

Population structure and growth acclimation of mountain maple along a successional gradient in the southern boreal forest¹

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Abstract: A range of stands was sampled in the southern boreal forest of eastern Canada to determine the impact of forest development stages and light availability on the dynamics of an abundant understory shrub: mountain maple (*Acer spicatum*). Mountain maple was studied at both the population and individual stem levels. At the population level, a total of 190 1-m² quadrats were sampled in five forest types representing a successional gradient (young aspen, mature aspen, mixedwood, shade-tolerant conifer, and old spruce budworm-affected conifer forests). At the individual stem level, a total of 100 stems of different sizes were harvested in a sub-sample of the quadrats. Mountain maple stem biomass, density, and population structure were found to be affected by forest composition, the coniferous forest being the least favourable. At the individual stem level, light availability and stem size were found to have an important impact on stem morphology and growth, suggesting a high level of plasticity in relation to canopy opening. From these results, four developmental phases of mountain maple population dynamics were identified: 1) following a drastic disturbance, a first phase of rapid growth, and potentially intense competition with aspen suckers, when present, takes place; 2) following the development of a closed aspen canopy, the overall density, biomass, and presence of mountain maple in the understory increase; 3) following recruitment of conifer trees into the overstory canopy, mountain maple enters a suppression phase associated with a decrease in light; and 4) following the occurrence of small scale disturbances, mountain maple quickly responds to rapidly dominate the openings, which further ensures its maintenance in the understory.

Keywords: *Acer spicatum*, boreal forest, light growth requirement, morphological and growth plasticity, population dynamics, spruce budworm-caused gaps.

Résumé : Plusieurs types de peuplements ont été échantillonnés dans la forêt boréale méridionale de l'est du Canada en vue d'évaluer l'impact du stade de développement forestier et de la disponibilité en lumière sur la dynamique de l'érable à épis (*Acer spicatum*). L'étude de cet arbuste abondant en sous-bois a été menée à l'échelle de la population et à celle de l'individu. Un total de 190 quadrats d'un mètre carré a été échantillonné dans cinq types de forêts suivant un gradient successional : jeune peupleraie, peupleraie mature, forêt mixte, forêt de conifères tolérants à l'ombre et forêt coniférienne affectée par la tordeuse des bourgeons de l'épinette. Dans un sous-échantillon de quadrats, 100 tiges de tailles différentes ont été récoltées. Il a été déterminé que le stade de développement forestier affecte la structure de la population, la biomasse et la densité des tiges de l'érable à épis, les forêts conifériennes étant les moins favorables. Au niveau de l'individu, la taille des tiges et la disponibilité en lumière avaient un impact majeur sur la morphologie et la croissance des tiges, suggérant une plasticité élevée par rapport à l'ouverture de la canopée. À partir de ces résultats, nous avons défini quatre phases dans le développement des populations d'érable à épis : *i*) une première phase de croissance rapide se produit à la suite d'une perturbation à grande échelle et une compétition intense avec les rejets de peuplier peut aussi avoir lieu lorsqu'ils sont présents; *ii*) lors de la fermeture de la voûte forestière, la densité, la biomasse et la présence de l'érable à épis augmentent en sous-bois; *iii*) une phase lente de suppression survient au moment de l'augmentation du couvert coniférien et de la diminution de la disponibilité en lumière qui en découle; *iv*) enfin, une réponse rapide et un fort développement de l'érable à épis se produisent à la suite de petites ouvertures créées dans la voûte forestière, assurant ainsi sa persistance dans le sous-bois.

Mots-clés : *Acer spicatum*, besoins en lumière pour la croissance, forêt boréale, plasticité de la morphologie et de la croissance, dynamique de population, ouvertures créées par la tordeuse des bourgeons de l'épinette.

Nomenclature: Gleason & Cronquist, 1991; Marie-Victorin, 1995.

Introduction

As with many temperate forests, some areas in the southern boreal forest have a very diverse and abundant understory herb and shrub cover (De Grandpré, Gagnon & Bergeron, 1993). From an ecological point of view, this understory vegetation contributes greatly to the composi-

tional, structural, and functional diversity of these forests. However, from a forest management point of view, this vegetation is often perceived as competition for the normal growth and development of commercial tree species. With an increasing desire for sustainable forest management, we need to ensure good tree growth while maintaining understory composition and structure.

One of the most important deciduous understory shrubs in eastern Canada and the northeastern United States is

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mountain maple, *Acer spicatum* (Farrar, 1996). It grows well in a large range of habitats and persists through all stages of forest development (Post, 1965; Vincent, 1965; De Grandpré, Gagnon & Bergeron, 1993). Mountain maple generally develops as a single dominant stem that produces basal suckers with age or when damaged (Jobidon, 1995). Following disturbance, mountain maple often forms a dense sub-canopy that greatly reduces understory light availability (Aubin, Beaudet & Messier, 2000). Mountain maple is therefore generally regarded as a species that impedes tree seedling establishment, growth, and development after disturbance (Post, 1965; Vincent, 1965; Batzer & Popp, 1985; Jobidon, 1995).

