

Development of stunted black spruce (*Picea mariana*) clones in the subarctic environment: A dendro-architectural analysis¹

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Abstract: Black spruce (*Picea mariana* [Mill.] BSP.) is the dominant tree species across the North American boreal forest. In the northernmost parts of its natural range, the species thrives in the form of scattered or aggregated stunted clones (krummholz) in winter-exposed subarctic and arctic sites. In this study, we have examined the mechanisms and developmental sequence that allow the growth, maintenance and expansion of long-lived (several hundred years old to more than one thousand years old), stunted black spruce using architectural and tree ring analyses. The development of stunted black spruce clones is the result of the reiteration potential of the species through layering. Exposed snow-drift sites are favourable to layering because branches are maintained close to the soil surface; these site conditions promote layering through adaptive reiteration associated with dedifferentiation of growing axes. Because the lower branches are held near the soil surface and buried beneath the litter, the formation of adventitious roots is accelerated and facilitates the physiological autonomy of clonally-born units. Newly formed units with an expanding root system lead to self-pruning of inter-branch connections and physiological autonomy. The age structure of all physiologically autonomous units within a clone often exhibits an inverse J-shaped distribution suggesting a stable population of units with prevailing site conditions. The average life span of a unit was 170 ± 70 years, but individual units may reach an age of more than 450 years. The dynamics of establishment and death of units (fragmentation of layers) through adaptive reiteration is the mechanism ensuring the great longevity of prostrate clones. In the absence of fire disturbance, stunted black spruce clones can perpetuate indefinitely.

Keywords: tree architecture, clone, layer, tree ring, black spruce, *Picea mariana*, subarctic, tundra, treeline, krummholz.

Résumé : L'Épinette noire (*Picea mariana* [Mill.] BSP.) est de loin l'espèce arborescente la plus abondante de la forêt boréale nord-américaine. À sa limite d'aire nordique, sous conditions subarctiques et arctiques de forte exposition nivéo-éolienne, l'Épinette noire survit sous la forme de clones prostrés individuels ou regroupés en formation (krummholz). Par le recours à l'analyse dendro-architecturale, nous avons cherché à comprendre les mécanismes et préciser le patron de développement morphologique assurant la croissance, le maintien et l'expansion des clones d'Épinette noire prostrés, dont plusieurs sont centenaires ou millénaires. Le développement des clones prostrés semble redevable à la capacité de réitération de l'Épinette noire associée au marcottage. Les conditions hivernales semblent favoriser le marcottage par l'intermédiaire de la réitération adaptative reliée à la dédifférenciation des axes en croissance. Puisque les branches inférieures sont maintenues près de la surface du sol, prêtes à être enfouies par la litière, il s'ensuit la production de racines adventives qui favorisent l'autonomie physiologique des marcottes. Grâce au transfert de la dominance apicale des axes endommagés vers les branches non endommagées qui développent un nouveau système racinaire, l'élagage du lien inter-branchial se produit et traduit l'atteinte de l'autonomie physiologique des marcottes naissantes. La structure d'âge des marcottes physiologiquement autonomes des clones étudiés montre souvent une distribution générale en J inversé qui suggère une population de marcottes stable au sein de chaque clone. La longévité moyenne des marcottes est de 170 ± 70 ans, mais chacune d'elles peut atteindre éventuellement un âge de plus de 450 ans. La dynamique démographique des marcottes (exprimée par leur fragmentation), à l'aide de la réitération adaptative, constitue le principal mécanisme favorisant la grande longévité des clones prostrés en milieu subarctique et arctique. En l'absence d'incendies dévastateurs, les clones d'Épinette noire prostrés, à leur limite d'aire de croissance, peuvent se maintenir et se développer à perpétuité.

Mots-clés : architecture des arbres, clone, marcottes, cernes de croissance, épinette noire, *Picea mariana*, subarctique, tundra, limite des arbres, krummholz.

Introduction

In boreal North America, black spruce (*Picea mariana* [Mill.] BSP.) is the dominant forest tree species and forms the treeline in many regions (Rowe, 1972; Larsen, 1980; Payette, 1983; Ritchie, 1987). Due to its phenotypic plasticity, black spruce displays a large array of contrasted growth forms in response to severe winter conditions and summer frosts (Payette *et al.*, 1996). Combined snow-drift abrasion and low temperatures damage most needles and meristems located at the snow-air interface (Hadley & Smith, 1986,

1987, 1989; Marchand, 1987), resulting in complex degraded growth forms (Payette *et al.*, 1996). In the most exposed sites of the subarctic forest-tundra and in the southern part of the arctic tundra across northern Canada, aggregated stunted black spruce clones form shrubby stands known as krummholz.

Stunted black spruce propagates vegetatively by layering of the lower branches; a layer is an autonomous or potentially autonomous rooted branch. The process of layering results in the formation of clones, *i.e.*, plants belonging to one genet (the same genotype) that proliferates horizontally (Silvertown & Lovett Doust, 1993). With time the

¹Rec. 2000-07-25; acc. 2001-06-20.

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clones divide into distinct morphological and functional layers or units (the term unit is used hereafter as a synonym for layer). Because these units are constantly renewed, clones may possess a longevity unequalled by normal trees. In subarctic Québec, the age of genetically identified stunted clones has been evaluated at 1800 calibrated ^{14}C years (Laberge, Payette & Bousquet, 2000). Long-lived stunted clones are fragmented into autonomous prostrate units that prevent the accumulation of structural tissue with a relatively stable leaf/wood ratio of approximately 10-15% through time. However, the decreasing leaf/wood ratio in ageing trees generally results in senescence because the accumulation of biomass becomes a burden over time (Kaufmann & Troendle, 1981; Mäkelä, 1986; Laberge, Payette & Bousquet, 2000). As a consequence, stunted growth forms are generally free of the biomechanical constraints associated with vertical growth. Interestingly, only a small number of tree species with normal vertical growth exceed 1000 years (Schulman, 1958; Connor & Lanner, 1990; Kelly, Cook & Larson, 1992). High longevity in trees is generally attributed to asymmetric radial growth due to the death of a part of the cambium (Kelly, Cook & Larson, 1992).

