

# Life span and biomass allocation of stunted black spruce clones in the subarctic environment

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## Summary

**1** Slow growth, maintenance of a high leaf: wood ratio and adoption of a clonal growth habit, more than size *per se*, may increase the life span in trees species. The longevity of black spruce (*Picea mariana* (Mill.) BSP.) is increased from 200 to 300 years, when it grows as a clonal shrub.

**2** We measured the surface area and above- and below-ground biomass of 25 post-fire, stunted black spruce clones identified from RAPDs markers. The maximum age of each clone was deduced from tree-ring dating or by radiocarbon dating of charcoal fragments. The oldest clone was > 1800 years of age. The total surface area of the clones increased with age, ranging from 2.8 to 691.3 m<sup>2</sup>. The ratio of living aerial parts to the total surface area decreased from 100% to < 50% with post-fire stand age, reflecting fragmentation of clones into many autonomous or potentially autonomous rooted branches (layers). The number of layers increased with age from 12 layers in a 100-year-old individual to more than 80 in a 1800-year-old clone.

**3** Biomass allocation and fragmentation can explain the maintenance of a relatively stable leaf: wood ratio of approximately 10% through time in stunted black spruce clones. The fragmentation of layers is the main mechanism ensuring the great longevity of prostrate clones in exposed sites. In the absence of perturbation, stunted black spruce clones may perpetuate for centuries or even millennia.

*Key-words:* black spruce, clone, clonal growth, senescence, longevity, layering, krummholz, subarctic, tree line

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## Introduction

According to current life-history theory, most variations of life span can be explained by differences in size: the larger the species, the longer its life (Peters 1983; MacKenzie 1999; West *et al.* 1999). However, tree species differ widely in life span and here the relation does not always hold true. Some trees live for only 100–300 years, while a few species exceed 1000 years, e.g. *Sequoia sempervirens* Endl., *Pinus longaeva* D. K. Bailey (Schulman 1958; Connor & Lanner 1990), where the oldest individual ever recorded was 4900 years of age (Currey 1965), and *Fitzroya cupressoides*, which is the second most long-lived tree species (Lara & Villalba 1993). Except for *S. sempervirens*, long-lived species are not always the biggest and they tend to occupy mar-

ginal, dry habitats, with adverse growth conditions. Furthermore, individuals growing in extreme sites within the natural range of a given species exhibit a higher longevity than those thriving in mesic sites (Schulman 1954; LaMarche 1969; Ward 1982; Kelly *et al.* 1992). Many of these ancient trees belong to the genera *Pinus*, *Cupressus* and *Juniperus*, and show morphological anomalies and asymmetric radial growth due to the death of a part of the cambium (Kelly *et al.* 1992).

Although there are clear advantages in achieving a high stature, such as a competitive advantage, the accumulation of dead material becomes a burden over time. According to the pipe model theory (Shinozaki *et al.* 1964), the surface area of phloem in trees is proportional to foliage biomass. The vertical growth of a tree requires an increasing amount of resources per unit of foliage biomass to ensure phloem development. Therefore, the important ratio between volume of the trunk and that of the crown

increases gradually with tree size and age, and the ratio between carbohydrate produced and carbohydrate consumed during respiration decreases. The decrease in water supply to the crown due to the lower ratio of phloem:foliage biomass is the main cause of foliage and branch mortality (Went 1942; Mäkelä 1986; Waring 1987).

According to Watkinson & White (1985) and Watkinson (1992), clonal plants, i.e. plants that belong to one genet (the same genotype) and proliferate and spread horizontally (Silvertown & Lovett Doust 1993), do not show signs of senescence because of the continuous production of new ramets (i.e. individually rooted parts of a clone, Silvertown & Lovett Doust 1993). Senescence is usually viewed as a decreasing probability of survival with age (Finch 1990). Several clonal species do indeed have exceptionally long life spans (Oinonen 1967; Kemperman & Barnes 1976; Vasek 1980; Smith *et al.* 1992). As the old parts of a clone die and decompose, clonal growth favours the rejuvenation of tissues, and the production of new ramets precludes senescence of the genet. Thus, the probability of mortality of the genet declines if the rate of ramet production exceeds that of ramet death (Cook 1979, 1983). In contrast, the vigour of other clonal organisms appears to decline with age (Griffiths 1992; Martinez & Levinton 1992) and even in long-lived species such as quaking aspen (*Populus tremuloides* (Michx.)) clones appear to vary in their rate of senescence (Shields & Bockheim 1981). Gardner & Mangel (1997) have shown that life history parameters such as the rate of sexual reproduction determine whether a particular clone experiences senescence, so that low rates could result in selection against senescence.

