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# Structure and Dynamics of Boreal Forest Stands in the Duck Mountains, Manitoba

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# Structure and Dynamics of Boreal Forest Stands in the Duck Mountains, Manitoba

SFM Network Project: Forest Succession and Post-Logging Regeneration
Dynamics in the Duck Mountain Ecoregion, west-central Manitoba

by

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**August 2000**

# EXECUTIVE SUMMARY

Knowledge of natural forest successional processes is critical to the long-term sustainable management and environmental stewardship of Canada's boreal forests. In this study we present a synoptic model for predicting long-term dynamics of forest stands in the Duck Mountains of west-central Manitoba. Predictive models of stand dynamics are critical to maintaining and promoting biodiversity, and in predicting the outcome of various forest management decisions.

Our approach involved reconstructing initial post-fire composition of 110 year old stands, by enumerating and aging the initial canopy cohort as well as standing dead and recently fallen trees. Five fire-initiated stand types were recognized: (1) trembling aspen, *n* = 17; (2) balsam poplar, *n* = 11; (3) white spruce, *n* = 14; (4) jack pine, *n* = 13; (5) black spruce, *n* = 7. For each stand type, stand dynamic patterns were summarized using age- and size-class analyses. 674 increment cores were obtained from canopy trees, and 740 subcanopy were aged at their base. In developing successional trajectories, consideration was also given to advance regeneration density, autecology of tree species, and natural disturbances such as ungulate herbivory and beaver activity. The following is a summary of stand dynamics for each stand-type:

1. Trembling Aspen: At initiation, these stands are dominated by trembling aspen, occasionally in mixture with balsam poplar, white spruce and/or white birch. Tall shrub cover is often high. White spruce may slowly invade, but regenerating trees are often stunted and slow-growing. Mature aspen trees may be blown over in older stands, resulting in a second flush of sucker shoots that perpetuates the stand.
2. Balsam Poplar: At initiation, these stands are often codominated by balsam poplar and trembling aspen, but pure balsam poplar occurs on floodplains and in wet depressions. White spruce and balsam fir invade into most stands, peaking at 60 to 70 years after stand establishment. These stands will be dominated by softwoods by age 150, but balsam poplar and white birch are expected to persist at low abundance.
3. White Spruce: At initiation, these stands are codominated by white spruce and trembling aspen, with some white birch and balsam poplar. Balsam fir invades many stands, with peak recruitment occurring 50 to 80 years after stand establishment. In moist sites, stands are increasingly dominated by balsam fir. In drier sites, balsam fir is less abundant and older stands consist of a diverse multi-aged canopy that includes trembling aspen, white spruce, white birch, balsam fir, black spruce and/or balsam poplar.
4. Jack Pine: At initiation, these stands are typically codominated by jack pine and trembling aspen, occasionally in mixture with black spruce, white spruce and/or white birch. Stand dynamics is highly variable and dependent on seed source availability, topography, and edaphic factors. White spruce, white birch and balsam fir invade 60 years after stand establishment. Late successional stands generally consist of an uneven-aged diverse mixture of black spruce, white spruce, balsam fir, white birch, and trembling aspen. In moist sites, balsam fir often dominates at the late-successional stage.
5. Black Spruce: Dense fire-initiated stands of black spruce occur on poorly-drained lowlands of poor to moderate nutrient status, on both mineral and organic substrates. Jack pine may

also be present at stand initiation, but is outcompeted by black spruce under these conditions. Black spruce forms an edaphic climax, with tamarack as a minor secondary component.

## ACKNOWLEDGEMENTS

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# INTRODUCTION

The Duck Mountain Provincial Park and Forest is a complex forested landscape incorporating elements of the Manitoba Escarpment, the Manitoba and Saskatchewan Plains, and the Grandview and Swan River Valleys. These underlying landforms, combined with Holocene glacial activity, have contributed to the complex and variable topography of the region. Largely as a result of this complex physiography, the area supports a remarkably diverse assemblage of forest communities. Other than the descriptive summary by Rowe (1956), however, no published studies have focussed on the boreal forests of western Manitoba.

Forest succession studies have been undertaken in many areas of the Canadian boreal forest, including central Saskatchewan (Dix and Swan 1971; Bridge and Johnson 2000), Alberta (Achuff and La Roi 1977), Ontario (e.g. Shafi and Yarranton 1973; Carleton and Maycock 1978; Zoladeski and Maycock 1990; Kenkel, Watson and Uhlig 1998), and Québec (e.g. Bergeron and Bouchard 1983; Cogbill 1985; Bergeron and Dansereau 1993; Bergeron and Charron 1994). The boreal forests of western Manitoba differ from those further west in Saskatchewan and Alberta, which are floristically different and somewhat drier. The boreal forests of Ontario and Québec are also floristically different, and unlike the Duck Mountains eastern boreal forest occurs on the Canadian Shield. A forest stand dynamic model was recently developed for Riding Mountain National Park (Caners and Kenkel 1998), but floristic composition, fire history, environmental conditions, and human disturbance differ between the Duck and Riding Mountains.

This study was undertaken to elucidate the structure and dynamics of major boreal forest stands in the Duck Mountain Provincial Park and Forest. Our objective was to determine stand structure and dynamics for major forest stand-types in the region, and to identify the major biological and non-biological processes determining forest composition, structure and change. The data used to achieve these objectives were acquired through detailed, intensive sampling of forest stands located throughout the study area. Forest stand dynamics were inferred by aging trees in both the canopy and regenerating layers, and by carefully examining processes such as canopy mortality and advanced recruitment into the regeneration layer. In addition, mature (> 100 years) forest stands were compared to stands from the large 1961 burn that occurred in the Duck Mountains, in order to infer post-fire recruitment patterns. Based on these data, a synoptic model was developed to predict long-term dynamics of forest stands in the Duck Mountains.

# MATERIALS AND METHODS

### Study Area

The 376,000 ha Duck Mountain Provincial Forest in west-central Manitoba is characterized by a complex interdigitation of small lakes, wetlands and forested uplands. The Duck Mountains form part of the Manitoba Escarpment, which includes the Turtle and Riding Mountains to the south and the Porcupine and Pasquia Hills to the north. The Escarpment is a distinctive physiographic feature that strongly influences the vegetation, soils, groundwater hydrology, mesoclimate, and natural disturbance regime of the region.

In 1996, the province of Manitoba awarded Louisiana-Pacific Canada Ltd. an Environmental License to sustainably manage the boreal mixedwood forests of the Duck Mountains. In addition to the hardwood volume harvested by Louisiana-Pacific (up to 900,000 $m^3$ annually), a number of family-owned sawmill operators harvest softwoods (primarily white spruce) in the region. The Duck Mountains are also an important recreation/tourism area, and represent a critical habitat resource for maintaining the biological and landscape diversity of western Manitoba. Wetlands in the region store vast quantities of water, making the Duck Mountains the principal watershed for extensive agrarian lands to the east, south and north.

## Stand Selection

Stands were sampled from June 23 to August 27 in 1998, and from June 2 to August 31 in 1999. Additional tree age data were obtained in June 2000. The study area was divided into non-overlapping strata to achieve a representative sample of the entire region. Strata were defined using both natural physiographic features and burn histories. However, access problems limited sampling to areas adjacent to roads and trails. Stands showing evidence of past logging were avoided: this often required walking in some distance from access roads and trails. Stands were selected using the following criteria: (a) no evidence of human disturbance; (b) uniform post-fire age; (c) uniform environmental conditions (e.g. slope, aspect, and edaphic conditions at the landscape scale). A cluster sampling approach was used, in which each stand was enumerated using three representative 10 x 10 m plots. A total of 68 stands (3 plots per stand, for a total of 204 plots) were enumerated over the 1998 and 1999 field seasons. Six stands were enumerated in the 1961 burn, while the other 62 stands were generally over 100 years in age.

## Data Collection

### *Trees*

The identity, bole size (diameter at breast height), and height of each living tree in each 10 x 10 m plot was recorded. In addition, the bole size and identity of all standing dead snags and fallen trees that had once occupied the initial post-fire canopy were recorded. At least two canopy trees of each species were aged using an increment borer. Most trees were cored at 20-30 cm from the base, but many were rotten at the base and had to be cored at 1.2 m. A total of 674 increment cores were obtained from canopy trees. Subcanopy trees (advanced regeneration layer) were aged by cutting them at their base, using a handsaw (smaller individuals) or chainsaw (larger individuals). A total of 740 regenerating trees were aged in this way.

### *Understory*

Percent cover of shrubs was estimated in each 10 x 10 m plot. Cover estimates for understory graminoids, forbs, ferns (and fern-allies), bryophytes and lichens were obtained from four 1 x1 m plots located within each 10 x 10 m plot.

### *Soils*

A soil pit was dug in each stand, and a representative soil core collected. Soils were classified, soil horizons measured, and depth to carbonates recorded. Soils were analyzed for pH and conductivity, and particle-size distribution (percentage sand, silt and clay).

### *Physiography and Landscape*

At each stand, distance to seed source was estimated for late-successional species such as balsam fir and white spruce. Detailed information on landform conditions (e.g. slope and slope position, aspect, drainage class) was also collected.

### *Disturbance*

Ungulate herbivory on all understory trees and shrubs was recorded using a browsing intensity index. Evidence of spruce budworm and other forest insect pests was also recorded. Beaver activity and nearby human disturbance were also noted.

## Data Analysis

### *Reconstruction of Initial Stand Composition*

The majority of stands enumerated in this study were approximately 110 years old, which corresponds to historical records of a very large forest fire in 1885 (Harrison 1934). The oldest living canopy trees were assumed to form the initial post-fire cohort. Reconstruction of initial stand composition was supplemented by the identification and aging (when possible) of standing dead and recently fallen trees. Consideration was also given to the known autecology of boreal tree species:

1. Jack Pine: This species produces serotinous cones that result in immediate establishment following a crown-killing fire. Jack pine is highly shade intolerant and fails to establish beneath an existing canopy, making it very useful in establishing stand age. Dense stands of jack pine undergo extensive self-thinning starting at about age 35 (Kenkel, Hendrie and Bella 1997).

2. Trembling Aspen and Balsam Poplar: These hardwood species produce sucker shoots from the root system immediately following a crown-killing fire or other disturbance (more rarely, these species may establish from seed). Both species are shade-intolerant. Dense stands established

from sucker shoots undergoes extensive self-thinning at an early age (Peterson and Peterson 1992).

