

Clonal development of *Maianthemum dilatatum* in forests of differing age and structure

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Abstract: The development of a dense tree layer in young coniferous stands can suppress understory plants, leading to very low herb abundance and diversity. In this study, clonal development of the rhizomatous herb *Maianthemum dilatatum* (Wood) Nels & Macbr. was compared among four types of coniferous forest (young, closed canopy; young, silviculturally thinned; mature; and old growth) on the western Olympic Peninsula, Washington. We predicted that (i) ramet turnover would be lowest, (ii) clonal fragment size would be smallest, and (iii) allocation of resources to leaves would be greatest in young, closed-canopy forests, and that these traits would increase (or decrease for leaves) as understory conditions became more favorable with stand development or thinning. The low frequency of new ramets in young, closed-canopy stands supported the first prediction. The second prediction was also supported: lateral spread and rhizome mass were smallest in these stands. However, allocation to leaves was not higher in dense young stands, indicating that *Maianthemum* does not respond to stress by increased investment in leaves. Clonal fragments in thinned, mature, and old stands showed no differences in traits, suggesting that once tree canopies rise, canopy gaps form, or young stands are thinned, resource levels are favorable for clonal growth. *Maianthemum* appears to persist in dense, young stands by maintaining long-lived ramets that produce leaves annually, rather than by increasing rhizome spread, rhizome storage, or allocation to leaves.

Key words: age structure, biomass allocation, canopy closure, forest herb, rhizome.

Résumé : Le développement d'une dense canopée dans les jeunes peuplements de conifères peut supprimer la végétation de sous-bois et conduire à de très faibles abondances et diversités de petites plantes herbacées. Dans cette étude, les auteurs comparent le développement clonal d'une plante herbacée, le *Maianthemum dilatatum* (Wood) Nels & Macbr., dans quatre types de forêts conifériennes (jeune à canopée fermée, jeune éclaircie par sylviculture, mature, surannée), situés dans la péninsule Olympique occidentale de l'état de Washington. Les auteurs ont prédit que (i) le cycle de ramettes serait le plus faible, (ii) la dimension des rameaux clonaux serait la plus faible, et (iii) l'allocation aux feuilles serait la plus élevée dans les jeunes forêts à canopée fermée, et que ces caractéristiques augmenteraient (ou diminueraient) à mesure que les conditions de sous-bois deviendraient plus favorables avec le développement ou l'éclairci du peuplement. La faible fréquence des nouvelles ramettes dans les peuplements jeunes à canopée fermée supportent la première prédiction. La seconde prédiction s'avère également juste : le développement latéral et la masse de rhizome sont plus faibles dans ces peuplements. Cependant, l'allocation aux feuilles n'est pas plus forte dans les jeunes peuplements denses, ce qui indique que le *Maianthemum* ne réagit pas à l'ombrage par un investissement accru dans les feuilles. Les fragments clonaux dans les peuplements éclaircis, matures et surannés ne montrent aucune différence de caractéristique, ce qui suggère qu'une fois la canopée arborescente élevée, que des trouées s'y forment ou que le jeune peuplement est éclairci, le niveau des ressources favorise la croissance clonale. Le *Maianthemum* semble persister dans les jeunes peuplements denses en maintenant des ramettes longévives qui produisent annuellement des feuilles, plutôt qu'en allongeant les rhizomes, les réserves dans les rhizomes, ou l'allocation aux feuilles.

Mots clés : structure d'âges, allocation de la biomasse, fermeture de la canopée, herbes forestières, rhizome.

[Traduit par la Rédaction]

Introduction

Species persistence during the development of a dense canopy stage in young coniferous stands often depends on long-term survival of ramets or formation of new ramets through clonal growth (Kudoh et al. 1999) because sexual reproduction

is very limited (Grime 1979; Ashmun and Pitelka 1984; Dahlem and Boerner 1987). As resource availability increases either through tree mortality during natural stand development or because of silvicultural thinning, many clonal herbs and shrubs increase in abundance, presumably by lateral growth (Tappeiner and Alaback 1989; Huffman et al. 1994; Halpern

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Table 1. Mean stand-level characteristics (± 1 SE) for the four forest types.