A key to understanding the competitive success of mountain maple may be related to its plasticity at the stem level. For example, Post (1967) observed that mountain maple can acclimate to a large variety of light conditions. Lei and Lechowicz (1990) also classified mountain maple as a shade-adapted species that shows a rapid response to very small openings. Although, these authors do not provide direct measurements of the morphological changes in mountain maple crown architecture, their observations do suggest a high level of phenotypic plasticity. Such plasticity has also been observed in other understory shrubs (Messier, 1992; Luken *et al.*, 1995; Ricard & Messier, 1996). We hypothesize that mountain maple's phenotypic plasticity allows it to respond to different canopy disturbances and to tolerate the changing light environments associated with the forest development stages that follow major disturbances (Whitney, 1976; Silander, 1985).

In addition to an absence of information on mountain maple growth acclimation at the individual level, there is little information on population-level responses to different disturbances or stand development stages. In the southern boreal forest, various stand compositions in combination with openings of the canopy caused by insect outbreaks and tree senescence create a diversity of understory environments. Canopy openings are reported to stimulate mountain maple growth and abundance (Post, 1970; Batzer & Popp, 1985; Jobidon, 1995). However, their impacts may vary according to forest development stage (Oliver & Larson, 1990; Kneeshaw, 2001). For example, light availability and patch structure are greatest in very early and very late successional stages (Park *et al.*, 2005).

To understand the development of mountain maple populations in various environments, we conducted this study at two levels: individual stem growth and morphology, and population dynamics. The objectives of this study were to 1) evaluate the growth and morphological plasticity of individual mountain maple stems and 2) document mountain maple population structure and dynamics in relation to stand development. This information will permit a better understanding of the response of this competitive shrub species to various forest conditions.

Methods

STUDY AREA

The study was undertaken in 1995 and 1996 in the southern part of the boreal forest of Québec in and around the Lake Duparquet Experimental Research and Teaching Forest (Abitibi, Québec; 48° 30' N; 79° 27' W). The region is

part of the Québec-Ontario clay belt left by large post-glacial lakes formed during the last retreat of the ice sheets (Vincent & Hardy, 1977). The area experiences a cold and continental climate characterized by an average annual temperature of 0.8 °C, an annual precipitation of 856 mm, and a 64-d frost-free period (Anonymous, 1993).

The research forest is composed of a mosaic of mostly unmanaged stands recruited following fires and insect outbreaks. Forest composition has been related to time since last stand-destroying fire, which varies in this area from 34 to 281 y (Dansereau & Bergeron, 1993). Paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and jack pine (*Pinus banksiana*) dominate the forest after fire (Bergeron & Dubuc, 1989). Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and white cedar (*Thuja occidentalis*) progressively become more dominant as stands age (Bergeron & Dubuc, 1989). The most recent spruce budworm (*Choristoneura fumiferana*) outbreak occurred from 1972 to 1987 (Morin, Laprise & Bergeron, 1993), with a peak between 1977 and 1981, killing most of the mature balsam fir (Bergeron *et al.*, 1995). Thus, spruce budworm gaps of various sizes are frequent in mixed and coniferous forests (Kneeshaw & Bergeron, 1998). Forest harvesting was negligible in the region before 1978.

SAMPLING

PLOT LOCATION

A total of 19 plots (radius = 15 m) were studied. These plots were located in five post-fire stand development stages (Table I) (post-fire aspen, mature aspen, mixedwood forest, intact conifer dominated forest, and spruce budworm-affected forest) that have been previously described for the area by Bergeron (2000). Sample plots were located in distinct stands more than 1 km apart to minimize spatial autocorrelation. All stands are located on modal, mesic, clay soils (grey luvisols) with a drainage class of 3-4 (moderate to good) (Anonymous, 1992). The stands were chosen to cover a broad range of understory forest conditions. Plots were located in areas with uniform tree structure, composition, and age in each of the stand types. Three plots were located in pure young aspen stands, four in pure mature aspen, four in mixed broadleaf-coniferous stands (between 25-75% aspen and paper birch, with the rest being white spruce and balsam fir), and the remaining eight in old-growth stands composed of shade-tolerant conifers (white cedar, white spruce, and balsam fir). We separated the old-growth coniferous stands into those with an intact forest canopy (four plots) and those that were affected by the most recent spruce budworm outbreak (four plots). An unbalanced sampling design was used due to plot availability. For the individual stem response part of the study we also evaluated the response of individuals across a light gradient from understory to open conditions.

Tree basal area and density (tree with DBH > 5 cm) were measured for each tree species within each plot. Mountain maple density and diameter distribution were sampled in ten 4-m² subplots systematically established in each of the 19 main plots. Subplots were placed every 5 m along two parallel transects that were 7 m apart. Mountain maple was sampled at both the population and the individual level.