3. Black Spruce: This species produces semi-serotinous cones, allowing it to establish immediately following a crown-killing fire. Dense post-fire stands often occur on wet to moist, organic or mineral substrates. Dense black spruce stands undergo limited self-thinning (Carleton and Wannamaker 1987). The species is somewhat shade-tolerant, and may invade into older stands (Carleton 1982).

4. White Spruce: This species may establish immediately following a crown-killing fire provided there is a nearby seed source. Later recruitment into established stands is episodic and highly variable (Lieffers, Stadt and Navratil 1996).

5. Balsam Fir: This is considered a later-successional species, as it rarely establishes immediately following a crown-killing fire. Balsam fir requires moist organic seedbeds, such as well-rotted logs in moderately dense forests, for successful germination and establishment. Balsam fir is highly shade-tolerant, but grows very slowly under a closed canopy. Once established, growth is most rapid in canopy gaps. It is generally considered to be drought-intolerant (Galipeau, Kneeshaw and Bergeron 1997).

6. White Birch: This species may establish immediately following a crown-killing fire from seeds or sucker shoots emanating from the root collar. White birch may also invade established stands, often germinating on well-rotted logs. It is considered moderately shade-tolerant.

For each stand, initial floristic composition was reconstructed using the following rankings for each tree species (note: each stand is represented by three 10 x 10 m plots):

| | |
|---|---|
| 0 | = species absent at stand initiation. |
| 0.1 | = single tree present in the stand at initiation. |
| 1 | = species at low abundance at initiation (2-5 trees per stand). |
| 2 | = species codominant at stand initiation. |
| 3 | = species dominant at stand initiation. |

Initial floristic composition was determined for each of the 62 mature stands enumerated. The resulting data were subjected to cluster analysis. Five fire-initiated stand types were recognized (these are described in more detail in the Results section):

| Name | No. Stands | Description |
|---|---|---|
| Trembling Aspen | 17 | Aspen; occasional balsam poplar, white spruce. |
| Balsam Poplar | 11 | Balsam poplar; some aspen and/or white spruce. |
| White Spruce | 14 | White spruce and aspen; occasional birch. |
| Jack Pine | 13 | Jack pine and aspen; some birch, black spruce. |
| Black Spruce | 7 | Black spruce; occasional jack pine. |

***Forest Stand Dynamics***

Patterns of forest stand dynamics were summarized separately for each of the 5 fire-initiated stand types. We used an approach based on age- and size-class analyses. Total basal area and density of each species were determined for each of four canopy strata:

1 = greater than 15 m in height (canopy) .
2 = 10 to 15 m in height (upper subcanopy).
3 = 2 to 10 m (lower subcanopy).
4 = 40 cm to 2 m (sapling layer).

Seedlings (< 40 cm in height) were also enumerated in this study, but were not considered in developing successional trends.

When inferring forest stand dynamics, consideration was also given to the density of advance regeneration, the autecology of tree species, and disturbance features such as ungulate herbivory and beaver activity. Stand age was determined by counting rings from cores taken from canopy trees, supplemented by available fire history maps for the Duck Mountains. We also examined the age structure of trees in the subcanopy, to determine temporal patterns of advance recruitment (saplings and small trees 2-10 m in height). Only a subset of the trees sampled for age analysis is included in this report, since age determinations are not yet completed (all ages will be determined by late October, 2000).

In this report, only stands resulting from the 1885 fire (i.e. approximately 110 years in age) were considered when summarizing stand dynamic trends. Six stands from the 1961 burn were used to confirm post-fire recruitment patterns of later-successional species such as balsam fir, white birch, and white spruce. Synoptic physiognomic profiles were developed for each stand-type, at ages 110 and 160. Standard tree symbols were used (Fig. 1).

# RESULTS

## Fire-Initiated Stand Types

### *1. Trembling Aspen*

At initiation, these stands are dominated by trembling aspen, occasionally in mixture with small amounts of balsam poplar, white spruce and/or white birch (Table 1). These stands are characterized by moderate to high cover of tall shrubs, typically beaked hazelnut, mountain maple, and/or green alder. Trembling aspen stands are typically found in moderately-drained uplands, particularly on well-drained southern and northern slopes of the Duck Mountains and along the upper slopes of major valleys in the western portion of the study area.

Stands containing contemporaneously-established white spruce are common on the upper slopes near Baldy Mountain, and occur sporadically throughout the study area. Dense productive stands of trembling aspen, often in mixture with white birch, balsam poplar and/or white spruce, are commonly encountered on north-facing slopes. Mountain maple or green alder often dominate the understory of these stands, suggesting moist and nutrient-rich conditions. This dense shrub layer may limit advance regeneration of white spruce.

### *2. Balsam Poplar*

The initial cohort of these stands consists of balsam poplar, often in mixture with trembling aspen (Table 2). The proportion of trembling aspen is a function of site drainage, being lowest on floodplains and areas subject to spring flooding and highest in moderately drained sites. Birch may also be present at stand establishment, and occasionally white spruce may establish contemporaneously as well. These stands generally contain few tall shrubs, but green alder may be abundant in some stands.

### *3. White Spruce*

At stand initiation, these stands are typically codominated by white spruce and trembling aspen: pure post-fire stands of white spruce are rare (Table 3). Balsam poplar and white birch may also be present at low abundance, and very occasionally balsam fir may establish contemporaneously. These stands are most commonly found on gently rolling hummocky terrain, where lakes and wetlands are interspersed with upland forests.

### *4. Jack Pine*

These stands are typically codominated by jack pine and trembling aspen at stand initiation (Table 4). The proportion of jack pine and trembling aspen varies considerably within stands and is often difficult to predict. Unlike many areas of the boreal forest, extensive pure jack pine stands are uncommon in the Duck Mountains. In areas where jack pine is most abundant, black spruce may establish contemporaneously at low to moderate density. By contrast, contemporaneously-established white birch is more common in mixed jack pine - trembling aspen stands. Jack pine stands are most commonly encountered on well-drained substrates in the uplands of the Duck Mountains, and on sandy beach ridges along the eastern Escarpment base. Tall shrub cover is generally low in these stands.

### *5. Black Spruce*

At initiation, these stands are strongly dominated by black spruce (Table 5). Black spruce often establishes at very high density, particularly on poorly drained mineral substrates. On better-drained sites, it may occur in mixture with jack pine. On organic peatland substrates, black spruce forms almost pure stands. Burned organic substrates may also be colonized by jack pine, but this species cannot tolerate the wetter condition and is generally extirpated by age 50. Depth to water table varies in these stands: if the water table is close to the surface, trees are stunted. Dense black spruce stands are most commonly encountered in the north-central uplands of the Duck Mountains.

## Stand Dynamics

### *Trembling Aspen*

The current (110 years in age) composition and structure of trembling aspen stands, and predicted structure-composition 50 years hence, are summarized in Fig. 2. Two major sub-types are recognized: (a) hardwood component only, with trembling aspen dominating and small amounts of balsam poplar and/or white birch; (b) hardwood component predominates, but with limited contemporaneous establishment of white spruce.

| | Strata | | | |
|---|---|---|---|---|
| **(a) Basal Area** | **1** | **2** | **3** | **4** |
| Trembling Aspen | 2763.88 | 150.88 | 45.29 | 0.205 |
| Balsam Poplar | 130.24 | 3.24 | 7.06 | 0.004 |
| White Birch | 179.71 | 31.47 | 7.35 | |
| Jack Pine | | 8.88 | | |
| Black Spruce | 1.47 | | 3.71 | 0.001 |
| White Spruce | 562.65 | 103.41 | 56.94 | 0.143 |
| Balsam Fir | | | | |
| **(b) Density** | | | | |
| Trembling Aspen | 6.10 | 1.52 | 4.83 | 1.098 |
| Balsam Poplar | 0.23 | 0.06 | 0.20 | 0.098 |
| White Birch | 0.63 | 0.27 | 0.52 | |
| Jack Pine | | 0.02 | | |
| Black Spruce | 0.03 | | 0.21 | 0.029 |
| White Spruce | 1.17 | 0.52 | 1.71 | 0.275 |
| Balsam Fir | | | | |

Table 1. Mean species basal area ($cm^2/10\ m^2$) and density ($no./10\ m^2$) values for 17 trembling aspen stands, in four canopy strata: 1 = > 15 m; 2 = 10 – 15 m; 3 = 2 – 10 m; 4 = 40 cm – 2m

| | Strata | | | |
|---|---|---|---|---|
| **(a) Basal Area** | **1** | **2** | **3** | **4** |
| Trembling Aspen | 1225.09 | 22.82 | 27.40 | 0.103 |
| Balsam Poplar | 2278.00 | 29.55 | 4.55 | 0.008 |
| White Birch | 234.91 | 18.36 | 12.91 | 0.005 |
| Jack Pine | | | | |
| Black Spruce | | 5.18 | 12.36 | 0.002 |
| White Spruce | 631.18 | 312.27 | 62.82 | 1.345 |
| Balsam Fir | 114.00 | 276.82 | 60.64 | 0.024 |
| **(b) Density** | | | | |
| Trembling Aspen | 2.61 | 0.36 | 1.58 | 0.333 |
| Balsam Poplar | 3.76 | 0.21 | 0.09 | 0.243 |
| White Birch | 0.82 | 0.24 | 1.00 | 0.091 |
| Jack Pine | | | | |
| Black Spruce | | 0.09 | 0.27 | 0.045 |
| White Spruce | 0.53 | 1.62 | 1.71 | 0.834 |
| Balsam Fir | 0.30 | 2.02 | 2.77 | 0.742 |