Forest type	Young, closed canopy	Young, thinned	Mature	Old-growth
Number of stands	4	3	2	3
Age (years)*	28–46	36–49	~75	>200
Tree DBH (cm)	27.3 \pm 1.2	38.9 \pm 0.6	48.9 \pm 0.7	54.6 \pm 8.3
Canopy cover (%) [†]	97.3 \pm 0.4	88.1 \pm 0.3	94.9 \pm 1.5	90.9 \pm 1.0
CV of canopy cover [‡]	1.3 \pm 0.36	3.1 \pm 0.28	1.3 \pm 0.31	2.5 \pm 0.11
Tree density (no./ha)	1019 \pm 184	288 \pm 19	415 \pm 2	204 \pm 14
Canopy height (m)	27.6 \pm 1.6	31.6 \pm 1.5	44.3 \pm 0.9	40.4 \pm 1.6 [§]
Understory vascular plant cover (%)	10.3 \pm 2.3	38.7 \pm 15.2	38.5 \pm 3.5	59.7 \pm 5.2

Note: Stand-level characteristics are average values from four to six, 0.01–0.06 ha plots.

*Stand ages were determined using historical records, increment cores of canopy trees, and ring counts of stumps in adjacent clear-cut sites. In combination, these sources of information provided accurate ages for all but old-growth stands, which are uneven aged with dominants >200 years old.

[†]Canopy cover was measured with a spherical densiometer at five points in each plot.

[‡]Mean coefficient of variation (CV) of the five canopy cover readings per plot.

[§]In old-growth stands, *Pseudotsuga* and *Picea* emerged at heights of ca. 65–85 m, well above a lower canopy of *Tsuga*.

and Spies 1995; Huffman and Tappeiner 1997; Lezberg 1998; Thomas et al. 1999). Thus, for understory herbs, the dynamics of populations during stand development and the abundance of species in older or thinned stands is strongly influenced by two characteristics related to clonal growth: ability to survive through the dense canopy stage and effectiveness in expansion as conditions become more favorable. However, few studies have compared clonal growth in stands representing different stages of forest development (but see Tappeiner and Alaback 1989; Cain and Damman 1997).

Low resource availability leads to low overall growth of clonal forest herbs, as shown by both greenhouse and field transplant experiments (Ashmun and Pitelka 1984; Salonen 1994; Marino et al. 1997), and may also lead to changes in resource allocation that increase the probability of survival during such periods. Clonal species may show adaptive responses that improve fitness in stressful environments by increasing resource acquisition or reducing expenditures (Hutchings and de Kroon 1994; Soukupová 1994). Resource expenditures can be reduced by slower turnover of plant parts, that is, through decreased production and greater persistence of ramets. Clonal spread and maintenance of connections among ramets also require resources, so that stressful conditions should limit rhizome growth and connectivity, resulting in a decrease in clonal fragment size (Stoll et al. 1998). Conversely, ramet connectivity could be advantageous in resource-poor forests because it can facilitate sharing of spatially separated resources, exploitation of dispersed resources, or support of newly formed ramets (Jónsdóttir and Watson 1997). However, most of these benefits accrue under heterogeneous environments (Stuefer et al. 1996; Alpert 1999), and both light and belowground resources tend to be uniformly low in dense, closed-canopy forests. Greater access to limiting resources could be achieved by greater allocation to foraging organs (e.g., roots or leaves) or by translocation of carbon or nutrients from storage to foraging organs (Hutchings and de Kroon 1994; Soukupová 1994; Hutchings 1997). Low light intensity and quality often limit clonal growth in dense stands (Anderson et al. 1969; Messier et al. 1989; Lieffers et al. 1999), which should translate into increased allocation to leaves (Givnish 1982). However, nutri-

ents or water may also be limiting under these conditions (Toumey and Kienholz 1931; Cole et al. 1990; Coomes and Grubb 2000), which would favor increased allocation to roots.