TABLE I. Characteristics of sampled plots and mountain maple populations.

Forest type	Plot characteristics				Mountain maple characteristics		
	Tree basal area m ² ·ha ⁻¹ (% conifer/aspens) ^a	Tree density n·ha ⁻¹	Light ^b % PPFD	Biomass ^c kg·ha ⁻¹	Density number·ha ⁻¹	Maximum stem height cm	
Young aspen forests	* 38.0 (0/93)	2,006	11.0 (16.3)	1,959	14,500	345	
	29.0 (0/90)	1,847	14.8 (16.6)	2,069	12,750	345	
	38.6 (4/93)	1,636	8.0 (13.9)	5,006	29,750	550	
Mature aspen forests	* 34.6 (2/92)	948	12.5 (26.9)	6,437	39,000	505	
	57.6 (5/92)	1,529	11.0 (30.5)	4,211	36,000	510	
	37.4 (5/92)	1,943	11.4 (23.9)	4,205	55,750	495	
Mixed forests	* 38.3 (3/94)	622	21.2 (52.1)	2,117	27,000	360	
	54.1 (15/80)	1,528	14.3 (20.1)	477	14,000	235	
	56.2 (44/39)	1,051	18.8 (43.1)	336	11,750	365	
Intact conifer forests	* 31.0 (26/68)	1,560	14.3 (13.9)	7,307	30,250	565	
	36.1 (32/44)	1,321	17.6 (23.0)	3,801	14,500	425	
	38.2 (69/24)	594	10.2 (51.8)	544	15,750	325	
Budworm-affected conifer forests	* 38.9 (100/0)	1,274	19.8 (72.1)	1,191	10,000	355	
	40.9 (89/0)	904	8.6 (60.7)	2,426	19,250	400	
	41.1 (91/5)	692	12.2 (64.0)	2,491	5,750	487	
Budworm-affected conifer forests	* 17.6 (89/11)	707	41.7 (21.8)	1,560	2,000	285	
	27.9 (36/0)	212	37.9 (54.3)	15,859	30,750	595	
	3.7 (52/0)	255	59.5 (26.3)	9,257	11,000	520	
	* 14.5 (5/48)	311	45.0 (24.6)	9,781	29,250	660	

^a Percent basal area of shade-tolerant conifer and aspen are given in parentheses; trees are stems > 5 cm DBH.

^b Light above understory vegetation. C.V. (%) is given in parentheses; PPFD = photosynthetic photon flux density.

^c Total oven dry biomass estimated from equation [2], see Methods.

* Subsample used for stem scale analyses.

STEM LEVEL MEASUREMENTS

Precise measurements were made at the stem level to a) develop allometric relationships and b) address the first objective of the study, to evaluate the growth and morphological plasticity of mountain maple stems along a light gradient. A total of 100 stems of different sizes were systematically selected in a variety of understory environments within a sub-sample of seven plots chosen to represent all conditions found in the 19 sampled plots (Table I) as well as in three plots located in nearby 400-m² patch cuts. In each of these 10 plots, 10 stems were harvested from two subplots (subplots 3 and 8). Stems were chosen in an evenly distributed gradient over the range of stem basal diameters found in the subplots (4 to 68 mm). Care was taken to select stems without any obvious structural damage. When it was not possible to find 10 stems corresponding to these criteria in subplots 3 and 8, stems adjacent to the subplot were selected. For each of these stems we measured the basal diameter at 5 cm above the ground (to the nearest 1 mm) and the projected crown area (m²). The shape of each stem crown was projected vertically to the ground. This area was then subdivided into triangles and estimated using the equation for area of a triangle (length × height/2). We also evaluated age (by counting annual rings from a disk taken at 5 cm above the ground) and the above-ground biomass (using harvested stems). The biomass of each stem was divided into (a) leaves, (b) petioles, (c) new shoot growth, and (d) branches and stem. Dry mass of each part was determined after oven-drying at 70 °C for at least 48 h, except for stems, which were dried for 96 h. Finally we determined the total foliage area of each stem by calculating a leaf mass/leaf area ratio (Gartner, 1991). To calculate foliage area, foliage subsamples were taken. Twenty small discs of known area were

removed from the leaves of each stem. Each disc was taken from a different leaf selected at regular intervals from the top to the bottom of the stem. Foliage subsamples were used to calculate a specific area/mass ratio for each stem. The leaf area of each stem was calculated from the dry mass as:

$$A_i = M_i \cdot a_i / m_i \quad [1]$$

where A_i is the total leaf area (m²) of stem i , M_i is the leaf dry mass (g) of stem i , and a_i/m_i is the leaf area to leaf dry mass ratio (m²·g⁻¹) of stem i (obtained from its subsample of foliage discs).