Table 2. Mean species basal area ($cm^2/10\ m^2$) and density ($no./10\ m^2$) values for 11 balsam poplar stands, in four canopy strata: 1 = > 15 m; 2 = 10 – 15 m; 3 = 2 – 10 m; 4 = 40 cm – 2m

| | Strata | | | |
|---|---|---|---|---|
| **(a) Basal Area** | **1** | **2** | **3** | **4** |
| Trembling Aspen | 1381.21 | 63.21 | 7.36 | 0.004 |
| Balsam Poplar | 103.71 | 44.21 | 4.21 | 0.004 |
| White Birch | 150.79 | 155.57 | 40.64 | 0.047 |
| Jack Pine | | | | |
| Black Spruce | | 10.79 | 15.93 | 0.007 |
| White Spruce | 1692.50 | 134.57 | 24.93 | 0.038 |
| Balsam Fir | 674.71 | 336.79 | 151.21 | 0.243 |
| **(b) Density** | | | | |
| Trembling Aspen | 2.90 | 0.79 | 0.38 | 0.142 |
| Balsam Poplar | 0.33 | 0.19 | 0.21 | 0.143 |
| White Birch | 0.33 | 0.98 | 0.76 | 0.620 |
| Jack Pine | | | | |
| Black Spruce | | 0.14 | 0.71 | 0.238 |
| White Spruce | 1.86 | 0.74 | 1.67 | 1.214 |
| Balsam Fir | 2.24 | 2.55 | 8.26 | 2.831 |

Table 3. Mean species basal area ($cm^2/10\ m^2$) and density ($no./10\ m^2$) values for 14 white spruce stands, in four canopy strata: 1 = > 15 m; 2 = 10 – 15 m; 3 = 2 – 10 m; 4 = 40 cm – 2m

| | Strata | | | |
|---|---|---|---|---|
| **(a) Basal Area** | **1** | **2** | **3** | **4** |
| Trembling Aspen | 1380.69 | 125.85 | 14.31 | 0.038 |
| Balsam Poplar | 25.62 | 4.69 | 0.31 | 0.004 |
| White Birch | 155.31 | 172.69 | 34.46 | 0.065 |
| Jack Pine | 1133.23 | | | |
| Black Spruce | 223.46 | 234.69 | 47.08 | 0.061 |
| White Spruce | 259.31 | 181.00 | 11.00 | 0.097 |
| Balsam Fir | 60.46 | 189.08 | 158.08 | 0.468 |
| **(b) Density** | | | | |
| Trembling Aspen | 2.69 | 1.69 | 0.79 | 0.473 |
| Balsam Poplar | 0.05 | 0.03 | 0.03 | 0.128 |
| White Birch | 0.73 | 2.41 | 2.95 | 0.385 |
| Jack Pine | 2.88 | | | |
| Black Spruce | 0.68 | 1.51 | 1.51 | 0.449 |
| White Spruce | 0.44 | 0.73 | 0.77 | 0.333 |
| Balsam Fir | 0.26 | 1.56 | 8.91 | 2.178 |

Table 4. Mean species basal area ($cm^2/10\ m^2$) and density ($no./10\ m^2$) values for 13 jack pine stands, in four canopy strata: 1 = > 15 m; 2 = 10 – 15 m; 3 = 2 – 10 m; 4 = 40 cm – 2m

| | Strata | | | |
|---|---|---|---|---|
| **(a) Basal Area** | **1** | **2** | **3** | **4** |
| Trembling Aspen | 123.29 | | 0.14 | 0.017 |
| Balsam Poplar | 48.43 | | | 0.001 |
| White Birch | | 145.00 | 5.71 | |
| Jack Pine | 718.71 | 7.29 | | |
| Black Spruce | 2152.29 | 1259.29 | 130.29 | 0.511 |
| White Spruce | | | | |
| Balsam Fir | | 3.71 | 2.29 | 0.156 |
| Eastern Larch | 34.71 | 39.29 | 0.43 | 0.091 |
| **(b) Density** | | | | |
| Trembling Aspen | 0.24 | | 0.10 | 0.523 |
| Balsam Poplar | 0.05 | | | 0.047 |
| White Birch | | 0.24 | 0.14 | |
| Jack Pine | 2.52 | 0.05 | | |
| Black Spruce | 12.76 | 12.24 | 8.91 | 3.190 |
| White Spruce | | | | |
| Balsam Fir | | 0.05 | 0.14 | 0.286 |
| Eastern Larch | 0.14 | 0.29 | 0.14 | 0.429 |

Table 5. Mean species basal area ($cm^2$/10 $m^2$) and density (no./10 $m^2$) values for 7 black spruce stands, in four canopy strata: 1 = > 15 m; 2 = 10 – 15 m; 3 = 2 – 10 m; 4 = 40 cm – 2m

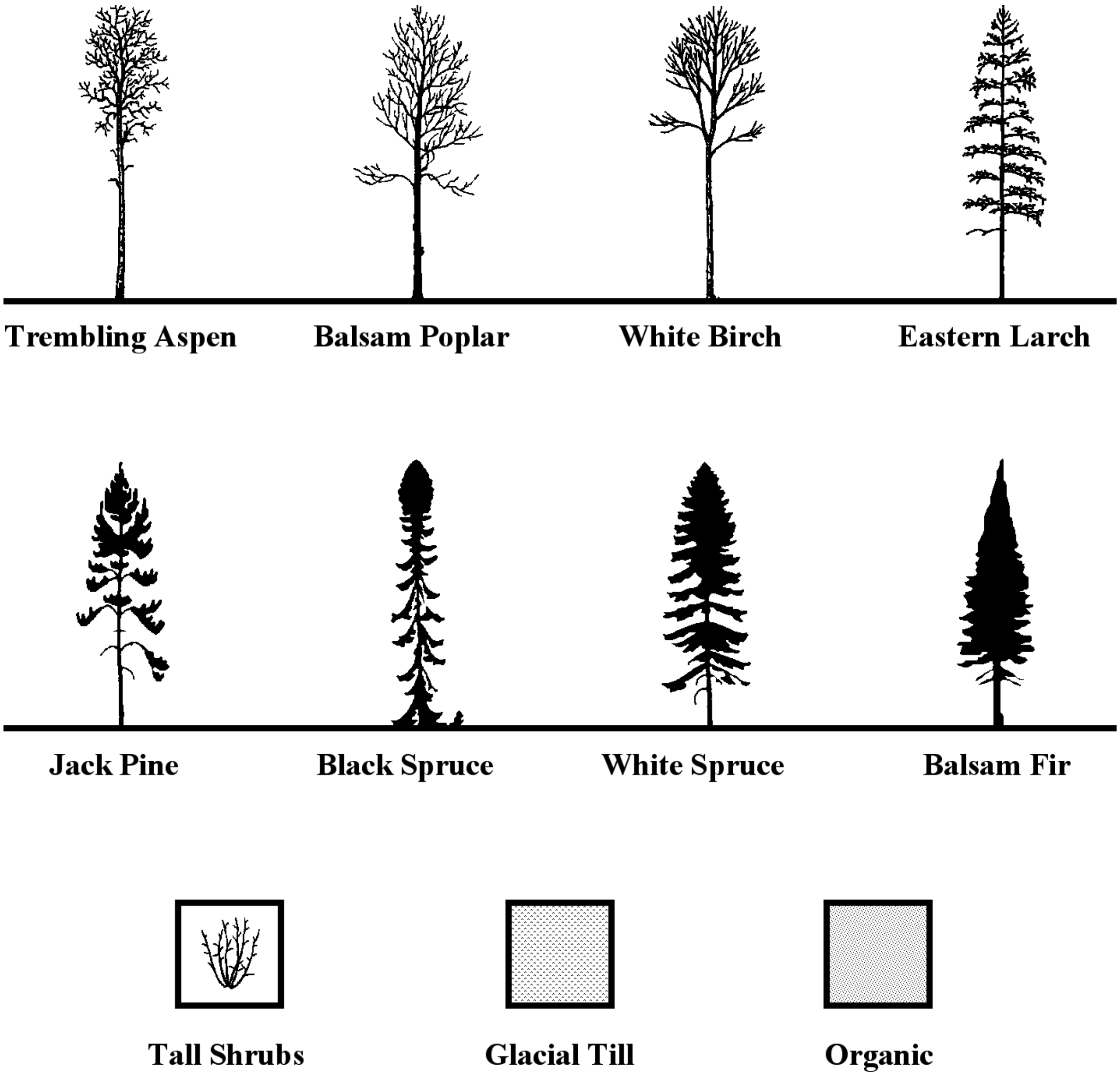



Figure 1. Symbols used in the synoptic physiognomic profiles of stand-types.