We document the relationship between the size, morphology, biomass and age of postfire, stunted black spruce (*Picea mariana* [Mill.] BSP.) clones growing at tree line sites. The individuals are genetically identified and their stand age is known from the absolute date of the last fire. At tree line, a high degree of phenotypic plasticity enables black spruce to adopt a large variety of growth forms in response to harsh winter conditions (Lavoie & Payette 1992). In exposed environments, this species is prostrate and rarely exceeds 30 cm in height, equivalent to the average snow cover. When stunted in this way, black spruce propagates vegetatively by layering of the lower branches (a layer being an autonomous or potentially autonomous rooted branch), resulting in clones (Filion *et al.* 1985). With time, the clones divide into distinct units or layers, but erect stems never develop and therefore there is no production of sexual cones. We hypothesize that the intrinsic longevity of stunted clones will be high, providing that the absence of fire allows their long-term spatial development and that a favourable ratio of leaf:wood biomass can be maintained. We assume that,

following initial establishment after fire, genets will self-perpetuate by layering. Given sufficient time after the most recent fire, genets may reach considerable size and the surface area and diameter of the clones is likely to be proportional to their presumed age, which can be deduced from fire dating at the site. We then predict that maintenance of a stable leaf:wood ratio will allow the stunted clones to reach a life span unequalled by arborescent forms.

## Methods

### STUDY AREA

The study area is located in subarctic Québec, along the rivière Boniface, about 35 km east of Hudson Bay (Fig. 1). The regional landscape is part of a low, Precambrian plateau at an average altitude of 200–250 m above sea level. Climatic data from the nearest weather station located at Inukjuak, about 145 km north-west, show that the annual mean temperature is  $-7^{\circ}\text{C}$ , with a mean temperature of  $-26^{\circ}\text{C}$  in February and  $9^{\circ}\text{C}$  in July. The average frost free period lasts for about 60 days. The growing season extends from mid-June to mid-August. The mean annual precipitation totals 550 mm, 40% of which falls as snow (Environment Canada 1993).

The rivière Boniface sites are located at the north-west limit of the forest tundra and at the northern tree line (Payette & Morneau 1993). Open forest stands occupy wet depressions and protected valleys, whereas wind-exposed hills with thin soils are colo-

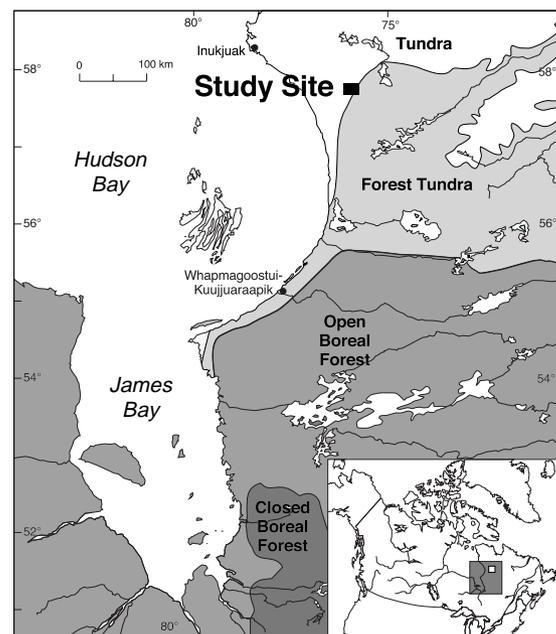


Fig. 1 Location of the study area.

nized by stunted spruce, dwarf birch, heath and lichen. Black spruce is the dominant species in the area, with rare tamaracks (*Larix laricina* (Du Roi) K. Koch). Charred dead stems lying on the ground and charcoal fragments beneath the vegetation cover indicate that fire influence is widespread, except at several sites scattered along the tree line where no signs of fire were recorded. The present vegetation cover reflects a long history of harsh climatic conditions combined with infrequent fires and this has determined the extent of forest regeneration. The distribution and dates of recent fires along a north-south transect (Payette *et al.* 1989a), from the continuous boreal forest to the arctic tundra, show that the number, surface extent and frequency of fires all decrease progressively towards the tree line. Those spruce stands that have been untouched by fires for several centuries or millennia consist of old trees that persist through layering.