MOUNTAIN MAPLE POPULATION ATTRIBUTES

Stem abundance (defined as individual stems > 7 cm in height) was quantified in each subplot (ten 4-m² subplots per plot). For each stem in each subplot, the basal diameter at 5 cm above the ground (to the nearest 1 mm) and the total length of the stem (to the nearest 1 cm) were recorded. Juvenile stems less than 7 cm in height were not considered as established, so they were not included in this measurement but were instead counted separately.

Individual stem biomass (2.2 to 6483.2 g) was estimated from basal diameter (4 to 68 mm) based on an allometric relationship developed from subsamples analyzed at the stem level. Equations were modified using a factor (1.034 for our study) developed by Sprugel (1983) to correct for a bias that is known to occur in log-transformed allometric equations.

$$\ln(\text{biomass}) = [2.717 \ln(\text{diameter}) - 2.733] * 1.034 \quad [2]$$

This relationship ($R^2 = 0.980$, $P < 0.001$, $n = 100$) was then used for all stems found in the 19 sampled plots. Total

biomass (g), basal area (m²), and density of the 10 subplots were calculated for each plot and are presented on a per hectare basis. Mean and maximum stem height (m) were also calculated for each plot. In each plot, we calculated the mean density of stems in each 5-mm basal diameter class. Stem frequency (%) (for individuals > 7 cm in height) was calculated as the proportion of subplots that contained at least one ramet or genet. Juvenile frequency (%) was calculated as the proportion of subplots that contained at least one juvenile.

LIGHT MEASUREMENTS

The percentage of above-canopy photosynthetic photon flux density (% PPF) was measured at the centre of each subplot above the understory vegetation (approximately 5 m). All light measurements were made under completely overcast sky conditions following the method proposed by Messier and Puttonen (1995) and validated by Gendron, Messier, and Comeau (1998). Photosynthetic photon flux density (PPFD, 400-700 nm) was measured using a point quantum sensor (LI-190, LI-COR, Lincoln, Nebraska, USA). A second point quantum sensor was installed in an open area close to each study site and was linked to a datalogger (LI-1000, LI-COR, Lincoln, Nebraska, USA) that recorded the above-canopy PPF. The percentage PPF was calculated as a ratio of the PPF obtained from measurements made in the understory and PPF recorded at the same time in the open area.

DATA ANALYSIS

STEM LEVEL RESPONSE

Leaf area density (LAD), specific leaf area (SLA), and leaf area ratio (LAR) were calculated for each stem ($n = 100$) based on the various biomass and leaf area components measured (equation [1]). Leaf area density (*i.e.*, the proportion of the crown area that is covered by leaf surface) provides an index of the light interception capacity of an individual plant, SLA provides a coarse index of the photosynthetic capacity of a sample of individual leaves of an individual, and LAR is a coarse indicator of photosynthesizing tissues to non-photosynthesizing tissues. A growth parameter, the relative annual shoot biomass production in 1995 (R_{shoot}), was also calculated. This ratio is an index of annual growth and was calculated as the mass of the shoot extension from a given year divided by the age of the ramet. Table II describes these parameters. Variation in these indices provides an indication of the plasticity of woody plant species (Claveau *et al.*, 2002). Previous work has shown that these indices vary as a function of both light and individual size. We used multiple linear regressions to test for the contribution of light (%PPFD) and size (height) to variation in each of the above mentioned indicators of plasticity. Dependent variables were natural log transformed to ensure that they met assumptions of both normality and homoscedasticity. A significance level of 0.05 was used. Statistical analyses were performed using Systat 10.0 (SPSS, 2000).

POPULATION-LEVEL RESPONSE

The diameter–density distributions were analyzed by stand development stage. Differences in density for each

diameter class were tested using a two-way ANOVA followed by a multiple comparison Bonferroni test on the interaction terms (Sokal & Rohlf, 1981) (forest development stage \times diameter class).

To determine differences in mountain maple attributes among the five forest types (19 undisturbed plots) we used a one-way ANOVA performed with a permutation test of 9,999 permutations (Legendre & Vaudor, 1991) as some of the data failed to meet the assumptions of normality and homoscedasticity. In the permutation analysis, the reference value for the statistic is included in the data in order to obtain the distribution for the statistical test. The statistical decision is therefore made by comparing the reference value of the F statistic with the distribution obtained using H_0 . If the F reference value is between the extremes of the distribution then H_0 is refused. A significance level of 0.05 was used. ANOVA with permutations were performed using R 3.0 (Legendre & Vaudor, 1991). All other statistical analyses were performed using Systat 10.0 (SPSS, 2000).