## *Trembling Aspen*

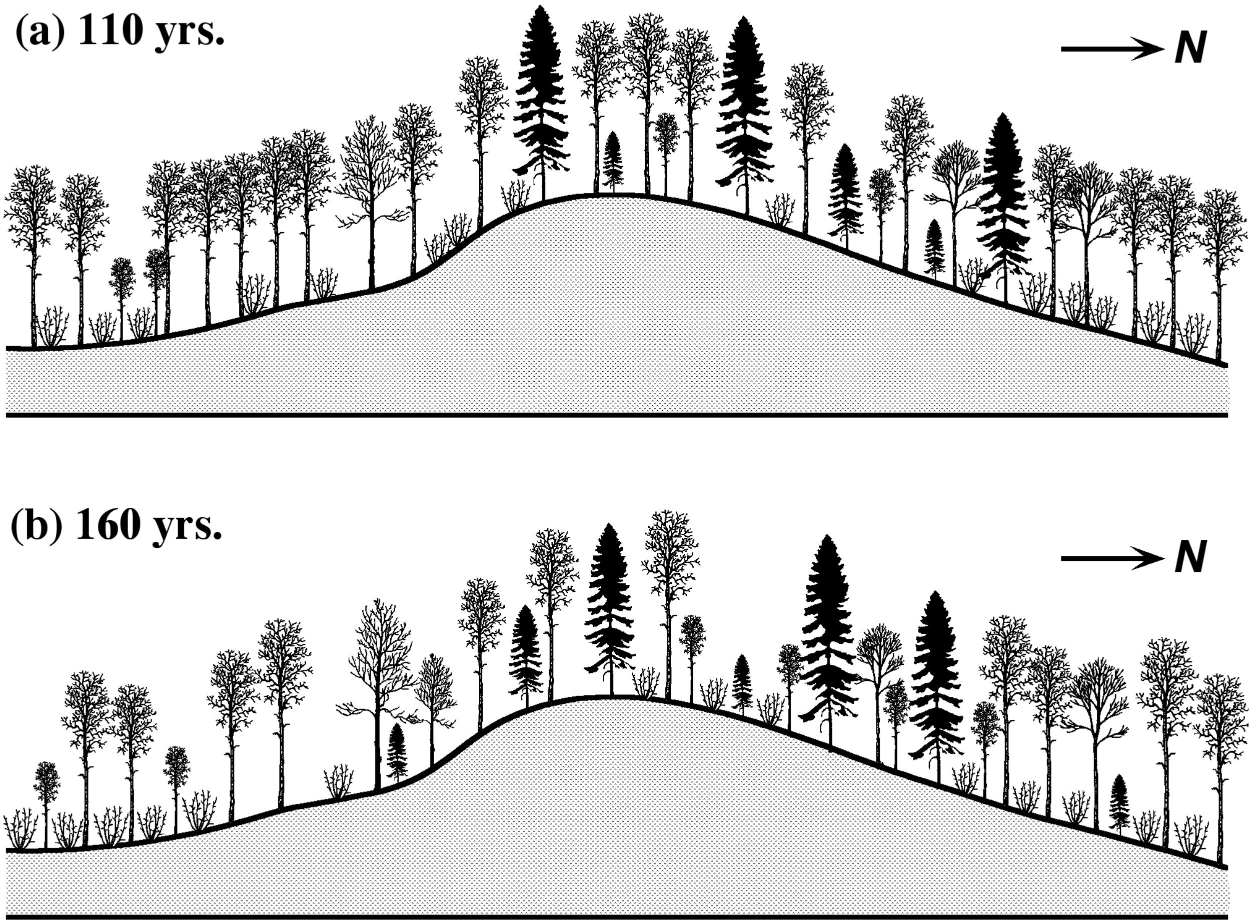



Figure 2. Synoptic physiognomic profile of (a) extant trembling aspen stands, age 110; (b) projected structure and composition of stands at age 160.

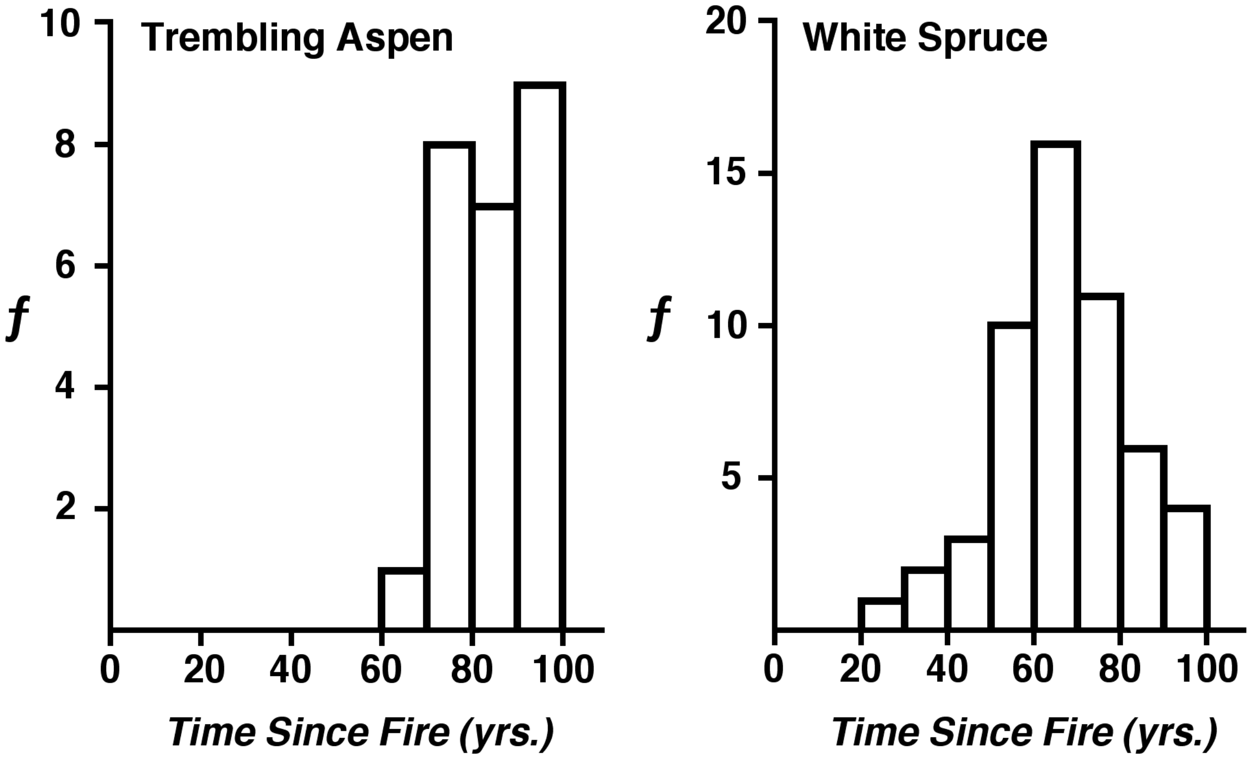
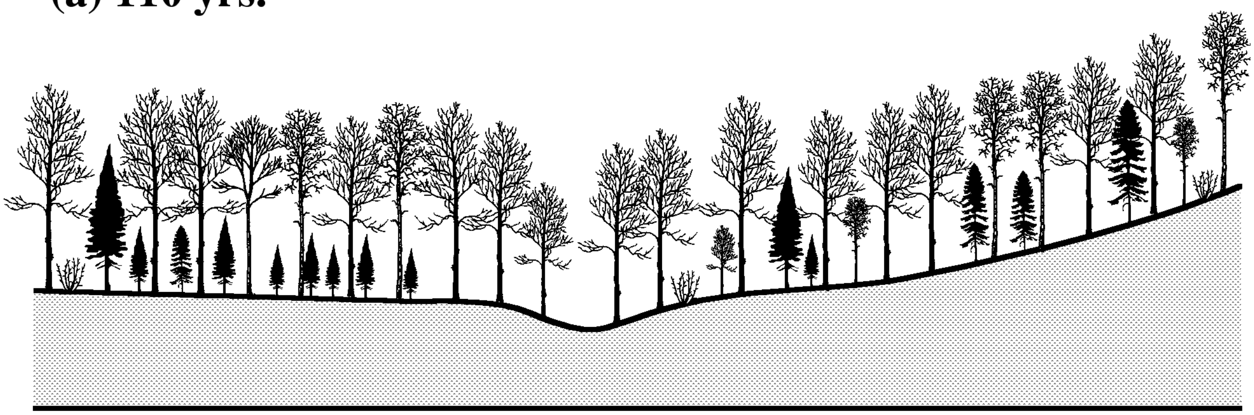



Figure 3. Age distribution of a random sample of trees in the advance regeneration layer of trembling aspen stands. Advance regeneration: trembling aspen, 4-10 m in height; conifers, 2-10 m in height.

## *Balsam Poplar*

**(a) 110 yrs.**



**(b) 160 yrs.**

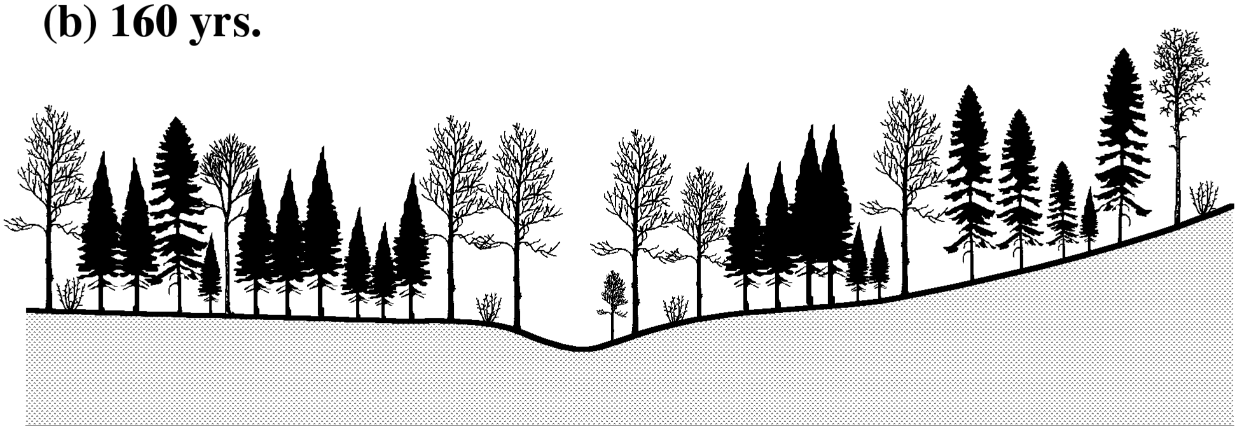


Figure 4. Synoptic physiognomic profile of (a) extant balsam poplar stands, age 110; (b) projected structure and composition of stands at age 160.

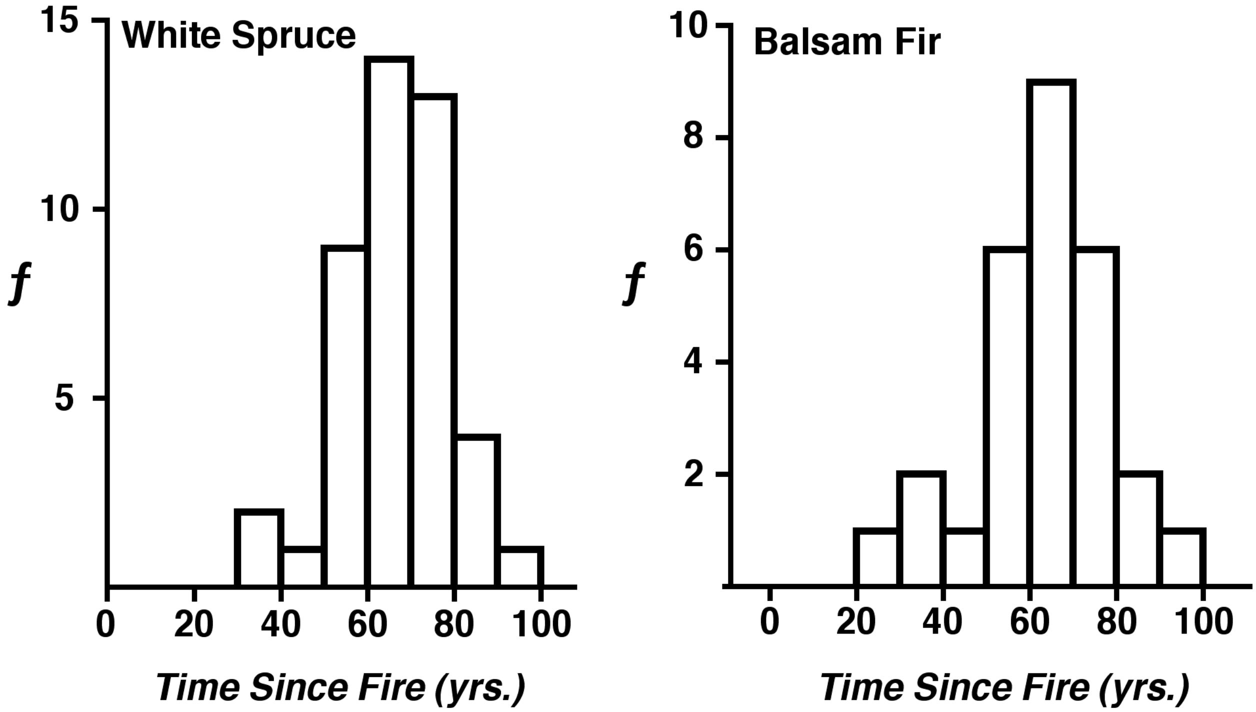



Figure 5. Age distribution of a random sample of trees in the advance regeneration layer of balsam poplar stands. Advance regeneration: conifers, 2-10 m in height.