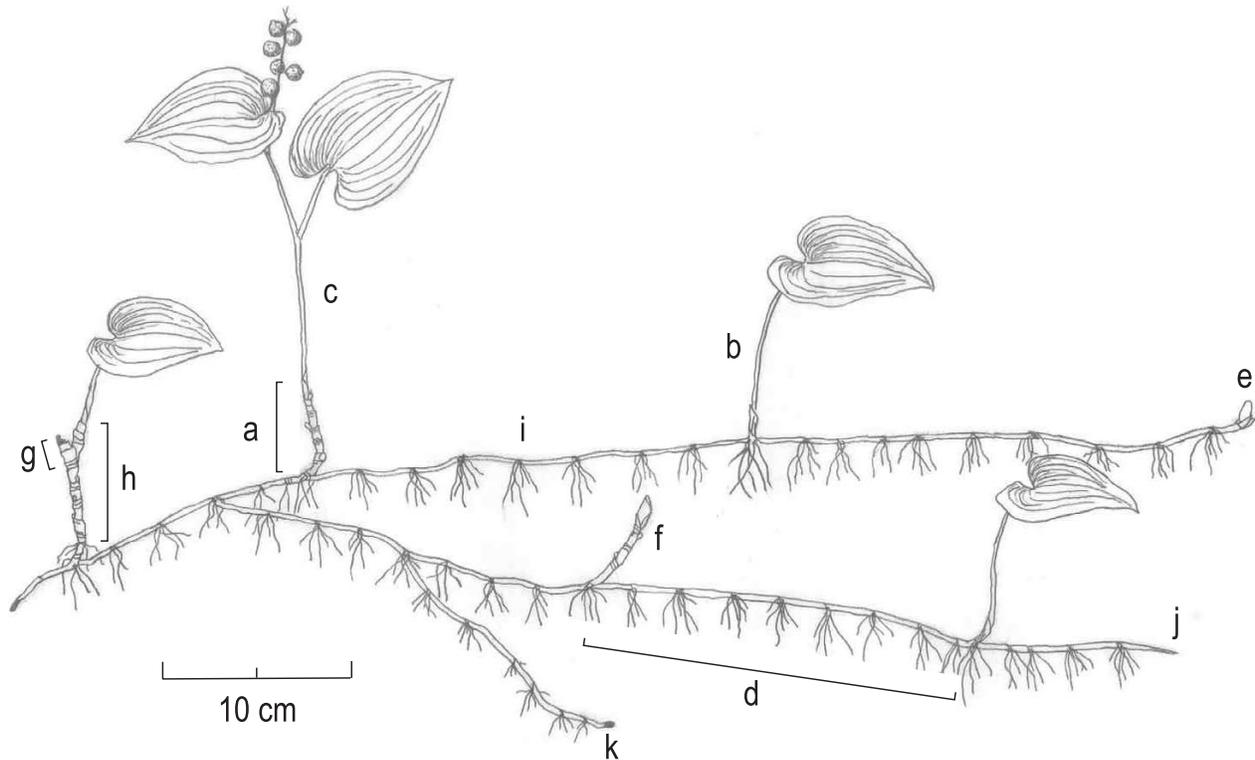
Maianthemum dilatatum (Wood) Nels & Macbr. is a common rhizomatous herb that shares attributes of both a shade-tolerant species and a successful pioneer of open habitats (Kawano et al. 1968). In this study we compare the clonal traits of *Maianthemum* in stands representing distinct stages in the successional development of northwestern coniferous forests (young, closed canopy; mature; and old growth) as well as silviculturally thinned stands. These are forest types with distinct structural characteristics (Spies and Franklin 1991) and levels of resource availability. Stem densities are very high and light levels are uniformly low in young, closed-canopy stands, whereas recently thinned stands typically have the most open canopies (Table 1). As stem densities decline, light levels gradually increase in mature and old-growth stands. Variability in canopy cover is highest in thinned and old-growth stands. It is likely that belowground resources also increase in abundance and variability as canopy cover decreases and canopy gaps form. We evaluate the following predictions with respect to these gradients in stand structure and resource availability: (i) ramet turnover (initiation and mortality) as inferred from age distributions and (ii) clonal fragment size (mass and lateral spread) will be smallest in young, closed-canopy stands and will increase with forest successional age and canopy openness, and (iii) allocation to leaves will be highest in young, closed-canopy stands and will decrease with successional age and canopy openness.