The developmental patterns of clonal plants may be addressed using architectural analysis based on a number of basic characteristics inherent to each species (McPhee, Bonser & Aarssen, 1997; Bégin & Filion, 1999). With simple criteria such as ramification mode (continuous, diffuse or rhythmic), type of growth (monopodial or sympodial), axis orientation (orthotropic or plagiotropic), and position of reproductive organs, 23 architectural models have been described so far to identify the development patterns of most extant tree species (Hallé, Oldeman & Tomlinson, 1978). Black spruce is characterized by a rather simple architectural device corresponding to Rauh's model (Bégin & Filion, 1999). This species has a monopodial and orthotropic trunk with spiral phyllotaxis and indefinite rhythmic growth. Rhythmic ramification is expressed by the formation of an apical bud. After emergence, scars of the bud scales remain and allow the identification of growth modules. Trunk ramification is also rhythmic. Branches are borne in pseudovercils on the subterminal parts of the growth modules. Branches are also orthotropic monopodes with indefinite rhythmic growth and spiral phyllotaxy. The reproductive organs are born laterally on ultimate axes, and thus do not interfere with the growth of vegetative axes (Bégin & Filion, 1999). This development pattern involves the rapid establishment of the four ramification orders, *i.e.*, the trunk corresponding to axis of order 1 (A1), and the branches corresponding to axis of orders 2 (A2), 3 (A3) and 4 (A4). Under normal growth conditions, a black spruce tree adopts an erect, spire form and completes its architectural program within 10-15 years, whereas in the subarctic, this may take up to 25 years. Subsequently, black spruce continues its development through an array of reiterative processes enabling the maintenance of its basic architecture (Bégin & Filion, 1999).

Reiteration (*sensu* Tomlinson, 1983) is fundamental to the development of trees in subarctic regions, where harsh climatic conditions may cause severe damage to exposed plant parts. Reiteration allows the preservation of the architectural integrity by replacing damaged limbs with shoots

possessing the same architecture. It originates from latent or dominated meristems (proleptic or differed), or from meristems that are already active (immediate or by dedifferentiation). The reiteration process may take many forms such as apical recovery or layers. These axes reproduce the growth model (Tomlinson, 1983), and the process involves a step back in the differentiation sequence of axes (Édelin, 1981). Phenotypic plasticity of trees thus depends on their reiteration potential.

The objectives of this study are: *i*) to identify the reiterative processes responsible for the development of the prostrate habit in black spruce, *ii*) to evaluate their role in the longevity of black spruce clones in exposed environments, and *iii*) to define the development model of the prostrate clonal form. To carry out this study, the clonal development of stunted black spruce has been analyzed along a long postfire chronosequence that includes 20 genetically identified clones whose inferred ages range between 114 calendar years and 1800 calibrated ^{14}C years. A dendro-architectural approach was used to describe the development patterns of the stunted growth form and to reconstruct the main stages from seedling establishment to horizontal expansion of large, old-aged clones.

Material and methods

STUDY AREA

The study was conducted in the Rivière Boniface area ($57^{\circ} 45' \text{ N}$, $76^{\circ} 15' \text{ W}$) (northern Québec, Canada), at the northwestern limit of the forest tundra and at the northern treeline (Payette, 1983). Open forest stands occupy wet depressions and protected valleys, whereas the top and sides of wind-exposed hills with thin soils are colonized by stunted spruce, dwarf birch (*Betula glandulosa* Michx.), heath and lichen. Black spruce is the dominant species in the area, with rare tamaracks (*Larix laricina* [Du Roi] K. Koch). The charred wood and subfossil trees lying on the ground, as well as charcoal fragments beneath the vegetation cover indicate that fire influence is widespread, except in scattered treeline sites where no signs of fire were recorded. Some spruce stands have been untouched by fire for several hundred years. In these old-growth stands, spruce is maintained mostly by vegetative propagation (layering). A recent study by Laberge, Payette and Bousquet (2000) in this area showed the presence of millennial stunted black spruce clones. The persistence of old clones is likely explained by the absence of human activities and major disturbances such as fire.

ARCHITECTURAL ANALYSIS

The aim of architectural analysis is to identify a general and consistent developmental sequence in individuals, while acknowledging that each plant has its own ramification design depending on local growing conditions (Bell, 1993). Architectural analysis is based on visual observation of morphological criteria in the form of sketches drawn to scale (Édelin, 1981; Tomlinson, 1983; Barthélémy, Édelin & Hallé, 1989; Bell, 1993). To understand the developmental sequence of stunted black spruce clones, we measured the size (diameter) and analyzed the internal structure of 20 genetically distinct individuals aged between 114 calendar

years and 1800 calibrated ^{14}C years (see Laberge, Payette & Bousquet [2000] for further information on clone selection, clone dating and genetic analysis), representing various growth stages. Individual clones were chosen from exposed lichen-heath-dwarf-birch sites exhibiting homogeneous conditions. The clones selected were growing on well-drained soils, without rock outcroppings or frost activity, to ensure homogeneity in terms of edaphic conditions, vegetation cover and free horizontal growth of stunted spruce. The age of clones was determined by tree-ring dating when macrofossils were present, or by radiocarbon dating of charcoal from the last fire on the sites.

A 400 year-old clone was selected to illustrate the spatio-temporal development of stunted clones. The aerial and below-ground parts of the clone were excavated and mapped to scale. A transverse wood section was sampled at the base of each independent unit. The wood sections were sanded and the establishment date of each unit was determined by tree-ring counts. The clone boundaries were extrapolated based on establishment dates of the units to reconstruct the spatial development of the clone.

Field surveys focused on the reiterative processes affecting the 20 clonal spruce chosen for architectural analysis. By comparing clones of different ages, we constructed a model based on morphological variability to characterize clonal development. Longitudinal sections along the branch pith were made to determine axis origin and to verify whether the axes originated from latent bud development (proleptic origin) or from the straightening of a branch, expressed by absence of pith disruption (adaptive reiteration) (Bégin & Filion, 1999). Sketches of these stages were then assembled to obtain a comprehensive illustration of the architectural development of the clones.

TREE-RING ANALYSIS

Eight clones were sampled to reconstruct their spatio-temporal development. To cover the longest period possible, the clones were selected along the postfire chronosequence (Table I). Once the clones were excavated and mapped, a section was taken at the base of each physiologically independent unit, as well as from every dead stem at the centre of the clones. A sketch of each unit was drawn

to scale. Transverse sections were sanded, dated and measured. Establishment date and physiological autonomy of the units were determined by tree-ring dating under a binocular microscope at 40 \times . A light-ring chronology was used to check the accuracy of all tree-ring dates (Filion *et al.*, 1986). One unit from each of the eight clones was then chosen for tree-ring analysis to provide a temporal framework of the architectural development of growth forms. All eight individuals were sampled every 10 cm along the main axes, as well as at any other level found to be significant, but only two representative examples are shown in this paper. Samples were sanded, dated and measured along two radii with a Velmex micrometer (± 0.002 mm precision) interfaced with a computer.