Results

STEM GROWTH AND MORPHOLOGY

Light availability (% PPF) affected all indicators of mountain maple plasticity except LAR (Table II and Figure 1). Variation in LAR was strongly and negatively correlated with stem height. This indicates that the ratio of photosynthesizing tissues to non-photosynthesizing tissues decreases with height. LAD was positively correlated with both light and size, while SLA was negatively correlated to both light and size (Table II). These indicators show that taller individuals growing in higher light conditions such as gaps adapt to those conditions through denser crowns that have thicker leaves. The relative annual shoot biomass production (as measured by the R_{shoot} indicator) was found to increase with increasing light. Interestingly, graphic evidence suggests that LAD and R_{shoot} may have reduced responses when light levels are over 60% PPF (Figure 1).

POPULATION STRUCTURE AND DYNAMICS UNDER VARIOUS FOREST TYPES

EFFECTS OF LIGHT AVAILABILITY

Even though significant effects of light availability on mountain maple crown morphology and growth were found at the stem level, no significant relationships were found for any of the population-level attributes presented in Table III ($P > 0.05$, analyses not shown).

DIFFERENCES AMONG FOREST TYPES

Variations in mountain maple population-level attributes were observed among plots both within and between forest types for the various canopy conditions sampled. Mountain maple density ranged from 2,000 to 55,750 stems·ha⁻¹, biomass from 336 to 15,859 kg·ha⁻¹, and maximum stem height from 235 to 660 cm. A high proportion of small stems, the highest found in the 5 to 10 mm class, in the mountain maple diameter-density distribution suggests good recruitment in almost all plots (Figure 2).

Mountain maple stem density varied significantly among forest types (ANOVA with 9,999 permutations, $P = 0.0262$,

TABLE II. Indicators describing stem morphology and growth.

Ratios	Definition	Abbreviation	Units	Formula	Range of values	Regression Model*	R ²
Leaf area density	Leaf surface area over projected crown area	LAD	m ² ·m ⁻²	A _i / CA _i	0.4164 - 6.9066	LAD = -0.6 + 0.13 Ht + 0.01 Light	0.45
Leaf area ratio	Photosynthetic surface over the total aboveground biomass of the plant	LAR	m ² ·g ⁻¹	A _i / M _{tot,i}	0.0008 - 0.0224	LAR = -4.4 - 0.3 Ht	0.79
Specific leaf area	Leaf surface area over leaf dry mass	SLA	m ² ·g ⁻¹	A _i / M _{leaves,i}	0.0182 - 0.0632	SLA = -2.8 - 0.008 Light - 0.06 Ht	0.52
Relative annual shoot biomass production	Index of the annual growth in 1995	R _{shoot}	g·y ⁻²	M _{shoot} / age ²	0.0042 - 0.6589	R _{shoot} = -4.5 + 0.03 Light	0.21

Note: A = total leaf area, M_{shoot} = annual shoot biomass in 1995, CA = crown area, i = of a stem i, M_{tot} = total biomass, M_{leaves} = leaf biomass, age = age of the plant, Light = light above the understory vegetation (% PPFD), Ht = stem height.

* All regression models are significant at P < 0.001, R² are adjusted.

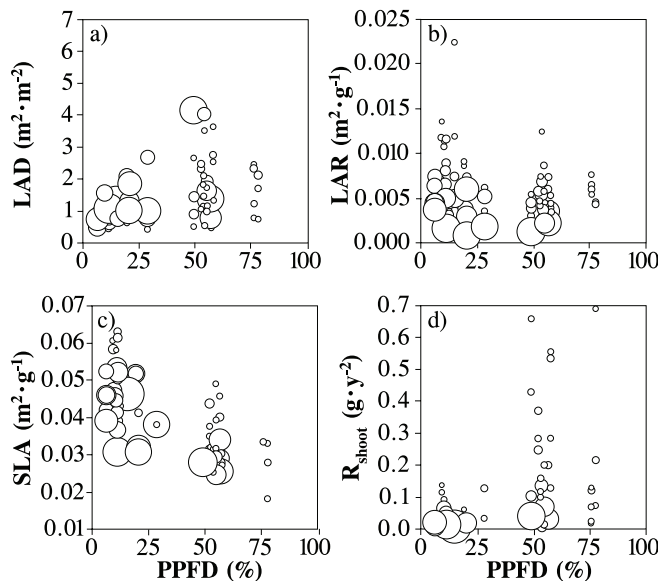


FIGURE 1. Relationships between mountain maple crown morphological and growth ratios and light above the understory vegetation (%PPFD): a) leaf area density (LAD), b) leaf area ratio (LAR), c) specific leaf area (SLA), and d) relative annual shoot biomass production (R_{shoot}). Dot size is function of stem size.

Table III), with mature aspen plots containing a significantly higher number of stems than tolerant conifer forests. The conifer forest had a high stem frequency (85%) despite having a low stem density. No differences were found in mountain maple basal area, stem height, juvenile frequency, or stem frequency between any of the evaluated stand types. Biomass, however, was significantly higher in spruce budworm-caused gaps than in the forested plots (Table III, P = 0.0478).