Methods

Study species

Maianthemum dilatatum (hereafter, *Maianthemum*) is a clonal, rhizomatous herb of moist temperate forests of the Pacific coast of North America, Japan, and coastal portions of eastern Asia (Kawano et al. 1968; LaFrankie 1986). In North America, it is most abundant in forests of the wet, coastal *Picea sitchensis* (Bong.) Carr. zone (Kawano et al. 1971; Henderson et al. 1989), but is also common farther inland in forests of the *Tsuga heterophylla* (Raf.) Sarg. zone. Although *Maianthemum* often increases in abundance near

Fig. 1. Clonal fragment of *Maianthemum dilatatum* illustrating the modular growth form. Each short shoot (*a*) gives rise to a vegetative (*b*) or a sexual shoot (*c*). A ramet or module (*d*) consists of a rhizome segment initiated at the base of a parent short shoot, a belowground short shoot, and an aerial shoot. New rhizome segments eventually turn upward, forming an overwintering bud containing a preformed shoot (*e*). Short shoots may remain dormant (*f*), failing to produce a leafy shoot while remaining connected to the clonal fragment. A short stub (*g*) on a branched short shoot (*h*) indicates abscission of a former sexual shoot. Roots emerge at nodes (*i*) along the rhizome, which extends laterally at growing tips (*j*) or terminates with a damaged or decayed end (*k*).



forest edges and openings, it occurs in all stages of forest development, surviving under a broad range of light and forest-floor conditions (Kawano et al. 1968; LaFrankie 1986; Henderson et al. 1989).

Seedlings develop a primary root and a buried orthotropic rhizome, from which one or two horizontal rhizomes eventually emerge to initiate clonal growth (LaFrankie 1986). The primary root eventually decays, masking evidence of seedling origin and genet age.

For our study, we define the buried orthotropic portion of the rhizome with its closely packed nodes as a short shoot (Fig. 1*a*) to distinguish it from horizontal rhizomes. Short shoots may bear an aboveground vegetative shoot (morphologically a leaf; Fig. 1*b*) or a sexual shoot (Fig. 1*c*). The interconnected short shoots, aerial shoots (i.e., vegetative or sexual shoots), rhizomes, and roots constitute the clonal fragment (sensu Antos 1988), the sampling unit of this study. A ramet (Fig. 1*d*) is considered to be a potentially independent module of the clonal fragment, analogous to the sympodial module of *Podophyllum peltatum* (Geber et al. 1997), and is comprised of a short shoot with or without an aerial shoot and a proximal rhizome segment with roots and lateral buds at the nodes (Silvertown and Lovett Doust 1993).

Aerial shoots arise from rhizome apices or from established short shoots. Clonal growth proceeds as the rhizome apex turns upward to form an overwintering short shoot with a swollen apical bud containing a preformed aerial shoot (Fig. 1*e*). From a basal node of the upturned short shoot, an axillary bud grows laterally, eventually forming the next modular unit of horizontal rhizome, short shoot, and aerial shoot (Fig. 1*d*). Established short shoots can produce aerial shoots for many years, however, they may remain dormant for at least one growing season (Fig. 1*f*). Flowering termi-

nates growth and leads to abscission of the sexual shoot (Fig. 1*g*), but new growth may be initiated from a nearby axillary bud, leading to an articulation in the short shoot (Fig. 1*h*). After autumn leaf senescence, the clonal fragment persists underground as a network of long-lived rhizomes and short shoots bearing overwintering apical buds. Growth from rhizome apices and branching at lateral buds leads to extensive spread across the forest floor (Kawano et al. 1968), although lateral spread of clonal fragments is limited by decay and fragmentation of the slender rhizomes.

Study sites

The study was conducted in low-elevation, coniferous forests of the western Olympic Peninsula, Washington, U.S.A. The climate is mild and wet with mean monthly temperatures ranging from ca. 4°C in January to 16°C in July, and mean annual rainfall ranging from 2900 to 3500 mm (Western Regional Climate Center 1999). Most precipitation occurs as rain between October and March, with <8% of annual precipitation falling between June and August (Henderson et al. 1989).

The 12 study sites (stands) were located within ca. 68 km of each other in the moist *Tsuga heterophylla* forest zone (Henderson et al. 1989) of the Hoh, Quinalt, and Humptulips watersheds. All sites were level or gently sloping (1–14% slopes) on upper valley terraces, flats, or toe slopes at 155–232 m elevation. Primary tree species at all sites were *Tsuga heterophylla*, *Pseudotsuga menziesii* (Mirb.) Franco, and *Picea sitchensis* (Table 1). Understories were dominated by *Vaccinium alaskaense* Howell, *Vaccinium parvifolium* Smith, *Oxalis oregana* Nutt. ex Torr. & Gray, *Polystichum munitum* (Kaulf.) Presl., or *Blechnum spicant* (L.) Roth, with *Rubus spectabilis*

Pursh common in silviculturally thinned stands. Bryophytes typically covered at least 30% of the forest floor.