Results

ARCHITECTURAL ANALYSIS

The 20 mapped clones, aged 114 calendar years to 1800 calibrated ^{14}C years, exhibited a similar spatial pattern, predominantly circular in outline (Figure 1). Openings at the centre of the clones occurred a few hundred years after their initial establishment. From 600 years onwards, clone fragmentation following death of the central parts was well under way, and several patches composed of live branches (units) could be distinguished. With the formation of new peripheral units, the oldest ones died out and decomposed, producing a litter of needle and wood remains at the centre of the clones. With time, the spreading clonal spruce reached 25 to 30 m diameter in ≥ 1300 year-old clones (Figure 2). This resulted in a fragmented cover composed of several independent units, > 40 units per clone being recorded in > 1000 year-old clones and > 80 units in a 1800 year-old clone (see below, the age structure of units in each clone).

SPATIAL GROWTH OF CLONES

To evaluate the spatial growth of stunted clones, we analyzed in detail the development of a 400-year clone using the age at the base of all living and dead branches above- and below-ground. Clonal growth showed a centrifugal pattern caused by the production of new branches along the expanding boundary and death of old and moribund

TABLE 1. Postfire stand age.

Site no.	Altitude (m)	Date of the last fire (laboratory no.)	Calibrated years BP ($\pm 2\sigma$)	Age (Calendar years)
1	115	1881 AD ¹	1881 AD	114
2	135	1568 AD	1568 AD	427
3	115	660 \pm 50 BP ² (Beta-35532)	1300 AD (1280 - 1407)	700
4	125	970 \pm 60 BP (Beta-35507)	1140 AD (985 - 1211)	850
5	125	1130 \pm 50 BP (Beta-35515)	900 AD (802 - 1001)	1100
6	115	1350 \pm 60 BP (Beta-31649)	670 AD (597 - 782)	1300
7	135	1480 \pm 50 BP (Beta-31661)	600 AD (530 - 660)	1400
8	165	1800 \pm 60 BP (Beta-31652)	240 AD (109 - 389)	1750

¹ Tree-ring dating

² Radiocarbon dating: maximum age of the fire

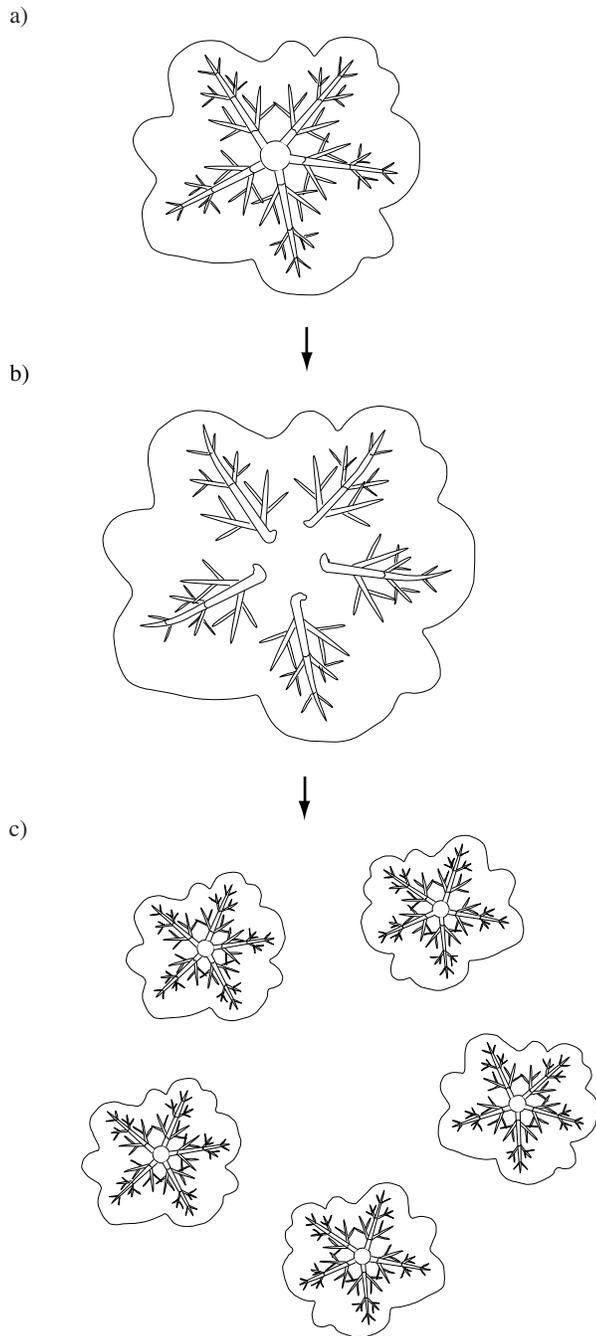


FIGURE 1. Changing morphology and size of stunted black spruce clones with time (a to c).

und branches at the centre of the clone (Figure 3). The oldest branch was located at the centre of the clone and dated back to 1639; however, a few dead branches were not dated because of wood decomposition. Based on all the tree-ring dates available, the centrifugal development of the clone seemed to rely on the production rate of peripheral branches. A few units have formed new loci of clonal development (particularly in the west part of the clone) (Figure 3a). The below-ground parts of the clone formed a tangle of roots and branches (Figure 3b). The absence of connections between units was direct evidence for their physiological autonomy. Live branches and roots were located generally

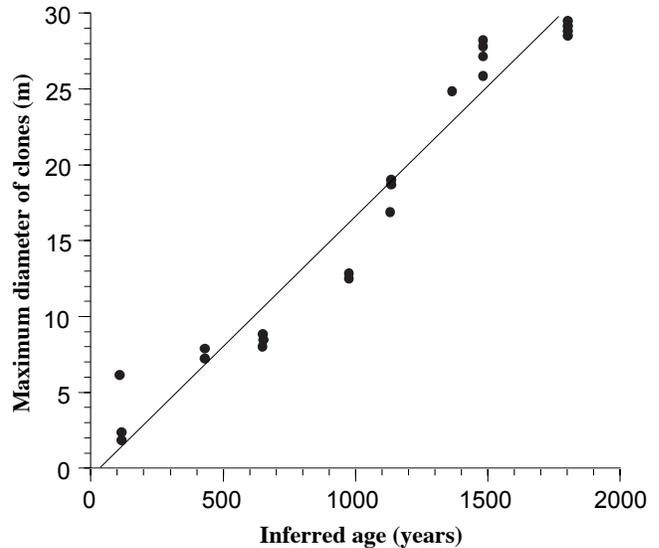


FIGURE 2. Maximum diameter of 20 genetically-identified black spruce clones according to inferred age based on time since fire at each site.

at the periphery of the clone, whereas branches in the central parts were dead, thus indicating that fragmentation was active. According to the maximum diameter and inferred age of eight genetically-identified clones, the lateral growth of each clone was remarkably constant through time, *i.e.*, 0.01-0.02 m year⁻¹ (Table II).