The diameter-density distribution of mountain maple stems among the various forest types is presented in Figure 2. Analyses of the interaction terms between class diameter and forest types showed that mature aspen forests had a significantly higher frequency of stems in the smallest size classes (0-5 and 5-10 mm diameter classes). This difference continued in the 10-15 mm diameter class with all stand types except the gap-dominated stand (Bonferonni P < 0.001, Figure 2). In the aspen and mixed forests, we found the highest proportion of stems in the 0 to 5 mm diameter class, occupying from 25 to 29% of the total stem density.

Recruitment into the smallest size class was lower in conifer plots, with only 18% being small stems. In most forests, we observed a sharp decrease in stem density above the 5 to 10 mm diameter class. However, in mature aspen forests this decrease occurred in the 10 to 15 mm class. The largest size class stems (larger than 30 mm in diameter) were most abundant in the spruce budworm-caused gaps. In fact these stems accounted for 15% of all the stems in the studied gaps, whereas they accounted for only 7% in the other forest types. We also noted that it was in spruce budworm-caused gaps that the largest stems (76 mm diameter, 6.5 m in height) were found.

Discussion

MOUNTAIN MAPLE SIZE, STEM GROWTH, AND MORPHOLOGY

Stem growth and crown morphology of mountain maple were strongly influenced by both light conditions and stem size. At high PPFD, smaller and thicker leaves (low SLA) and a structure that ensures high light interception (high LAD) are believed to maximize light interception and thus growth (Givnish, 1988; Niinemets, Kull & Tenhunen, 1998; Poorter & Werger, 1999; Farque, Sinoquet & Colin, 2001). This was clearly how mountain maple reacted with increasing light availability. Similar morphological and growth acclimations to a strong gradient of light have been observed for other understory shrubs, such as *Lindera benzoin* (Veres & Pickett, 1982), *Viburnum acerifolium*, *V. dentatum*, *V. prunifolia* (Nicola & Pickett, 1983), *Lonicera maackii* (Luken *et al.*, 1995), *Gaultheria shallon* (Messier, 1992), and deciduous tree seedlings (Beaudet & Messier, 1998). Furthermore, as found in many recent studies (King, 1986; Naumburg, Ellsworth & Percy, 2001; Claveau *et al.*, 2002; Delagrangue *et al.*, 2004; Claveau, Messier & Comeau, 2005), both stem growth and morphology were strongly affected by stem size as well as light. As shown in Figure 1, LAR was clearly influenced by stem size at all light levels. Therefore, any increase in size at low light will induce a strong carbon stress in mountain maple, while staying small at low light should increase its chance of survival (Figure 1d) (as does its ability to both increase SLA and decrease LAD with decreasing light availability). Clearly, light and size interact strongly to influence many of mountain maple's crown morphological variables; both factors need to be considered to explain the ability of mountain maple to survive and grow in various understory environments.

In our study, the best individual stem growth was noted between 40 and 60% full light, while a decrease in growth rate occurred above 60% light (Figure 1). These light levels are roughly equivalent to those previously suggested as being optimal for mountain maple growth (Post, 1967). Wilson and Fischer (1977) found a similar light growth requirement for striped maple. These light requirements are

characteristic of a gap-phase strategy species (Hibbs, Wilson & Fischer, 1980).

Trembling aspen stems, which may compete with mountain maple in high light environments, have a minimum light requirement of 30% full light (Kelly, Messier & Bergeron, 1999), with optimal growth occurring above 40 to 50% full light (Prevost & Pothier, 2003). Thus high growth occurs at roughly similar light levels for both mountain maple and aspen, but mountain maple's high plastic crown morphology and growth permit it to survive at lower light and to intercept more of the received light (Aubin, Beaudet & Messier, 2000).

TABLE III. Differences in the mean of six mountain maple population variables among forest types. One-way ANOVA among forest types, with comparisons performed using permutation tests. SE is in parentheses.

Variable	Young aspen forest	Mature aspen forest	Mixed forest	Conifer forest	Gap
Biomass ^γ (kg·ha ⁻¹)	3,011ab (998)	4,243ab (882)	2,980ab (1,650)	1,663a (478)	9,114b (2,930)
Basal area (kg·ha ⁻¹) [§]	2.80 (0.69)	4.57 (0.67)	2.66 (1.27)	1.76 (0.37)	6.10 (1.97)
Stem density (n·ha ⁻¹)	19,000ab (5,399)	39,438a (6,006)	17,625ab (4,251)	12,688b (2,997)	18,250ab (7,035)
Mean stem height (cm)	98 (4)	102 (4)	95 (29)	128 (22)	143 (11)
Stem frequency (%)	70 (6)	100 (0)	73 (8)	85 (7)	75 (19)
Juvenile frequency (%)	50 (27)	65 (19)	49 (17)	5 (29)	13 (13)

^γTotal oven dry biomass estimated from equation [2], see methods.