#### SAMPLING

Fire data were gathered from a set of about 400 hill sites distributed within a 40-km<sup>2</sup> area along the rivière Boniface (S. Payette, unpublished data). At each well drained site, the date and spatial extent of the last fire that occurred was recorded, using fire scar dating for recent fires, tree-ring cross-dating of charred dead stems lying on the ground for events *c.*100–600 years ago, and radiocarbon dating of charcoal at the ground surface for the oldest fire events. The accuracy of the date of the most recent fire at a given site was checked in the field against other evidence such as fire scars and charred stems. Fire scars are found on spruce trees located at the periphery of a fire, whereas clones tend to be centred well inside the fire area, so they are unlikely to have survived the fire. Where the last fire event was old enough for obvious field evidence to have been obscured, we compared the radiocarbon age of several charcoal fragments from the same site and from adjacent sites, as well as the patterns of tree regeneration. Each sample of radiocarbon dated charcoal fragments beneath the organic horizon originated from one burned tree. A normal curve was established for each <sup>14</sup>C date using the mean and two standard deviations associated with each date. All dates were then weighed using a normal distribution probability table ( $\pm 2$  SD) and calibrated in calendar age using the Stuiver & Reimer (1993) program. The <sup>14</sup>C dates of the charcoal fragments give a maximum value for the time since the last fire. Charcoal fragments generally come from wood that was present at the time of the fire; if the charcoal had been produced from wood that died several decades or one hundred years before the onset of the last fire, the charcoal dates would be correspondingly older.

#### CLONE SELECTION AND MAPPING

The genetic integrity and persistence of stunted black spruce clones were checked using 25 putative clones in eight different sites. Sites were selected from a data set to give a range of postfire ages with similar soil and wind-exposing conditions. As the age of the clones is deduced from the last fire date, the latter becomes a determining factor in the choice of the sampling sites. The presence of the relationship between the surface area of the clones and their age will therefore depend on the accuracy of the fire dates, and on the assumption that establishment occurs immediately after fire, as well as on the absence of any spatial constraints acting to limit the lateral development of the clones. The success of tree regeneration depends on the climatic conditions prevailing during the first few years after fire and the structure of the stands at the time of ignition (Vioreck 1973; Black & Bliss 1980; Sirois & Payette 1991). Seed germination is rare in the absence of fire in exposed sites. So by determining the date of the last fire at a given site, it becomes possible to evaluate the maximum date of establishment of black spruce individuals occupying the site. Among our putative clones, we found that the smaller ones were restricted to recent burned sites while those of larger size were found only at old postfire sites, supporting the existence of a close allometric relationship between clone size and age and postfire stand age.

We first identified all sites within the 40-km<sup>2</sup> study area that had < 10% cover of black spruce. These sites, which were generally wind-exposed, were the most likely to harbour free-growing stunted clones. We then selected those that: (i) showed free drainage; (ii) had vegetation dominated by lichens of the genus *Cladina*; (iii) were exposed to dominant winter winds (to ensure the development of stunted spruce); (iv) contained no spatial constraint, such as boulders or outcrops that would inhibit the lateral development of a clone; (v) lacked ground-frost disturbance that modifies the expansion pattern of clones; and (vi) contained at least one clone that showed neither vertical stems (dead or alive) nor damage by caribou hooves (e.g. as shown by trampling scars, Morneau & Payette 1998).

The selected sites were grouped in eight age classes (200-year intervals) from present to 1800 BP, based on date of the last fire and its associated age variability, and one representative was chosen at random from each class (Table 1). At each site, the spatial delineation of each putative clone was determined with a theodolite ( $\pm 50$  cm precision) to provide data for calculation of surface area. None of the sampled clones exceed 30 cm in height. Clones perpetuate by layering, so that several stems may belong to the same genet. Due to the growth pattern of black spruce, the clone generally exhibits a circular or elliptical form, often fragmented into distinct

**Table 1** Postfire stand age

Site no.	Altitude (m)	Date of the last fire (laboratory no.)	Calendar years ( $\pm 2\sigma$ ) (AD)	Age (calendar year)
1	115	1881 AD	1881	114
2	135	1568 AD	1568	427
3	115	660 $\pm$ 50 BP (Beta-35532)	1300 (1280–1407)	695
4	125	970 $\pm$ 60 BP (Beta-35507)	1140 (985–1211)	855
5	125	1130 $\pm$ 50 BP (Beta-35515)	900 (802–1001)	1095
6	115	1350 $\pm$ 60 BP (Beta-31649)	670 (597–782)	1325
7	135	1480 $\pm$ 50 BP (Beta-31661)	600 (530–660)	1395
8	165	1800 $\pm$ 60 BP (Beta-31652)	240 (109–389)	1755