FORMATION OF AN INDEPENDENT UNIT

Based on the morphology and layout of the below-ground parts of all studied clones, every physiologically independent unit has developed a dominant adventitious root several meters long, generally extending beyond the clone boundaries (Figure 4). The daughter unit developed from a branch of the mother unit (identified as the proximal part in figure 4); the dominant aerial root of the daughter unit exhibited thickening in the distal part, whereas the proximal part of the mother unit, when present, was thin and brittle. More frequently, the proximal part of the mother branch simply disappeared. The junction between the new branch unit and the aerial root formed a crank on which the decaying proximal part produced a scar. An independent unit is formed when the proximal part of the mother unit either ceases to be functional, is decayed or dead.

TREE-RING ANALYSIS

The physiological autonomy of the units is well illustrated by radial growth. The examples shown in Figures 5 and 6 summarize the main sequence of events involved. In Figure 5a, two units were identified: around 1760, unit 1 formed an inter-branch connection (corresponding to the proximal part of the mother unit 1) with unit 2 (corresponding to the daughter unit). Because of pith decomposition, the exact date of origin of unit 2 could not be determined (Figure 5b). The dominant aerial root of unit 2 was initiated around 1830 (Figure 5b), when burial of the branch below the litter began. As shown by the two tree-ring curves, the period of development of an independent root system in unit 2 was likely associated with an increase in radial growth around 1830. Around 1850, *i.e.*, 20 years after the formation

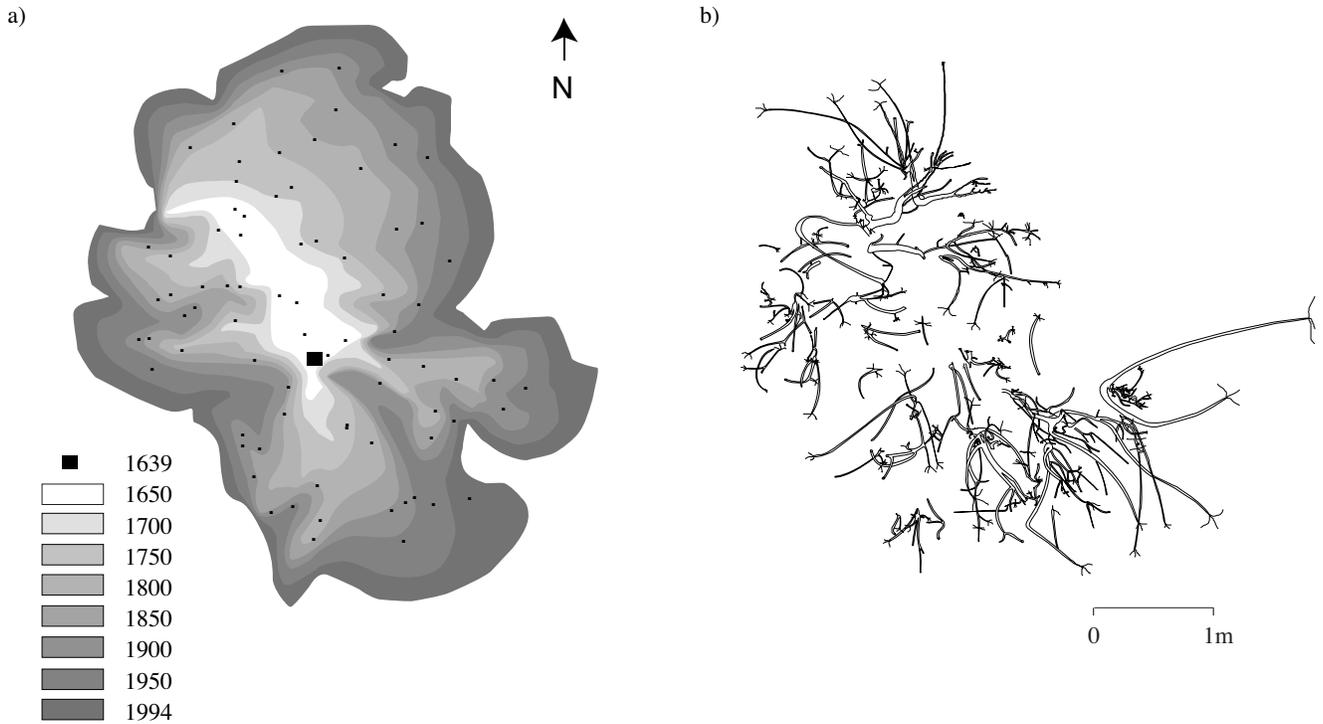


FIGURE 3. Spatio-temporal development of a stunted black spruce clone. a) above-ground parts. Black square: the oldest stem dated by tree rings at the center of the clone. Black dots correspond to tree-ring dated branches arranged in 50-year contour classes. b) below-ground parts including the main roots and buried branches.

TABLE 2. Annual average growth rate based on the maximal diameters of clones.

Clones	1	2	3	4	5	6	7	8
Age (years)	114	427	700	850	1100	1300	1400	1750
Diameter (m)	1.9	7.3	8.2	12.7	17.0	24.9	27.3	29.2
Growth rate (m year ⁻¹)	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02

of the adventitious root system, a decrease in growth was recorded, followed by death in 1863 and self-pruning of the proximal part of the mother-branch of unit 1. Then the distal part of the branch became a physiologically independent unit. Soon after, radial growth of the new unit 2 increased rapidly.

In the second example (Figure 6) the clonal spruce had a more complex elementary structure, with two units (2 and 3 in Figure 6a) developing from another unit (unit 1 in Figure 6a). The mother branch of unit 1 exhibited slow radial growth during its development (unit 1 in Figure 6b). The physiological autonomy of unit 2 occurred probably around 1815, coinciding with the death of the mother unit 1 (now forming a scar due to pruning of the mother branch of unit 1). The development of unit 3 from an A2 axis (or mother branch) of unit 2 began around 1868 (3 in Figure 6a,b). The radial growth of the branch of unit 3 was slow until the 1940s. Then unit 3 probably became autonomous with the development of an active adventitious root system, with a corresponding growth decrease of the mother unit 2 (2 and 3 in Figure 6b). Growth of the proximal part of unit 2 (not shown in Figure 6b) also decreased, soon resulting in death and self-pruning. Unit 3 then became physiologically independent.