[§]At ground level.

*Different letters mean significant differences at $P < 0.05$.

This high growth and morphological plasticity, combined with its ability to grow clonally (Jobidon, 1995), may explain the success of mountain maple in a wide range of habitats (Kempf & Pickett, 1981). For example, connections between stems may allow a redistribution of resources from unproductive ramets to those located in favourable microsites that support rapid growth (Pitelka & Ashmun, 1985). Simultaneously, high morphological and growth plasticity in its aerial sections, as we observed, allows mountain maple to produce ramets well adjusted to the highly varied understory light conditions found in late successional gap-prone forests (Table I).

IMPACT OF STAND DEVELOPMENTAL STAGE ON MOUNTAIN MAPLE POPULATION STRUCTURE AND DYNAMICS

Mountain maple's population structure and abundance varied among forest types. For instance, aspen stands had a

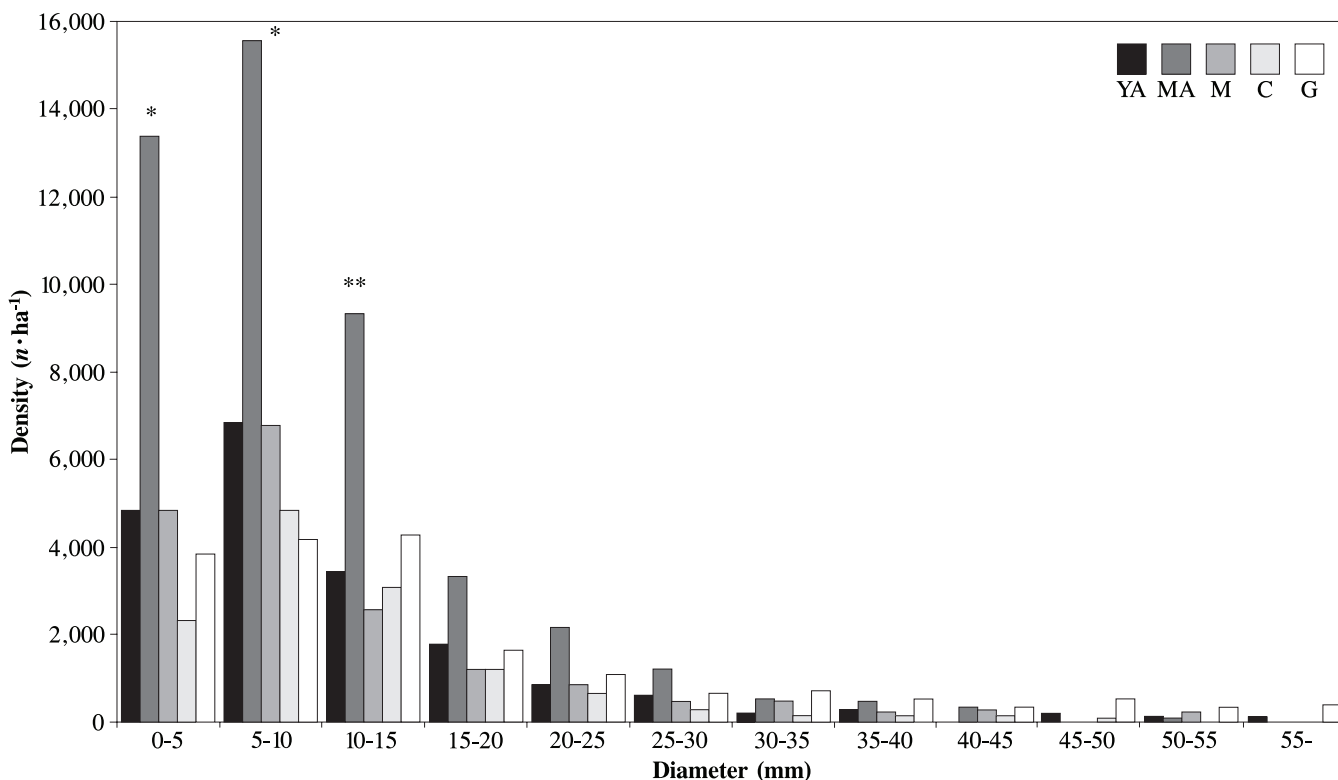


FIGURE 2. Diameter-density distribution of mountain maple population among forest types. * indicates that mature aspen forest type is significantly different from all other forest types, ** indicates that mature aspen forest type is different from young aspen, mixed, and intact conifer forests but not from conifer forests with spruce budworm-caused gaps (Bonferonni $P < 0.05$). YA = young aspen, MA = mature aspen, M = mixedwood, C = conifer, and G = spruce budworm-caused gap.

higher abundance of mountain maple and a higher proportion of small stems, suggesting a higher recruitment rate than in either the mixed or shade-tolerant conifer forests. There was a greater decrease in the abundance of individuals in the largest size classes in the mixed and intact conifer forests, which may reflect slower growth rates in these reduced light environments or poorer survival in the large diameter classes. Kurmis and Sucoff (1989) observed a similar decline in hazel populations (*Corylus cornuta*) as more fir and spruce enter the tree canopy. Young aspen stands also had less mountain maple and fewer small stems than mature aspen stands. This may be due to an abundant recruitment of aspen suckers shortly after disturbance that may compete with mountain maple stems.