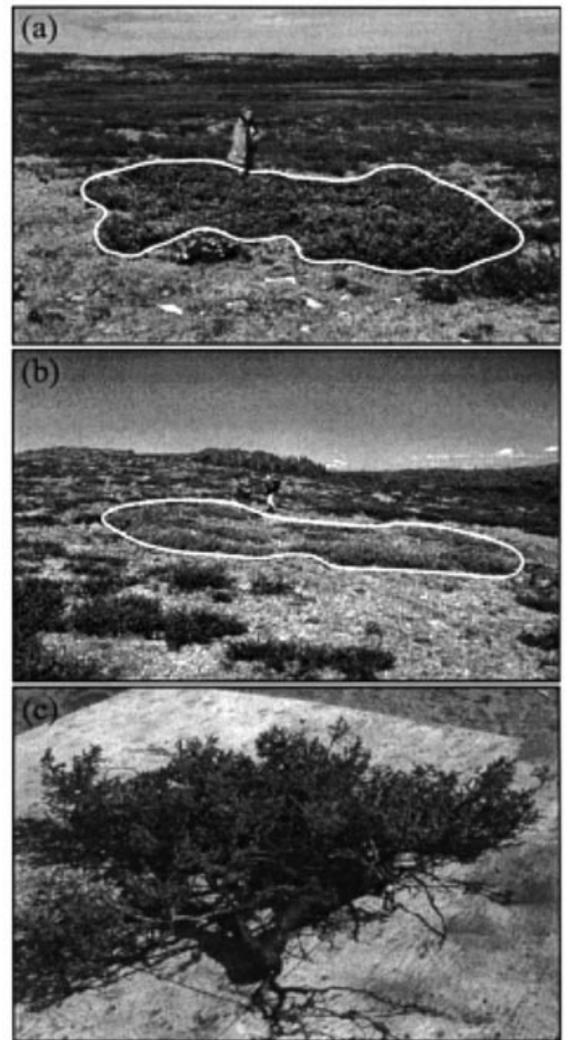
Tree-ring dating for sites 1 and 2. Radiocarbon dating (showing maximum age of the fire) for the remaining sites.

layers (Fig. 2). The oldest part of each clone, generally located at the centre, dies and rapid decomposition of its small branches creates an opening. Clones tend to fragment over time, but we were able to map the live parts of each clonal unit.

#### GENETIC ANALYSIS

The visual identification of the putative clones was validated by a genetic analysis using random amplified polymorphic DNAs (RAPDs). The genetic analysis was performed on leaf material. A total of 250 annual shoots were sampled from the 25 mapped clones, and included tissue from each of the layers within a given clone. Tissue was also taken from the stems of neighbouring spruce (within a radius of about 100 m). DNA extraction follows a protocol modified from Bousquet *et al.* (1990). The DNA concentration was evaluated by electrophoresis. The choice of primers was based on the work of Isabel *et al.* (1995) for black spruce populations in southern Québec. After preliminary trials, four primers were retained. The primers revealed at least four scorable RAPD fragments per primer, which could be used to reduce the number of amplifications necessary to deliver the genotypic information at a minimum of 15 loci. A total of 18 polymorphic fragments were used to generate the multilocus genetic fingerprints. DNA amplification follows the protocol described in Roy *et al.* (1992). Each amplification was repeated once to test replicability. Only the replicable fragments were included in the analysis.

Genetic integrity was tested by comparing the band patterns of the samples within each clone. Only the loci with well segregated bands were considered. Based on the combinations of amplification patterns from the four primers, genotypes were assigned to each sample. All the samples showing identical band patterns were considered to be part of the same clone. The probability of obtaining two identical patterns not belonging to the same clone was computed using the formula of Jeffreys &



**Fig. 2** Stunted black spruce clones (genetically identified) at tree line: (A) *c.* 400-year-old clone. (B) *c.* 1000-year-old clone. Snowdrift abrasion in association with low temperatures affects the needles and apical meristems at the snow–air interface, thus preventing the production of erect stems and sexual cones. In this growth form, black spruce propagates vegetatively by layering of the lower branches. With time, the clones divide into distinct layers. (C) Closer view of a single layer which has an independent root system.

Morton (1987). The mean similarity coefficient in the population ( $S$ ) was computed using Lynch's similarity index (Lynch 1990).

#### BIOMASS SAMPLING

One genetically distinct clone per postfire age class was randomly chosen for measurements of above- and below-ground biomass at ages from 113 to 1800 years. To avoid the complete destruction of the clones, a grid of 1-m<sup>2</sup> quadrats was laid out and only 20% of the total surface area of each clone was removed for biomass determination. The first quadrat was randomly chosen, and then the biomass was systematically sampled at 5 m intervals. The above-ground biomass (branches and needles) was collected first, after which all the roots > 0.2 cm in diameter were sampled. For comparison we also measured above- and below-ground biomass of 10 complete layers (randomly chosen from 120 layers located on a hill burned at about 1600 BP) and for 10 trees (from two forest stands growing in well-drained soils in protected valleys). Trees were selected according to their normal shape (absence of damage to branches or stem). A cross-section at the base of each layer and each tree was sampled and finely sanded for age determination from tree-ring counts.