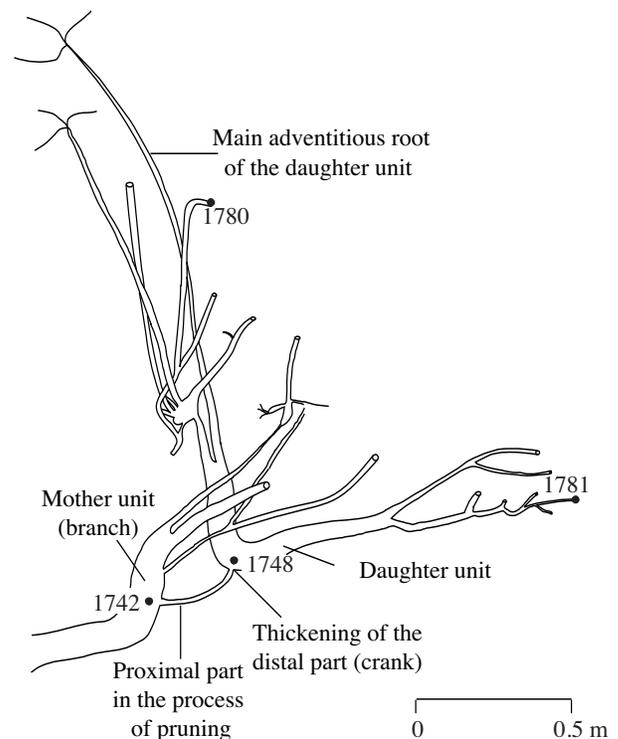


FIGURE 4. Below-ground structure of a unit in the process of physiological autonomy. The proximal part of the branch (inter-branch connexion) is currently in the process of pruning, whereas the distal part of the branch thickens resulting in the formation of a crank. Numbers correspond to dates of initiation of axes. The proximal part corresponds to the nearest part of the branch of the mother unit that initiates formation of the daughter unit. The distal part corresponds to the branch "tip" of the mother unit that is transformed to produce the daughter unit.

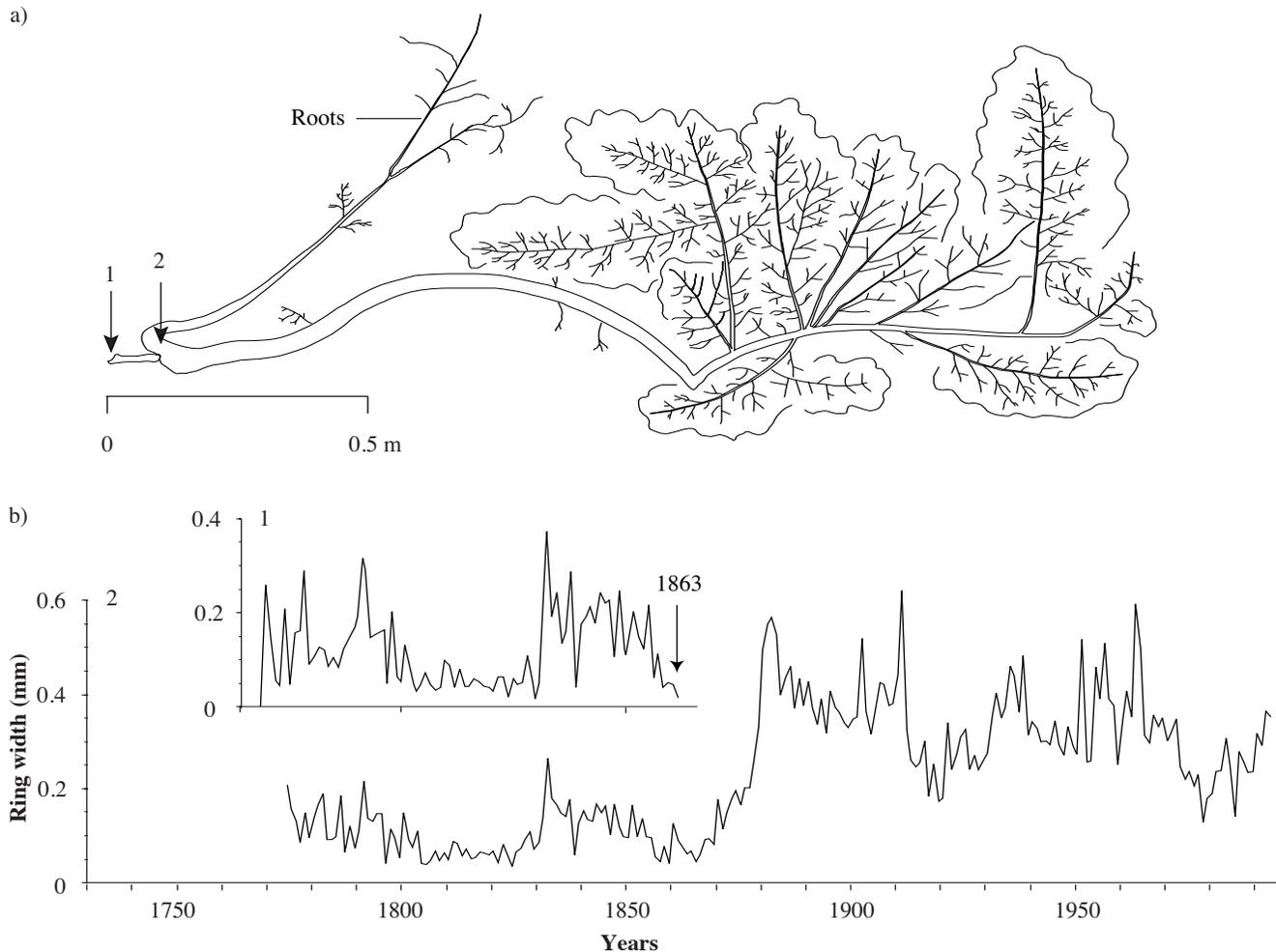


FIGURE 5. Temporal development of two units within a clone. a) layout of unit 1 and unit 2; b) radial growth of unit 1 and unit 2. Unit 1 is represented only by the distal part of the mother branch in the process of pruning. Unit 2 is represented in its entirety with the crank section near the mother branch of unit 1. Unit 2 acquired definitive physiological autonomy during the 1860s, resulting in increased radial growth.

AGE STRUCTURE OF UNITS

The age of a unit was determined by subtracting the period of physiological dependence (equivalent to the life span of the inter-branch connection) from the age of branches. New units were produced continuously, as shown by the age structure of physiologically independent units in each of the eight studied clones (Figure 7). Physiological independence occurred as early as 20 years after branch formation, but for the majority of units it was at an average of 50 ± 25 years. Most units living at the time of sampling reached physiological autonomy during the last 400 years. The average life span of a unit was 170 ± 70 years, with a maximum of 450 years.