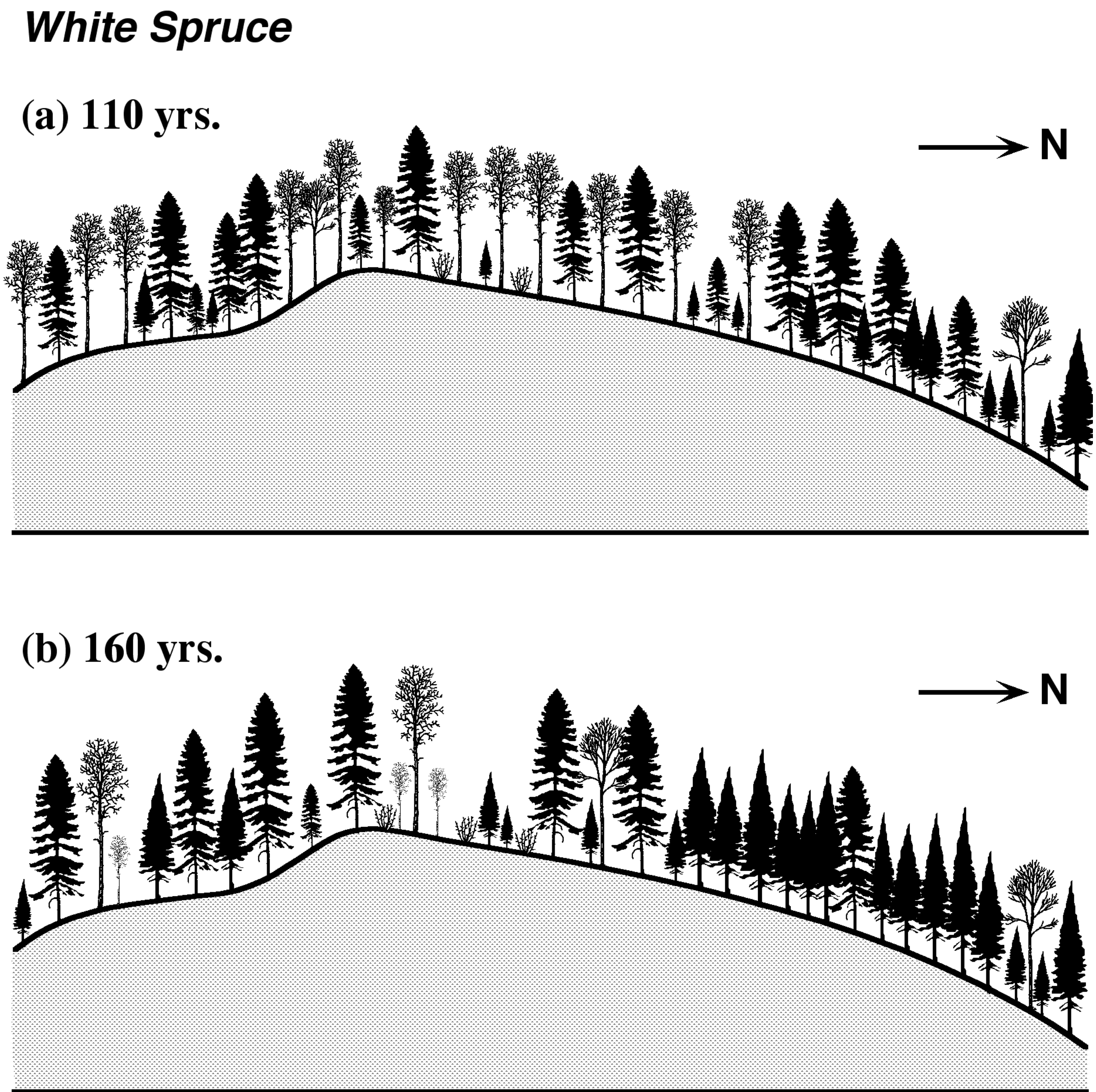



Figure 6. Synoptic physiognomic profile of (a) extant white spruce stands, age 110; (b) projected structure and composition of stands at age 160.

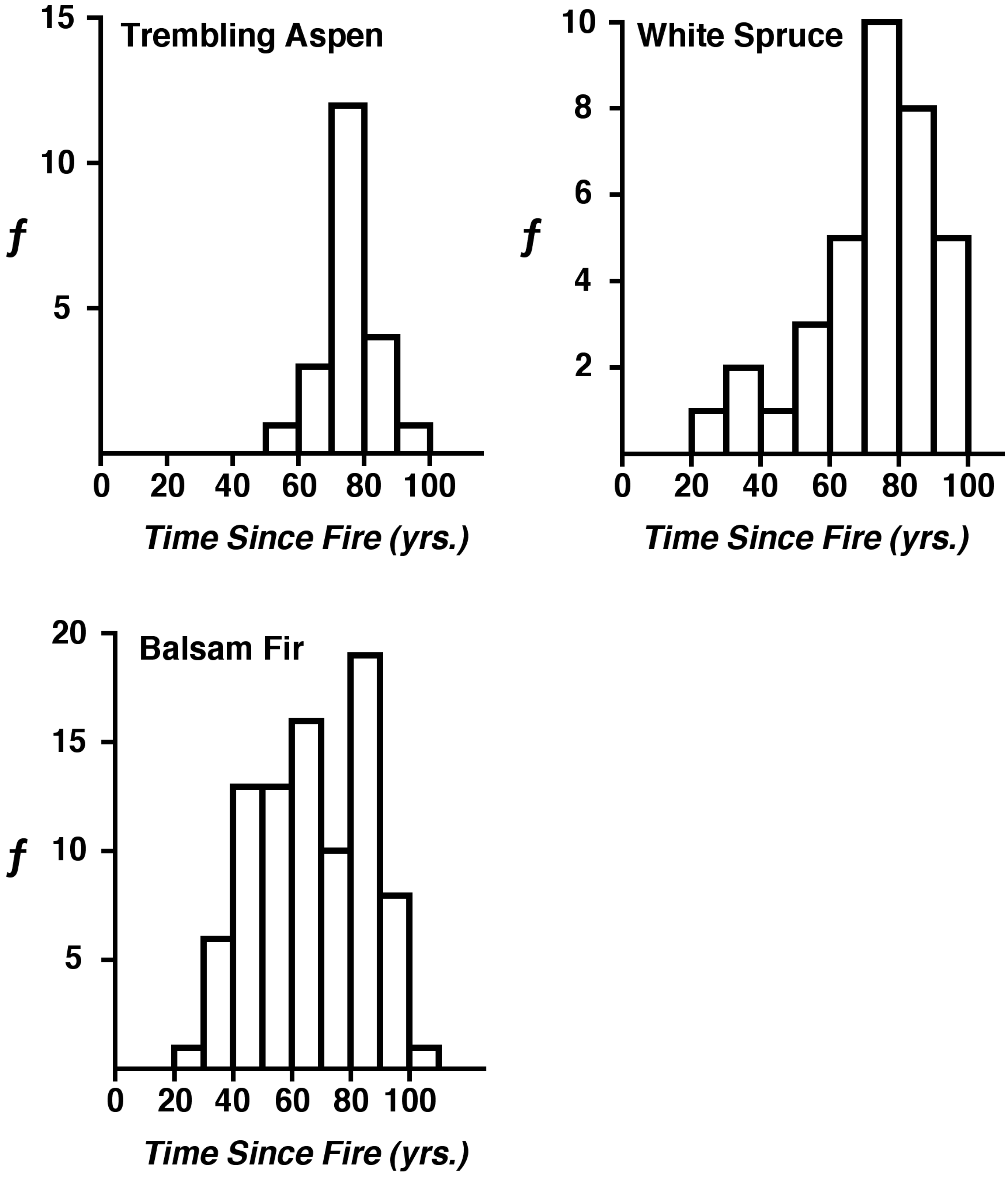



Figure 7. Age distribution of a random sample of trees in the advance regeneration layer of white spruce stands. Advance regeneration: trembling aspen, 4-10 m in height; conifers, 2-10 m in height.