The biomass samples from clones, layers and trees were placed in an oven at 65 °C for 48 h. The needles were then manually separated from the branches (and cones in the case of trees) and sifted to eliminate extraneous material such as lichen, sand and gravel. The needles and the above- and below-ground parts of all the clones, trees and layers were then weighed. Bark was also included in the mea-

surements, although biomass generally refers to the living parts of a plant (Ford-Robertson 1971).

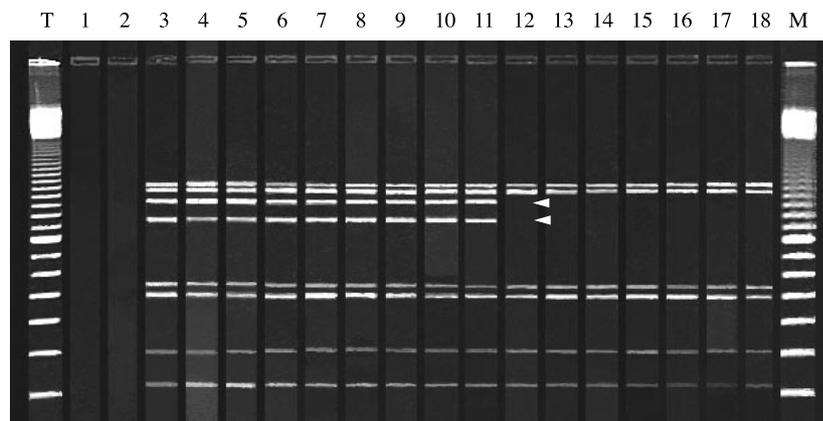
## Results

#### GENETIC IDENTIFICATION OF THE CLONES

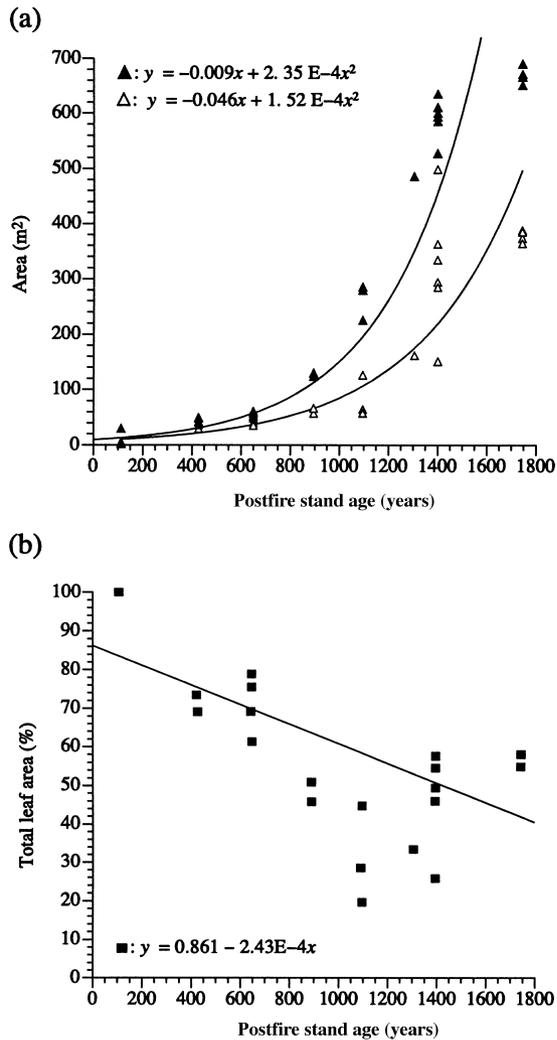
The genetic analysis enabled the identification of 30 genotypes, comprising the 25 mapped clones together with five further individuals located outside the clones. Eighteen fragments were retained among the band profiles generated by the four primers. All bands considered were polymorphic. Each genotypic profile was identified by the presence or absence of one or more bands (Fig. 3). Twenty-five of the 30 genotypes identified belonged to distinct clones in which each tested sample showed the same genotype. Similarity coefficients were used to compute the probability of obtaining two identical genotypes not belonging to the same genet. With a mean similarity coefficient of 0.885 and a mean number of presence of fragments of 15.5, the probability of obtaining matching genotypes from two distinct clones was 0.0186.