DEVELOPMENTAL MODEL OF UNITS

Based on the morphology and radial growth of all the excavated clones, a model describing the development of units was established (Figure 8). After germination, the seedling produces an orthotropic monopodial trunk and rhythmic ramification takes place progressively (Figure 8a). At a later stage, each stem adds several branches of A2, A3 and A4 (Figure 8b). Short-lived A3 branches are inserted by 2 or 3, and are generally positioned on a horizontal plane. A4

twigs complete the ramification sequence. The ultimate branches show a definite growth in time (Figure 8b,c). As they grow larger with time, the branches eventually lean against the ground (Figure 8c,d).

When branches reach the snowpack level, reiteration may intensify from latent buds (proleptic reiteration), resulting in the development of new branchlets on A3, and progressively spreading to all branches. Moreover, reiteration by dedifferentiation is translated by a step back in the ramification sequence: A2 branches are transformed in A1 axes (orthotropic habit and radial symmetry), A3 branches differentiate into A2 as they adopt an orthotropic position, and so on (Figure 8d). Reiteration is first expressed on the ultimate A3 and A4 branches, and can induce the formation of a ramification order not included in the architectural model, which progressively reaches the lower order branches (A2 and A1). Dedifferentiation of A2 into A1 involves important architectural changes, that is, the straightening of A2, and changes in the layout of A3 and A4 branches from a bilateral to a radial arrangement. The change in symmetry occurs after the straightening of A2. Dedifferentiation of A2 into A1 is completed when the first aerial root is formed (Figure 8d). When the branches are

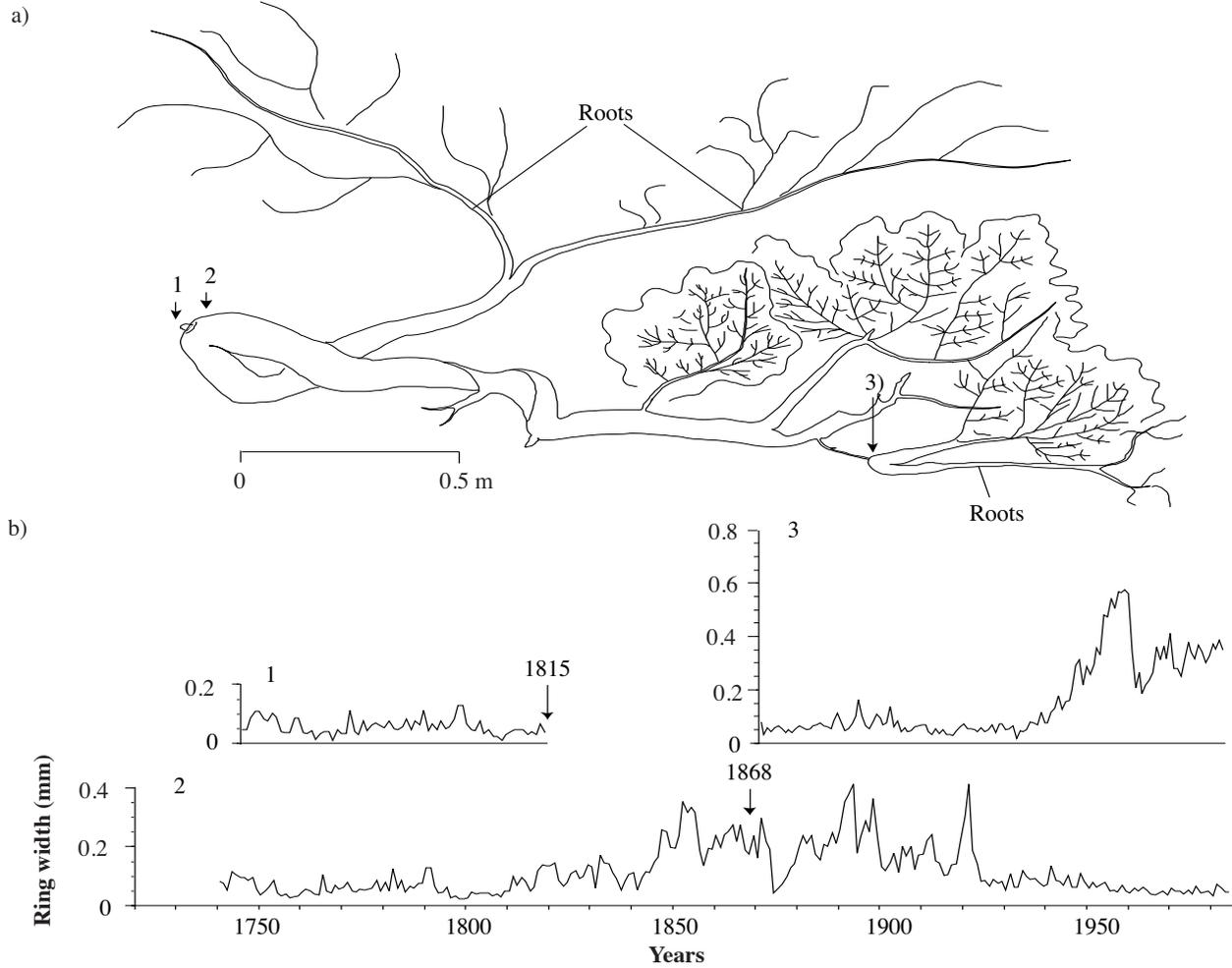


FIGURE 6. Temporal development of three units within a clone. a) layout of unit 1, unit 2 and unit 3; b) radial growth of unit 1, unit 2 and unit 3. Unit 1 is represented by only the tip of the distal part of the mother branch in the process of pruning. Unit 2 is represented in its entirety by the enlarged crank section near the mother branch of unit 1. Unit 2 acquired physiological autonomy around 1815, resulting in increased radial growth. 1) The inter-branch connection of unit 1 (corresponding to the “tip” of the distal part of the mother branch) near the pruning scar and its associated radial growth; 2) unit 2 and its associated radial growth in the crank section near the mother branch of unit 1; 3) unit 3 and its associated radial growth in the crank section near the mother branch of unit 2.