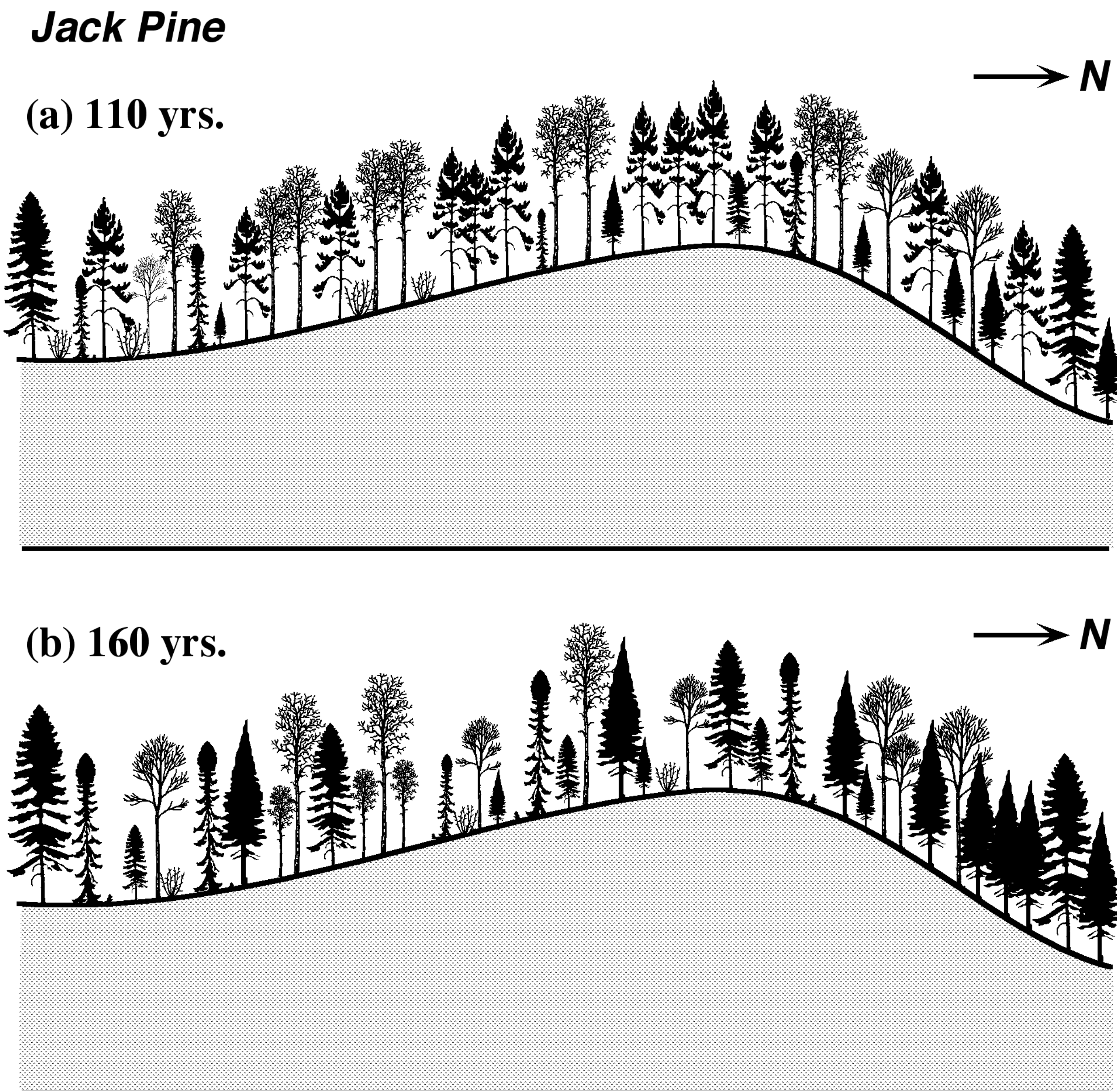



Figure 8. Synoptic physiognomic profile of (a) extant jack pine stands, age 110; (b) projected structure and composition of stands at age 160.

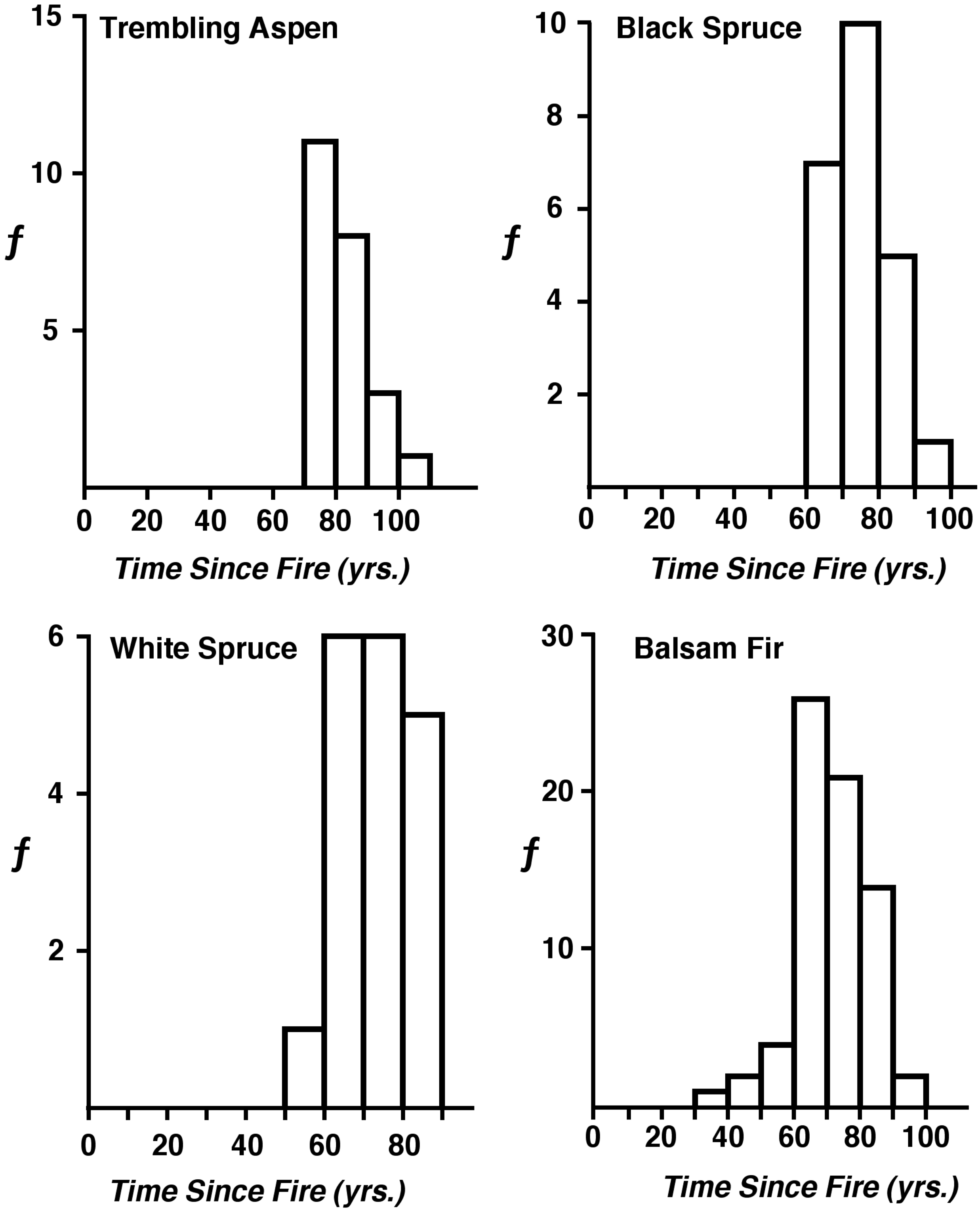
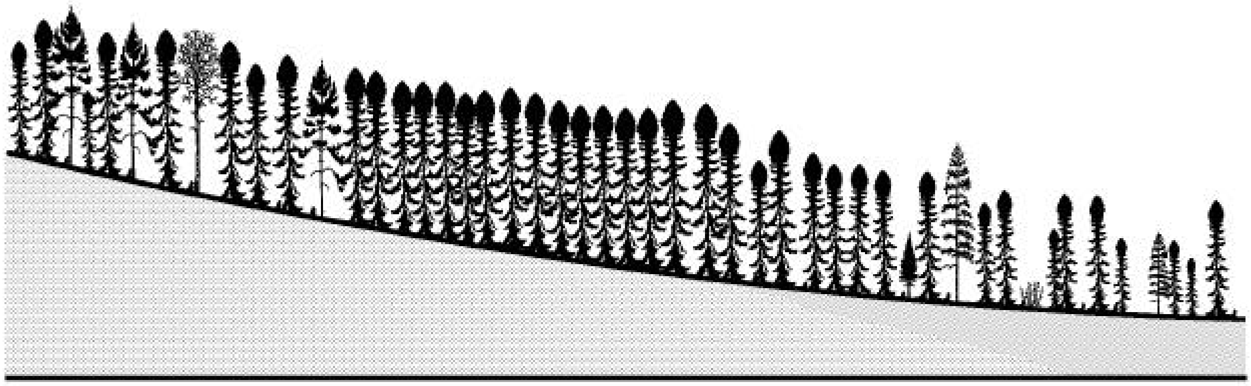



Figure 9. Age distribution of a random sample of trees in the advance regeneration layer of jack pine stands. Advance regeneration: trembling aspen, 4-10 m in height; conifers, 2-10 m in height.

## Black Spruce

**(a) 110 yrs.**



**(b) 160 yrs.**

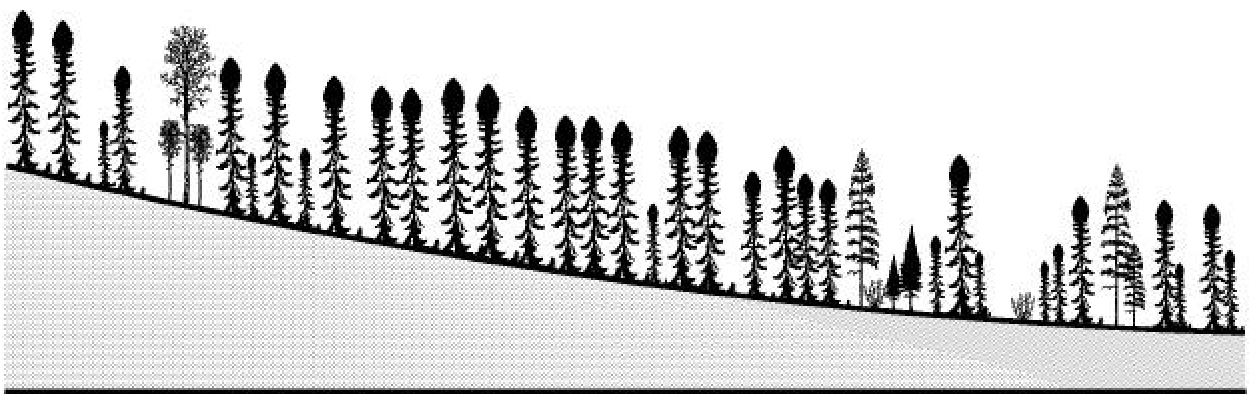


Figure 10. Synoptic physiognomic profile of (a) extant black spruce stands, age 110; (b) projected structure and composition of stands at age 160.