#### AGE-SURFACE RELATIONSHIPS

Genotypic data were used to calculate the surface area occupied by each clone. The size of the mapped clones ranged from 2.8 to 691.3 m<sup>2</sup> (Fig. 4a). The total surface area increases with postfire stand age, at a slow rate over the first 600 years, and then more rapidly ( $R^2 = 0.98$ ,  $P < 0.001$ ). The same trend was observed when considering only the living parts, although the increase in size was slower ( $R^2 = 0.92$ ,  $P < 0.001$ ). The ratio of living parts to the total surface area of the clones decreases with postfire stand age (Fig. 4b) ( $R^2 = 0.36$ ,  $P = 0.0015$ ). Clones < 400



**Fig. 3** Agarose gel electrophoresis of RAPD fragments obtained with the primer MUL11M1. Lanes T and M are the size standard. Lanes 3–11 show RAPD fragments from samples derived from the same clone, as do lanes 12–18 for another clone. Arrows show the absence of fragments 900 pb and 1100 pb in the second individual. Negative controls are shown in lanes 1 and 2.

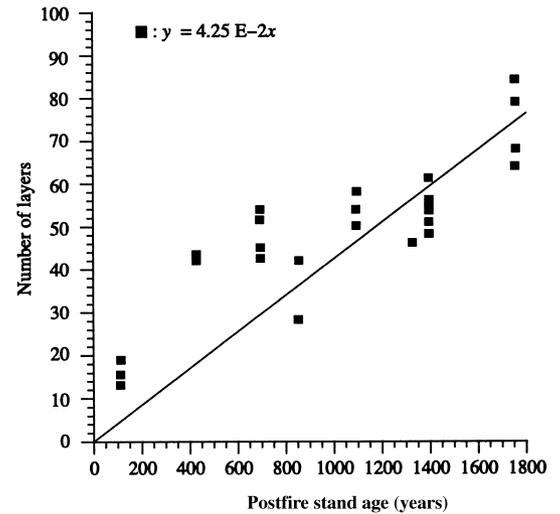


**Fig. 4** Surface area of clones of different ages deduced from postfire stand age. (a) relationship between total surface area (▲) and photosynthetic area (total surface area : non-leafy area, △) of the clones and age. (b) Percentage of clone that bears leaves [(photosynthetic area/total area) × 100] as a function of the presumed maximum age of clones deduced from postfire stand age.

years old form a compact mat at the ground surface, whereas clone fragmentation begins in 600-year-old clones with the death of the central part of the leafy mat. The number of independent layers increases according to postfire stand age (Fig. 5) ( $R^2 = 0.73$ ,  $P < 0.001$ ).

#### BIOMASS CHANGE WITH TIME

All components of biomass increase with age in both clones and trees (total biomass increased from 0.7 to 25 kg in 80 years), whereas biomass of individual layers shows only a small increase with age (Fig. 6a–d). The leaf : wood ratio decreases with age in trees and layers according to age, while it remains



**Fig. 5** Number of layers as a function of clone age deduced from postfire stand age.

constant over time in clones, regardless of postfire stand age (Fig. 7).

#### Discussion

The development of new techniques enables the genetic identification of clones (Smith *et al.* 1992; Steinger *et al.* 1996). RAPD markers allowed us to show conclusively that stunted clones are genetically identical. Also, no establishment of new genets within an existing clone was observed.

The determination of the age of individual clones is always problematic due to the death and decomposition of the oldest parts. In most cases, the age of clones is estimated from the size and the mean annual growth rate (Steinger *et al.* 1996). We deduced the age of clones from tree ring counts and radiocarbon dating of charcoal fragments from the last fires that had affected the studied sites. The strong correlation between the estimated age of clones deduced from postfire stand age and their size confirms the close relationship between the age of genets and time since the last fire. This is explained by the swift postfire establishment of spruce from seeds shed from semiserotinous cones at the time of the burn and their ready germination before the development of a dense vegetation cover (Black & Bliss 1980; Morneau & Payette 1989). Due to the disappearance of the forest after fire, the harsh new conditions of burned sites (Payette *et al.* 1989b) prevent the production of erect stems in the postfire tree cohort, thus causing the adoption of a stunted growth habit. Lateral expansion through layering has permitted the persistence of the clones up to the present day. Our data show that, in the