The mountain maple population structure was different in the spruce budworm-caused gaps. The higher proportion of large stems in spruce budworm-caused gaps suggests either an important establishment phase soon after the end of the outbreak, better growth, or a better survivorship of this cohort. In contrast with sudden disturbances such as windthrow, the slow, standing death of balsam fir trees (6-7 y) through gradual foliage consumption during spruce budworm outbreaks results in a very gradual increase in light availability (Morin, Laprise & Bergeron, 1993; Kneeshaw & Bergeron, 1999). This gradual increase of resources, combined with maple's persistence in the understory and its great plasticity are thought to favour mountain maple rather than aspen recruitment in these forests.

OVERSTORY FOREST DEVELOPMENT AND MOUNTAIN MAPLE POPULATION DYNAMICS

Four distinct hypothetical phases of mountain maple understory dynamics can be suggested based on the stands that we studied. As our stands have previously been associated with a time since fire gradient (Bergeron, 2000), our proposed phases of mountain maple dynamics can also be related to successional stages described for this part of the boreal forest. First, following a disturbance that removes most of the aboveground vegetation (clearcut or fire), young stems, probably resulting from basal suckering, show a rapid growth that is favoured by a multi-layer morphology well adapted to a high light environment. This stage can still be observed in our young aspen forests. A similar observation was made by Archambault, Morissette, and Bernier-Cardou (1998), who noted rapid expansion of mountain maple following clearcutting. Our results suggest, however, that competition with aspen can reduce mountain maple expansion.

Second, mountain maple tends to increase in density, size, and overall biomass with time as aspen forests get older. We speculate that during this expansion phase, mountain maple may increase in abundance and colonize a large part of the understory. Third, over time an increasing number of shade-tolerant conifer trees reach the overstory canopy. This tends to reduce understory light below 10% in the mixedwood forests of our region (Messier, Parent & Bergeron, 1998). Such a low light level is detrimental to mountain maple density, biomass and height; we thus observed greater monolayer or shade-adapted morphology and reduced density and biomass of maple compared to the

younger aspen-dominated forests. A process of dynamic dying back and resprouting (Vincent, 1965) may also be an important part of this phase. This could be associated with the observed reduction in biomass. Mountain maple may also initiate new stems in search of favourable understory patches. The clone thus "sits and waits" (Matlack, Gibson & Good, 1993) for a future opening in the canopy. De Grandpré, Gagnon, and Bergeron (1993) observed a similar pattern for much of the understory vegetation in the southern boreal forest of Québec.

Fourth, with trees ageing and with an increasing abundance of budworm host species (balsam fir and white spruce) dominating the canopy, these forests become more prone to gap formation (Kneeshaw & Bergeron, 1998). In the case of a small-scale disturbance where the understory mountain maple cover is already present and mainly unaffected by the disturbance, such as those produced by spruce budworm-caused gaps, mountain maple can quickly occupy the opening. In our study the largest mountain maple and highest biomass were found in spruce budworm-caused gaps. It has been suggested that the presence of only a few stems of mountain maple are necessary to rapidly form a dense sub-canopy (Vincent, 1965; Post, 1967). Even in our old growth conifer forests, where mountain maple stem density was low, a high stem frequency was found. The foraging behaviour of mountain maple (Bell, 1984; Lei & Lechowicz, 1990) and its ability to rapidly alternate between the suppression and expansion phase following small canopy openings form the basis of its persistence through succession in our gap-riddled boreal forest. It appears from our results that mountain maple's strategy is typical of that of other mid-shade-tolerant clonal understory shrubs, such as striped maple (Wilson & Fischer, 1977; Hibbs, 1979; Hibbs & Fischer, 1979; Hibbs, Wilson & Fischer, 1980), hazel (Kurmis & Sucoff, 1989), and salal (Messier, 1992).

Since mountain maple is prevalent in most southern boreal and temperate mixedwood forests of eastern North America, a sound knowledge of mountain maple autecology is necessary to develop silvicultural systems that will ensure the success of commercial trees. Mountain maple is known to have a strong regulatory effect on light availability and, more generally, on the diversity, structure, and composition of the understory environment (Aubin, Beaudet & Messier, 2000). Through its strong impact on light availability, mountain maple can play a major role in ecosystem functioning and successional processes. Furthermore, our study has shown that small and gradual openings in the canopy, such as those created by the spruce budworm, increase mountain maple dominance in the understory.

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