In the first sub-type, white spruce has not established contemporaneously and other softwood species (black spruce, jack pine, balsam fir) are not present. Distance to coniferous seed source is generally moderate to high. These stands are characterized by moderate to high tall shrub cover. Three variants are recognized:

1. Well-drained stands with a southern exposure: the understory is typical 'aspen parkland', with grassland species and low shrubs such as rose and snowberry.
2. Moderately well-drained stands with eastern or western exposure: the dominant shrub is beaked hazelnut, which often forms a continuous subcanopy.
3. Moderately well-drained stands on the northern slopes of the Duck Mountains: these are rich stands containing tall shrubs such as mountain maple and green alder.

In these hardwood dominated stands, secondary suckering of aspen and balsam poplar, and seeding and resprouting of white birch, tend to perpetuate a deciduous forest canopy. Tall shrub cover and deciduous leaf litter appear to limit the establishment of softwood species in these stands. White spruce may slowly invade, establishing on well-decomposed logs. Conifer advance regeneration is generally limited, however, and regenerating trees are often stunted and slow-growing. In older stands, mature aspen trees may be blown over, resulting in a second flush of sucker shoots that perpetuates the stand (Fig. 3). In some stands, ungulate herbivores may do significant damage to aspen suckers, favouring white spruce growth. Stands near water courses may be subject to beaver activity, resulting in removal of the aspen canopy and thus favouring white spruce recruitment and growth.

Contemporaneous establishment of white spruce may occur in some stands, particularly in moderately well-drained sites with southern, eastern or western exposures. The dominant shrubs in such stands are rose, snowberry and beaked hazelnut. White spruce may also occurs with trembling aspen on northern exposures, where green alder or mountain maple dominate the shrub canopy. These contemporaneously established trees provide a ready seed source for white spruce advance regeneration. White spruce typically occurs in the advance regeneration layer at low density, however, and trees are generally suppressed and slow-growing due to strong competition for light from the forest canopy, tall shrub layer, and understory. White spruce germinates on well-rotted logs in bouts of episodic recruitment, peaking at 50-70 years following stand establishment (Fig. 3). This corresponds to an increase in seedbed availability as trembling aspen undergoes self-thinning and boles fall to the ground.

Over the next 50 years, most of these stands will continue to be hardwood-dominated, although white spruce will slowly increase in abundance in some areas. Older trembling aspen stands on well-drained substrates may progress to open 'white spruce aspen parkland' characterized by an open, discontinuous canopy of tall white spruce, with some trembling aspen, balsam poplar and white birch derived from secondary suckering. Tall shrub cover is very high in such stands, impeding the advance regeneration layer.

***Balsam Poplar***

Like trembling aspen, these stands are currently dominated by hardwoods (Fig. 4). In general, softwood species do not establish contemporaneously. Balsam poplar typically occurs in moderately drained low-lying areas, and on nutrient-rich seepage slopes. Some groundwater flow is critical: balsam poplar cannot tolerate oligotrophic, poorly drained anoxic substrates (black spruce occupies such sites instead). Two sub-types are recognized: (a) Moderately drained sites: balsam poplar and trembling aspen are codominant in these stands, and white birch may also be present. These stands often occur in small 'bowls' on the landscape where the water table is closer to the surface, and snowmelt accumulates in the spring. Tall shrub cover is generally low to moderate, and declines as soil moisture levels increase; (b) Seepage slopes, floodplains and wet depressions: balsam poplar dominates such sites. Trembling aspen and white birch, when present, occur at low abundance. These stands are generally flooded for many weeks in the spring. Tall shrub cover is generally low.

Softwood species, particularly white spruce and balsam fir, invade into most of these stands. Conifer recruitment peaks at 60 to 70 years following stand establishment (Fig. 5), which corresponds to increased seedbed availability (rotting logs) resulting from self-thinning of the initial hardwood cohort. White spruce and balsam fir are the chief invaders of moderately drained stands, while balsam fir is increasingly favoured in sites where drainage is somewhat impeded. River floodplains are not invaded by conifers, however.

These stands will become increasingly dominated by softwoods in the next 50 years (Fig. 4). Trembling aspen will decline in abundance as a result of strong light competition from a canopy increasingly dominated by conifers, as well as ungulate herbivory of sucker shoots and beaver activity. Balsam poplar will also decline in abundance, but is expected to persist since the sucker shoots are not favoured by herbivores. Later-successional balsam poplar stands are therefore expected to be increasingly dominated by white spruce and/or balsam fir, but balsam poplar and white birch are expected to persist in many stands. Increased softwood abundance is favoured in moderately well-drained sites, but balsam poplar will persist on floodplains and in wet depressions.

***White Spruce***

Fire-initiated stands are very rarely dominated by white spruce; instead, trembling aspen and white spruce are codominant in virtually all stands. White birch and balsam poplar may also be present at stand establishment, but generally occur at low abundance. Very rarely, balsam fir may establish contemporaneously as well. These stands are most commonly encountered in the central highlands of the Duck Mountains, particularly in areas where wetlands, lakes and complex topographic features prevent fires from sweeping unimpeded across the landscape. Fire-initiated mixed trembling aspen – white spruce stands are most frequently encountered near lakeshores and wetlands where burns are less frequent and severe. At age 110, the canopy of these stands is dominated by white spruce and trembling aspen, with lesser amounts of white birch and balsam fir (Fig. 6). A dense subcanopy of balsam fir develops in many of these stands.

Balsam fir rarely establishes contemporaneously; instead, balsam fir recruitment peaks at 50 to 80 years following stand establishment (Fig. 7). The timing and intensity of balsam fir recruitment appears to be a function of seed availability, although microsite conditions and seedbed quality are likely also important. Balsam fir may form a very dense subcanopy beneath a mature white spruce - trembling aspen canopy, resulting in a 'thicket' that casts a deep shade and is virtually impenetrable to ungulate herbivores. This dense subcanopy prevents the development of a second cohort of aspen suckers, and impedes white spruce recruitment. In areas adjacent to wetlands, beaver may actively remove mature trembling aspen trees and thus hasten the conversion to conifer dominance. Older stands are increasingly dominated by balsam fir, and trembling aspen is extirpated from these stands after 120-150 years. White spruce and white birch can persist in the canopy for over 200 years. The deep shade cast by dense balsam fir advance regeneration often prevents white spruce and white birch from regenerating in these stands. The late-successional stage is therefore characterized by a balsam fir canopy with a 'super-canopy' of very old white spruce and white birch. Club-mosses and feathermosses dominate the understory.

In drier sites, and in areas lacking a proximate balsam fir seed source, white spruce is more commonly encountered in the advance regeneration layer. White spruce recruitment peaks at about 70-80 years following stand establishment (Fig. 7). Recruitment density of white spruce is generally low, however, resulting in secondary suckering of hardwoods (mostly trembling aspen) 70-80 years after stand establishment (Fig. 7). Older stands consist of a diverse multi-aged canopy that includes trembling aspen, white spruce, and white birch, with smaller amounts of black spruce and balsam poplar. These stands may also be colonized by balsam fir, but at lower density than occurs in moister sites.

Spruce budworm may attack mature and regenerating balsam fir, resulting in a cyclical succession of shrub-dominated gaps that are repeatedly invaded by balsam fir. Other tree species such trembling aspen, white spruce, balsam poplar and white birch may also colonize such canopy gaps. While spruce budworm has been recorded in the Duck Mountains, it appears to have done relatively little damage in the past century. If balsam fir abundance increases in the Duck Mountains, spruce budworm could prove to be a more serious pest.

***Jack Pine***

Unlike much of the boreal forests of eastern Manitoba, northwestern Ontario and central Saskatchewan, jack pine rarely forms extensive pure post-fire stands in the Duck Mountains (Fig. 8). Reasons for this include: (a) predominance of loamy to clay tills, and the comparative absence of sandy substrates except along ancient beach ridges and outwash plains; (b) strong topographic variability over relatively small spatial scales; (c) water table relatively near the surface. As a result, pure post-fire jack pine stands only occur locally on sandy, excessively drained hilltops, outwash plains and ancient beach ridges. Two sub-types are recognized: (a) Well-drained sands to sandy loams: jack pine dominates these stands, but trembling aspen, white birch and black spruce are generally also present. These stands are fairly localized in distribution

on the landscape. In very well-drained sites, jack pine may form a ‘
type, but such stands are very localized in distribution; (b) Moderately well-drained sandy to clay loams: these stands are codominated by jack pine and trembling aspen at stand establishment. Black spruce, white spruce and/or white birch may also be present at low abundance. Such stands are commonly encountered in the central and north-central highlands of the Duck Mountains, typically on well-drained sites of low nutrient status and with limited organic matter accumulation. The understory is dominated by herbs; tall shrubs are generally uncommon.

Stand dynamics is highly variable, and appears to be strongly dependent on seed source availability, topography, and edaphic factors. White spruce, white birch and balsam fir may recruit into these stands after about 60 years, following extensive self-thinning of jack pine (Fig. 9). Seedlings generally establish on rotting logs of jack pine and trembling aspen. Jack pine is largely removed from the canopy after 100-120 years, and trembling aspen shortly thereafter. However, trembling aspen often produces a second cohort of suckers 70-80 years after stand establishment (Fig. 9), and can successfully colonize canopy gaps created by natural tree mortality and windthrow. Late successional stands generally consist of an uneven-aged diverse mixture of black spruce, white spruce, balsam fir, white birch, and trembling aspen (Fig. 8). Under favourable conditions (e.g. moderately drained sandy loams on north facing slopes), and along water courses where beavers actively remove trembling aspen, dense balsam fir recruitment may occur. Balsam fir dominates these stands at the late-successional stage, but lesser amounts of white birch, white spruce and black spruce are generally also present.