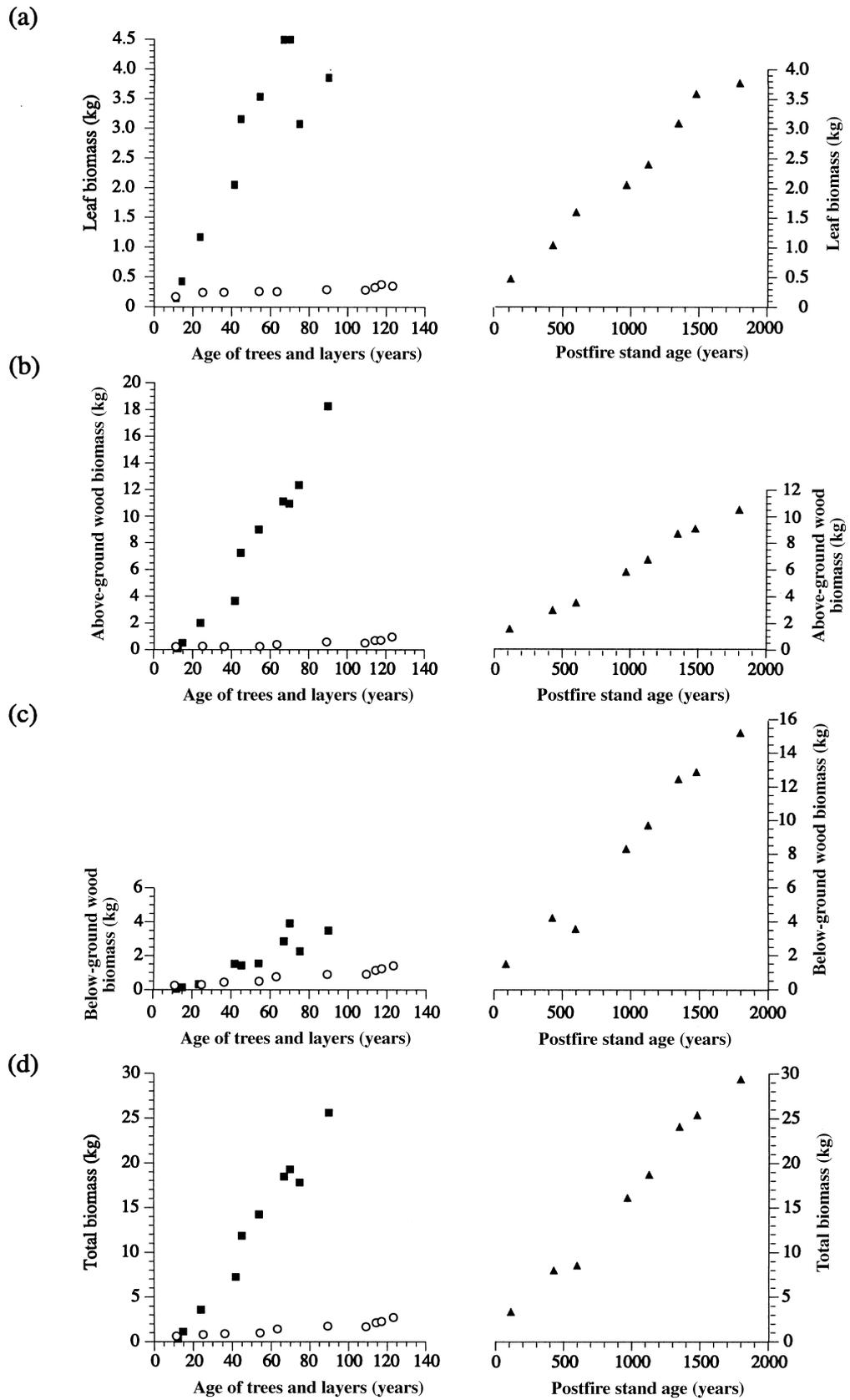


Fig. 6 Biomass (dry weight) of trees (■), layers (○) and clones (▲) as a function of age or postfire stand age; (a) needle mass; (b) above-ground wood mass; (c) below-ground wood mass; (d) total biomass.