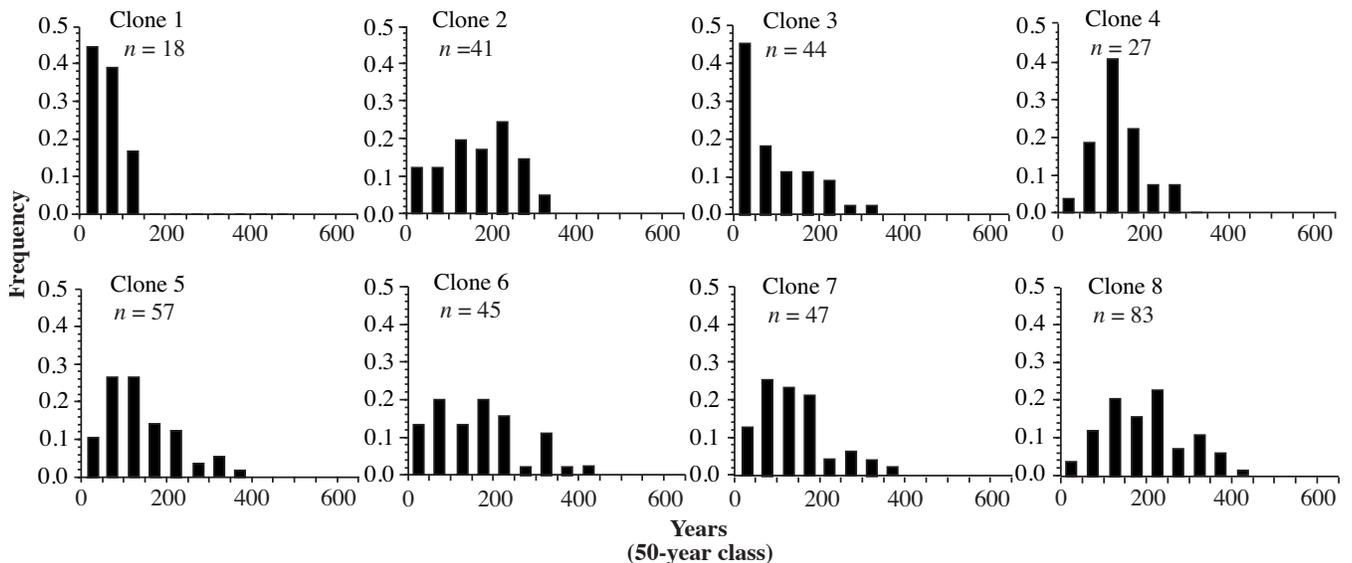


FIGURE 7. Age structure of physiologically independent units per clone (50-year class). The age of a physiologically independent unit = branch age – lifespan of inter-branch connection.

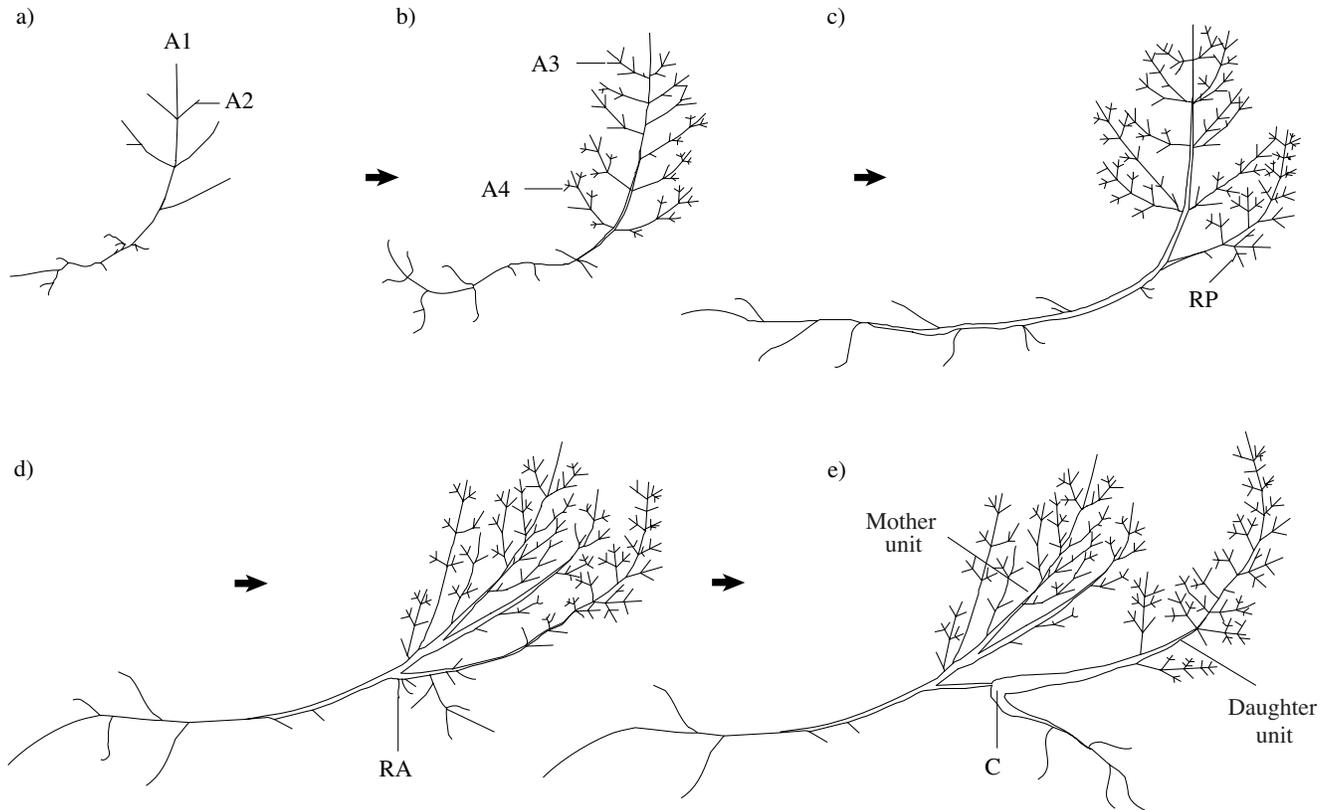


FIGURE 8. Development model of prostrate black spruce clone. a) seedling; b) establishment of the four ramification orders; c) beginning of dedifferentiation of A2 into A1 through proleptic reiteration (RP); d) development of adventitious roots (RA) on dedifferentiated A2; e) secondary growth (C: crank formation) and beginning of pruning of the proximal part of A2. A1: axis of order 1; A2: axis of order 2, and so on.

well rooted, the distal part of the axis thickens to the detriment of the proximal part (Figure 8e). If secondary growth continues, the junction between the dominant root and the new daughter unit forms a crank. Self-pruning of the proximal part eventually allows the physiological autonomy of the new unit.