***Black Spruce***

Dense fire-initiated stands of black spruce are found in poorly-drained lowlands of low to moderate nutrient status. Such sites are characterized by impeded groundwater flow, creating somewhat anoxic edaphic conditions. Two sub-types are recognized: (a) Mineral substrates: these stands generally occur on flat, poorly drained lowlands. Black spruce is the dominant species, but jack pine and occasionally trembling aspen may establish contemporaneously. These stands often establish at very high density, but jack pine and trembling aspen thin much more rapidly and are only a minor component by 110 years (Fig. 10). Feathermosses dominate the understory; (b) Organic substrates: these stands occur on a layer of organic peat that is often >1 m in depth. Such stands are characterized by a perched water table. Black spruce is the dominant post-fire species, but tamarack occurs at low abundance in richer fens. Jack pine may also occur immediately following a fire, but is generally extirpated by age 50. The understory is dominated by feathermosses, sphagnum mosses, and ericaceous shrubs. Black spruce density is rarely as high as on mineral substrates. As a result, the lower branches are retained and form ‘layers’ in the organic peat substrate that perpetuate the species. Advance recruitment of tamarack and occasionally balsam fir may occur in older stands. Balsam fir trees grow very slowly on organic peat, however, and retain their root system very close to the surface (above the water table).

Black spruce forms an edaphic climax in these sites, with tamarack as a minor secondary component (Fig. 10). In drier stands, secondary suckering by trembling aspen may perpetuate small groves of the species.

## MANAGEMENT APPLICATIONS

A common theme of boreal ecosystem research is forecasting the future composition, structure, function, diversity and dynamics of forest stands and landscapes (e.g. Bergeron and Dansereau 1993). Boreal forest ecosystems in central and western North America have evolved under a disturbance regime overwhelmingly dominated by recurrent, large-scale catastrophic fires. However, during the 20$^{th}$ century many of these forests underwent a paradigm shift in disturbance regime: large-scale catastrophic fires were suppressed, while smaller-scale disturbances related to timber harvesting were imposed. This fundamental shift in disturbance intensity, severity and spatial extent is expected to affect the composition, structure and successional pathways of boreal stands. In turn, these effects are expected to 'cascade' through the ecosystem, with largely unknown consequences on biodiversity, pest and pathogen outbreaks, landscape structure and complexity, stand regeneration dynamics, soil development and nutrient cycling, and hydrological and geomorphological processes. Given these recent changes in the disturbance paradigm, it is imperative that boreal forest researchers focus their efforts on obtaining knowledge that will aid in the development of models to predict the structure, composition and functioning of future boreal forests.

The objective of our study was to obtain information on the structure and dynamics of the Duck Mountain boreal forests. With such information, tools and protocols for the forecasting, monitoring, and sustainable management of the boreal forests of west-central Manitoba can be developed. It is increasingly recognized that a critical aspect of sustainable forest management is the emulation of natural disturbance processes. Our results offer some valuable insights into the natural forest fire regime of the Duck Mountains:

1. Much of the study area was burned in 1885, suggesting that recurrent catastrophic wildfires may be characteristic of the region.

2. The presence of jack pine in the Duck Mountains suggests that recurrent wildfires probably occurred at least every 150 years, since otherwise jack pine would have been extirpated from the area.

3. Balsam fir is relatively common in the Duck Mountains, particularly when compared to the boreal forests of central Saskatchewan, eastern Manitoba, and north-western Ontario. Balsam fir is not well adapted to fire, suggesting that the historical frequency, severity and/or spatial extent of catastrophic fires is lower in the Duck Mountains compared to much of central and western Canada.

What emerges is a complex fire history for the region. Some areas of the Duck Mountains apparently burned rather infrequently, as evidenced by the abundance of white spruce and balsam fir in many regions of the central uplands. These sites tend to occur in areas of complex topographic relief interspersed with lakes and wetlands. In such areas, fires were prevented from sweeping unimpeded across the landscape. By contrast, the topographically less complex northern region of the Duck Mountains has abundant jack pine and black spruce, suggesting more regular and recurrent fires. Similarly, the slopes of the Duck Mountain Escarpment are dominated by relatively young stands of trembling aspen, indicating that fires regularly swept into these forest stands from the adjacent plains and parkland. Based on this information, it can be inferred that the Duck Mountains forests historically consisted of various forest stand types at different successional stages. This state of affairs helped maintain high structural and compositional diversity, thus promoting habitat diversity and maintaining diverse wildlife populations. Sustainable management of the Duck Mountain forests must recognize this natural state of affairs and attempt to emulate it. Since burning (natural or otherwise) is clearly no longer an option, other strategies must be found to maintain a sustainable mixture of younger and older forest stands. Sustainable forest harvesting has been practiced in the region for over 100 years, and has undoubtedly helped to promote and maintain structural and compositional diversity in the Duck Mountain forests. Forest harvesting must be sensitive to both stand composition and landscape configuration. Stands that have been subjected to regular fires may be harvested sustainably, since they are well adapted to a recurrent disturbance paradigm. Conversely, areas that have traditionally burned less frequently and/or severely should be harvested with great caution, if at all. These include areas protected from severe wildfires such as islands, wetlands, lakeshores, and steep valleys and slopes. Detailed information on stand composition and structure, together with landform and spatial configuration, must be available to make informed decisions regarding the emulation of natural disturbance. Some forest stands, in some locations, should probably not be disturbed by human activities.

Different stand types must also be managed differently. In hardwood stands, clear-cut logging appears to emulate natural disturbance processes quite well, since trembling aspen, balsam poplar and white birch successfully sucker back immediately following both fire and logging. Clear-cut harvesting of jack pine and black spruce is more problematic, since the seed source is largely removed and mineral soil is not exposed (mineral substrates are required for early seed germination and establishment). Selective harvesting of mature white spruce is quite sustainable, and has in fact been practiced in the area for over 100 years. The key to this harvesting strategy is to take only the largest trees, leaving the advance regeneration intact in order to fill the canopy gaps that result from felling the oldest trees.

## Sustainable Forest Management by Stand Type

### *Trembling Aspen*

Our results indicate that upland aspen stands may be slowly invaded by white spruce, but that aspen will naturally regenerate from secondary suckers and so maintain itself. However, older stands (> 120 years) may degenerate into unproductive open 'parkland' or shrubland with discontinuous canopies. Wildfire undoubtedly played an important role in perpetuating this stand type, but edaphic and geomorphic processes are undoubtedly important as well. Specifically, trembling aspen is best adapted to warmer, drier south-facing slopes and more nutrient-rich north-facing slopes. Trembling aspen recovers quickly from wildfire by suckering, and responds in the same way to clear-cut logging. Logging therefore emulates natural fire disturbance quite well. Sustained efforts must be made to ensure that harvesting rotations are such that various age and size structures of aspen stands are maintained at the landscape level. Clear-cuts should be of relatively small spatial extent and well separated by buffers of natural uncut forest. Careful logging of trembling aspen stands, which involves leaving white spruce advance regeneration, is to be promoted as a method for maintaining high biodiversity. Spreading slash on site is recommended as a method for recycling nutrients and providing substrates for the recruitment of later-successional species such as white spruce and white birch.

***Balsam Poplar***

Our results suggest that balsam poplar stands are often succeeded by softwoods, particularly white spruce and balsam fir. In the absence of fire, many of these stands will become increasingly dominated by softwoods. The exception occurs in seasonally flooded areas where softwoods cannot colonize. Like trembling aspen, balsam poplar suckers from the root system following wildfire or clear-cut logging. Balsam poplar often occurs in mixture with trembling aspen in cutblocks, but it is not a favoured timber species.

***White Spruce***

White spruce often occurs in mixture with trembling aspen, particularly at early stages of succession. The largest white spruce trees have long been harvested from older stands. This appears to be a sustainable practice, provided that only the largest trees are taken and that efforts are made to protect the advance regeneration. Many of these stands are becoming increasingly dominated by balsam fir, and selective logging of white spruce or the cutting of trembling aspen in such areas could conceivably speed up this process. Increased balsam fir abundance may result in increased frequency and/or severity of spruce budworm outbreaks. Balsam fir saplings are a favoured winter forage for large ungulates such as moose and elk, and their presence may help sustain higher ungulate populations. Ungulate herbivory of balsam fir may prevent or greatly slow the succession toward balsam fir dominance in boreal mixed wood stands.

***Jack Pine***

Extensive monodominant stands of jack pine are rare in the Duck Mountains. Most post-fire stands contain both jack pine and trembling aspen, with high density phases of jack pine alternating with dense groves of trembling aspen at a relatively fine spatial scale. Black spruce, white spruce and white birch are often present at low abundance at stand initiation, and become increasingly important canopy components as jack pine and trembling aspen undergo self-thinning. In the absence of fire, jack pine is removed from the canopy by age 120 to 150 (the large 1961 fire has undoubtedly helped perpetuate jack pine in the Duck Mountains). By age 100, these stands consist of an uneven-aged mixture of many species, making them less desirable for logging. The harvesting of larger patches of trembling aspen in this complex canopy matrix could help perpetuate the hardwood component and thereby promote stand-level biodiversity. Selective logging of white spruce is also sustainable in these stands, as this opens the canopy (emulating a windthrow) and thus promotes recruitment from the advance regeneration layer. Active fire suppression in the Duck Mountains will result in a decline in jack pine abundance over time. Perpetuation of jack pine would require clear-cut logging followed by planting of jack pine seedlings and suppression of other species (e.g. trembling aspen suckering), which is a very expensive proposition.

***Black Spruce***

Black spruce is a comparatively long-lived, slow-growing species that generally establishes at very high density in moist, poorly drained lowlands on mineral and organic peat substrates. Few other tree species can survive these nutrient-impoverished, anoxic and water-logged substrates. Layering will perpetuate black spruce stands occurring on organic substrates. There is currently little if any advance regeneration in black spruce stands on mineral substrates. Such stands are very dense and thin very slowly, resulting in a deeply shaded understory and poor seedbed conditions (a combination of a thick feathermoss layer, cold soils, few rotting logs). Dense upland black spruce stands often fringe open wetlands, forming a natural buffer to the boreal mixedwood stands further upslope. These fringe forests may be the result of past activity by beaver, which consolidated the abundance of black spruce by felling trembling aspen trees adjacent to wetlands. Clear-cut harvesting of upland black spruce, if undertaken, should be followed by planting and the suppression of herbaceous vegetation and tall shrubs. Clear-uctting of black spruce growing on organic substrates should undertaken in winter to ensure minimal damage to established layers.

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