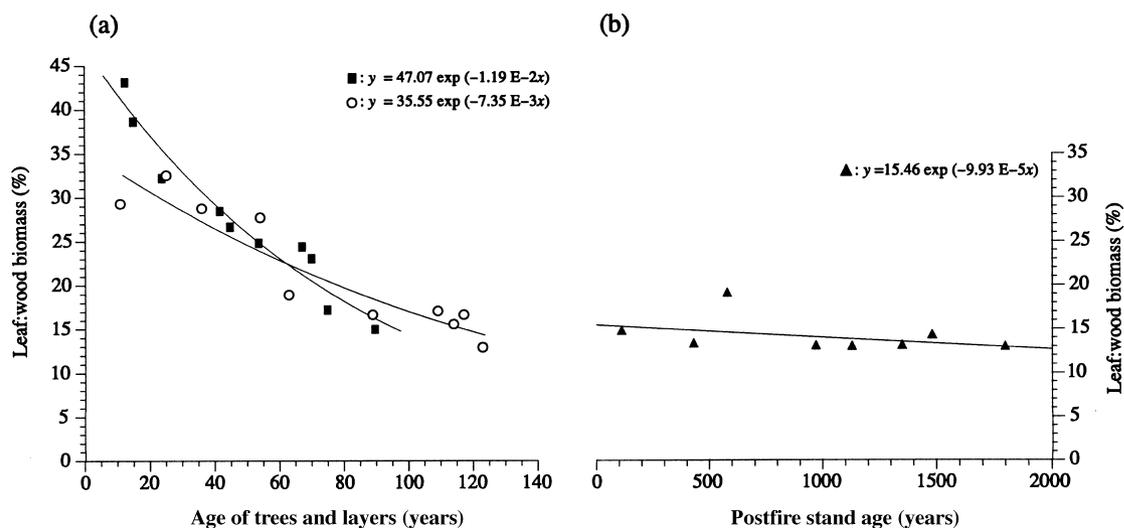


Fig. 7 Leaf: wood biomass ratio according to (a) age of trees (■) and layers (○), and (b) postfire stand age of clones (▲) (trees:  $R^2 = 0.94$ ,  $P < 0.01$ ; layers:  $R^2 = 0.88$ ,  $P < 0.01$ ; clones:  $R^2 = 0.38$ ,  $P < 0.05$ ).

absence of any spatial constraints, the surface occupied by stunted clones is indicative of their age.

The continuous lateral expansion suggests that clonal growth can go on indefinitely in absence of disturbance. Most non-clonal organisms show exponential growth in the juvenile stage and a later asymptotic growth phase. This characteristic growth plateau generally corresponds to the onset of senescence, but there is no evidence of this occurring, even in 1800-year-old clones, suggesting an even longer potential longevity. The vigorous lateral growth of old aged clones is clearly associated with the increasing number of independent layers with time (Fig. 5). The continuing trend to increase in size may mask interannual variation in the rate of lateral growth. The residence time of spruce macrofossils on the ground at the studied sites is at least 600 years (Payette & Morneau 1993) and no major environmental changes have affected wind-exposed sites at tree line during the past thousand years (Payette *et al.* 1989b). The morphological similarity of all stunted clones and the absence of wood remains strongly suggest that the clones have shown this pattern, with no upright growth since their initial establishment.

Biomass shows an increase with time in trees and clones whereas it remains relatively constant in layers. The sharp increase of biomass in trees is mainly due to the accumulation of non-photosynthetic material, although needles do increase, whereas in clones the different biomass components (above-ground, below-ground and needles) increase more similarly with postfire stand age (Fig. 6). As they mature, trees accumulate an important biomass in both leaves and wood, but because needles are

mainly concentrated at the tips of branches to optimize light interception, branch biomass must increase disproportionately to accommodate the increased weight. This change is marked in trees but only moderate in layers (which can be compared to small trees), whereas the leaf:wood ratio remains constant with time in clones (Fig. 7). Maintaining a small size probably avoids the need to accumulate wood and the problems associated with hydraulic transport. The variation in the leaf:wood ratio with age in layers resembles that observed in trees, despite the more moderate slope (Fig. 7). Within the clones, layers develop like trees until their height becomes limited by snow-drift abrasion. The tendency of layers to divide once they have achieved a certain size may explain the apparent absence of an increase in their biomass with age (Fig. 6a–d).

The longevity of stunted black spruce clones exceeds that of most other tree species in subarctic Québec. The pattern of spatial development of clones along the postfire chronosequence suggests that still older clones may be present at other sites in this area which have been dated at > 3000 years postfire. The maximum longevity of prostrate clones may be directly associated to the extent of their fragmentation. Lateral expansion without fragmentation would result in an accumulation of wood and a reduction of the leaf:wood ratio as in trees, whereas fragmentation of clones into physiologically independent layers enables the maintenance of a constant leaf:wood ratio. Stunted clones can therefore reach a very old age because they grow in an environment where catastrophic disturbances like fires and epidemics are infrequent and fragmentation can proceed at a regular pace.

The discovery of such long-lived organisms provides a unique opportunity to study the mechanisms of longevity in clonal trees. Our results show the absence of senescence in 1800-year-old stunted clonal spruce living in a harsh environment where sexual reproduction is absent. Unless future climatic changes are substantially larger than those of the past 2000 years, stunted clones will continue to ensure the presence of tree species beyond tree line.

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