham, R. M. 1984. The surface waters of Winnipeg - rivers, streams ponds and wetlands, 1874-1984, the cyclical history of urban land drainage. MLA practicum. University of Manitoba, Winnipeg.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Hesse, P.R. 1971. A textbook of soil chemical analysis. John Murry, Great Britain.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol., 61: 237-249.

_____ and Gauch, H.G. Jr. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio, 42: 47-58.

Hilderman and Associates. 1975. Background data - soils and drainage, vegetation, riverbank typology. Vol 2. of The Red and Assiniboine Rivers tourism and recreation study. pp. 302-304.

Horn, H.S. 1981. Some causes of variety in patterns of secondary succession. In Forest succession: concepts and application. Edited by D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York.

Hosie, C.R. 1973. Native trees of Canada, 7th edition. Canadian Forestry Service, Department of Environment, Canada.

Hosner, J.F. 1957. Effects of water upon the seed germination of bottomland trees. For. Sci., 3: 67-70.

_____ 1958. The effects of complete inundation upon seedlings of six bottomland tree species. Ecol., 39: 371-373.

_____ and Minckler, L.S. 1963. Bottomland hardwood forests of southern Illinois - regeneration and succession. Ecol., 44: 29-41.

Huenneke, L.F. 1983. Understorey response to gaps caused by the death of Ulmus americana in central New York. Bull. Torrey Bot. Club, 110: 170-175.

Hupp, C.R. and Osterkamp, W.R. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecol., 66: 670-681.

Johnson, D. F. 1950. Plant succession on the Missouri river floodplain near Vermillion, South Dakota. MA thesis, University of South Dakota, South Dakota.

Johnson, W.C., Burgess, R.L. and Keammerer, W.R. 1976. Forest overstory vegetation and environment on the Missouri river floodplain in North Dakota. Ecol. Monogr., 46: 59-84.

Jones, R.H., Sharitz, R.R. and McLeod, K.W. 1989. Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. Am. Midl. Nat., 121: 165-175.

Keammerer, W.R. 1972. The understorey vegetation of the bottomland forests of the Missouri river, North Dakota. PhD thesis. University of North Dakota, North Dakota.

_____, Johnson, W.C. and Burgess, R.L. 1975. Floristic analysis of the Missouri river bottomland forests in North Dakota. Cd. Field Nat., 89: 5-19.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. Ecol., 34: 44-54.

Kenkel, N.C. and Orloci, L. 1986. Applying metric and non-metric multidimensional scaling to ecological studies: some new results. Ecol., 67: 919-928.

Looman, J. and Best, K.F. 1979. Budd's flora of the Canadian prairie provinces. Research Branch, Agr. Canada publication 1662. Canadian Government Publishing Centre Supply and Services Canada, Hull.

MacHardy, W.E. and Beckman, C.E. 1973. Water relations in American elm infected with *Ceratocystis ulmi*. Phytopathology, 63: 98-103.

Macoun, J. 1882. Manitoba and the great Northwest; the field of investment, the home of the immigrant, being a full and complete history of the country. The World Publishing Co., Guelph.

Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr., 44: 73-88.

Martinez-Ramos, M., Alvarez-Buylla, E. and Sarukhan, J. 1989. Tree demography and gap dynamics in tropical rain forests. Ecol., 70: 555-558.

McBride, J. 1973. Natural replacement of disease-killed elms. Am. Midl. Nat., 90: 300-306.

McConnaughay, K.D.M. and Bazzaz, F.A. 1987. The relationship between gap size and performance of several colonizing annuals. Ecol., 68: 411-416.

96

McKeague, J.A. ed. 1978. Manual on soil sampling and methods of analysis, 2nd ed. Canadian Society of Soil Sciences, Ottawa.

Menges, E.S. 1986. Environmental correlates of herb species composition in five southern Wisconsin floodplain forests. Am. Mid. Nat., 115: 106-117.

_____. 1987. Biomass allocation and geometry of the clonal forest herb *Laportea canadensis*: adaptive responses to the environment or allometric constraints? Am. J. Bot., 74: 551-563.

_____. 1990. Environmental correlations with male, female and clonal biomass allocation in the forest herb, *Laportea canadensis*. Am. Midl. Nat., **124**: 171-180.

Michalyna, W., Gardiner, Wm. and Podolsky, G. 1975. Soils of the Winnipeg region study area. Province of Manitoba, Dept. Municipal Affairs, Municipal Planning Branch, Manitoba.

Moore, M.R. and Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. Am. Midl. Nat., **115**: 338-347.

Moss, E.H. 1938. Longevity of seed and establishment of seedlings in species of *Populus*. Bot. Gazette, **99**; 529-542.

Nebel, B. 1981. Soil, ecosystems and agriculture. *In* Environmental science: the way things work. Prentice-Hall, New Jersey.

Niering, W.A. and Goodwin, R.H. 1974. Creation of relatively stable shrublands with herbicides: arresting "succession" on right-of-way and pastureland. Ecol., **55**: 784-795.

Noble, M.G. 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota river. Am. Mid. Nat., **102**: 59-67.

Osborne, P. 1982. Some effects of Dutch elm disease on nesting farmland birds. Bird Study, **29**: 2-16.

_____, 1983. The influence of Dutch elm disease on bird population trends. Bird Study, **38**: 27-30.

Parker, G.R. and Leopold, D.J. 1983. Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bull. Torrey Bot. Club, **110**: 482-488.

Pielou, E.C. 1984. The interpretation on ecological data - a primer on classification and ordination. John Wiley & Sons, New York.

_____ and Thomas, J.B. 1979. Seasonal development of Dutch elm disease on white elms in Central Ontario, Canada. *II* Following feeding by the North American native elm bark beetle. Can. J. Bot. 57: 353-359.

Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. Am. Midl. Nat., 104: 176-184.

_____ and Willson, M.F., 1978. Disturbance and the dispersal of fleshy fruits. Science, 200: 1161-1163.

Wanek, W.J. 1967. The gallery forest vegetation of the Red River of the North. PhD. thesis. University of North Dakota, North Dakota.

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience, 37: 569-574.

Wartenberg, D., Ferson, S. and Rohlf, F.J. 1987. Putting things in order: A critique of detrended correspondence analysis. Am. Nat., 129: 434-448.

White, P.S. and Pickett, S.T.A. *In* The ecology of natural disturbances and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Orlando. pp. 3-13.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. Ecol., 70: 536-538.

Wikum, D.A. and Wali, M.K. 1974. Analysis of a North Dakota gallery forest: vegetation in relation to topographic and soil gradients. Ecol. Monogr., 44: 441-464.

Wilson, R.E. 1970. Succession in stands of *Populus deltoides* along the Missouri river in southeastern South Dakota. Am. Mid. Nat., 83: 330-342.