Discussion

Stunted black spruce clones persist in exposed environments through the continuous production of physiologically autonomous units. Centrifugal growth of clones is the result of the establishment and mortality dynamics of units originating from total reiteration by dedifferentiation. The production by rooting of the lower branches of physiologically autonomous and genetically identical individuals is known as layering, a common phenomenon in black spruce (Stanek, 1961; 1968; Bégin & Filion, 1999). This type of reiteration, *i.e.*, the transformation of a branch into a stem, is possible because of the great phenotypic plasticity of black spruce. The orthotropic secondary axes (A2, A3) are predisposed to layering (Bégin & Filion, 1999).

The production of new units at the periphery of the clones, when the lower branches bend under their own weight, induces centrifugal clonal growth (Figure 8). Burial of the proximal part of the branches beneath the litter promotes the production of adventitious roots, preceding the formation of new units. Such roots develop rapidly from latent buds located on the secondary axes (Fayle & Scott,

1995). One of these roots then becomes dominant and spreads readily outside the clone boundaries. The outward growth of the root system reduces inter-branch competition and enables the roots to avoid the drier and nutritionally impoverished soils beneath the clone mass. Because black spruce is particularly sensitive to hydric stress, an additional aerial root extending beyond the clone boundary may increase water intake. Moreover, the production of roots beyond the clone boundaries helps prevent a decrease in growth rate and photosynthesis associated with low temperatures beneath the clone mass (Delucia, 1986; Hadley & Smith, 1987).

The continuous formation of adventitious roots results in successive unit independence, which is expressed by the lateral growth of the clone and self-pruning of the proximal part of the secondary axes (Figures 5 and 6). Long after the disappearance of the proximal parts of the new units, the mother-branch scar is still visible on the outward part of the crank formed by secondary growth (Figure 6a). Like a hilum, the scar marks the past connection to the mother unit. From the orientation of the scar, one may locate the position of the mother unit long after its death.

The prostrate habit promotes the rapid production of new units, thus ensuring clone persistence. Exposed sites are favourable to layering because vertical axes are absent and branches are maintained close to the soil surface. Branches may be lowered by the weight of snow accumulated in the centre of clones during winter (Scott *et al.*, 1987). In the study area, the production of units in open forests is

often limited by spatial constraints, as well as by the death of lower branches due to a deficit in light intensity (Bégin & Filion, 1999). The absence of vertical axes in exposed sites facilitates the production of new units, which will multiply with time. The increase in the number of units with clone age indicates a rate of establishment of units higher to the rate of extinction, explaining the absence of senescence even in 1800 year-old clones (Laberge, Payette & Bousquet, 2000).

The proliferation of units with time is attributable to rapid physiological autonomy. This is facilitated by the loss of apical dominance in the mother plant. The inductive role of the apical meristem is transferred to the new units, thus resuming the maintenance of the global architecture of black spruce. Rapid development of the new units causes the decrease of radial growth in the mother plant (Figures 5 and 6). This process is irreversible because a large share of energy is transferred to the development of the new unit. This also leads to the rapid die-off and self-pruning of the proximal part of the mother unit. Radial growth of the new unit then increases following the development of its adventitious root system and the acquisition of physiological autonomy.

In most clones, the roughly inverse J-shaped age structure of independent units exhibits a general decrease in the number of units with age, suggesting a stable population of units within each clone (Figure 7). However, young units on their way to physiological autonomy are difficult to identify in the field. At the beginning of the dedifferentiation process, it is often impossible to distinguish any future independent units from the secondary axis bearing adventitious roots. Nevertheless, the age structure of physiologically autonomous units in most clones shows an equilibrium in the production of units with time. The age structure of a mature clone is, in a way, similar to that of a mature, undisturbed forest. Individual units may reach an age of more than 450 years, which is a sign of clone vitality, and an indication of a higher longevity than is usually found in vertical stems.

Climatic variations seem to have little influence on the establishment of units. The fact that no increase in layering was recorded during periods of known harsh conditions (*i.e.*, the Little Ice Age [1600-1880 AD] [Grove, 1988; Bradley & Jones, 1992]) may be attributable to the relative inertia of stunted black spruce in “permanently” wind-exposed sites. Black spruce trees in the study area responded to the severe conditions of the Little Ice Age by a major shift in growth forms (Lavoie & Payette, 1992) except in wind-exposed sites (Payette *et al.*, 1989), thus explaining why the frequency of unit formation in prostrate clones remained constant (Figure 7). The morphological inertia of stunted spruce in exposed environments is probably caused by the overwhelming influence of local, persistent snow-drift conditions. The ultimate cause is past deforestation of exposed sites resulting from scarce postfire regeneration which exacerbates the impact of exposure to winter winds. Regional climatic improvements during the 16th and 20th centuries (Arseneault & Payette, 1997a,b) were not sufficient to counter the severity of exposure prevailing at these sites. Reduced photosynthetic mass of stunted black spruce and recurrent death of the apical meristem at the snowpack level are the main obstacles for a positive

response of exposed black spruce to recent climate warming (Filion, Payette & Gauthier, 1985; Payette *et al.*, 1989). Under present climatic conditions, the lateral expansion of clones takes place at a pace of 2 cm year⁻¹, regardless of age (Table II). This rate represents an average of the lateral growth rates and have likely varied little, according to changes in snow-drift conditions since the period of initial establishment of the clones. The winter conditions required to initiate development of stunted clones were more frequent after 1000 AD (Arseneault & Payette, 1997b). The constant rate of lateral expansion of clonal spruce during this period is thus likely due to the relative constancy of snow-drift exposure in winter.

Conclusion

The persistence of long-lived, stunted black spruce clones in the subarctic environment is the result of the reiteration potential of the species through layering. The maintenance of the prostrate habit due to abrasive winter conditions promotes layering through adaptive reiteration resulting from dedifferentiation of a growing axis. The fact that the lower branches are held near the soil surface and readily buried beneath a thick litter accelerates the formation of adventitious roots and facilitates the physiological autonomy of units. The transfer of apical dominance from axes damaged by snow-drift abrasion to newly formed units leads naturally to self-pruning of inter-branch connections and to physiological autonomy. Physiological independence of units is important for the persistence of clones in harsh environments. The dynamics of establishment and death of units through adaptive reiteration is the main mechanism ensuring the great longevity of prostrate clones in exposed sites. The production of units increases with clone age and size, explaining the lack of senescence in clones up to 1800 calibrated ¹⁴C years old. In the absence of fire disturbance, stunted black spruce clones can perpetuate for centuries, and even millennia.

Acknowledgements

This study was financially supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Department of Indian and Northern Affairs (Canada), and the Ministère de l'enseignement supérieur et de la science of Québec (FCAR program). We are grateful to Julie Gauthier, Dominic Lavoie, and Martin Simard for field and laboratory assistance, to A. Delwaide for assistance in figure preparation, and to P. A. Scott and an anonymous reviewer for useful comments on the manuscript.

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