The 12 sites represent four forest types of distinct age and stand structure (Table 1), and share comparable climate and surficial geology. To minimize any potential confounding of genetic differences among populations and forest type, stands of each type were chosen from within each of the three watersheds to the extent possible (Lezberg 1998). Three forest types (young, closed canopy ($n = 4$); mature ($n = 2$); and old growth ($n = 3$)) correspond to the stem exclusion, understory reinitiation, and late-successional stages of forest development, respectively (Oliver and Larson 1996; Lezberg 1998). The fourth type, young, thinned forest ($n = 3$), is comparable in age, tree size, and composition to young, closed-canopy forest, but sites were silviculturally thinned 3–7 years prior to sampling, thus permitting comparison of the effects of stand density and canopy openness not confounded by stand age. All young stands (closed canopy and thinned) originated after clear-cut logging and slash burning; all were planted with *Pseudotsuga menziesii*, but uniformity of planting and survival varied considerably, as did the amount of natural regeneration of *Tsuga heterophylla* and *Picea sitchensis*. Mature stands (ca. 75 years old) had a single-layered canopy of *Tsuga heterophylla*; most trees established after a major windstorm in 1921. Old-growth stands were vertically complex, uneven-aged forest originating more than 200 years ago, with no visible signs of human disturbance.

Tree density and canopy cover decreased, but mean tree diameter, canopy height, and variation (coefficient of variation; CV) in canopy cover generally increased with forest developmental stage or thinning (Table 1). Total understory vascular plant cover, perhaps the best indicator of resource availability or favourability of the understory environment, was sparse in young, closed-canopy stands, but increased with developmental stage or thinning (Table 1). All forest types had abundant woody debris in various stages of decay and organic horizons that varied in depth (ca. 1–15 cm) within and among stands (data not shown).

Plant excavations

In the late summer and early fall of 1996, just before plant senescence, we excavated 9–15 clonal fragments per stand (a total of 140 clonal fragments) and recorded their demographic and morphological traits. Within each stand, we randomly selected aerial shoots from three to six 0.04-ha plots spaced ≥ 60 m apart, coinciding with areas measured for forest structural attributes. The entire clonal fragment associated with the initially chosen aerial shoot was carefully excavated until decayed ends or new rhizome tips were encountered (Antos and Zobel 1984). Excavated clonal fragments were placed in plastic bags, stored on ice, and transported to the laboratory. Fresh rhizomes were gently washed, air dried, and frozen in plastic bags along with leaves for future analyses of short-shoot age and dry mass of clonal fragments.

Plant measurements

Age structure and demography of shoots

Using the established understanding of morphological development (Silva et al. 1982; LaFrankie 1986), we aged each live short shoot on a clonal fragment by counting the number of lateral buds and the number of clusters of three to four scale-leaf scars subtending the leaf. Branched short shoots (i.e., those that had previously flowered; Fig. 1h) with live apical meristems were assigned an age equal to the summed age of the primary and secondary branches. In the 1.4% of short shoots where age of ramets was obscured by basal decay, a minimum age was assigned according to the remaining scars.

All live ramets were assigned to one of three demographic conditions: vegetative shoot, sexual shoot, or dormant short shoot.

Vegetative shoots had a single basal leaf or the remains of a petiole (if laminae had been browsed). Sexual shoots had two to three stem leaves and a flowering or fruiting stalk (Fig. 1c). Dormant short shoots lacked any aboveground structure, but had fully formed apical buds (Fig. 1f) subtended by at least one cluster of scale-leaf scars. The apical buds of each short shoot were inspected with a dissecting microscope to distinguish dead (decayed or aborted apical buds) from dormant short shoots.

Morphology and biomass

Area of each leaf was determined in the field by counting grid squares on a mylar overlay. Total and specific leaf area (leaf area per dry mass) for each clonal fragment were obtained using the summed area of leaves. Belowground traits were measured in the field on freshly excavated clonal fragments. These included maximum linear distance occupied by the rhizome system (rhizome lateral spread), summed length of all horizontal rhizome segments (total rhizome length), number of rhizome apices (new tips) and decayed rhizome ends, and maximum rhizome diameter (Antos and Zobel 1984). From these, we derived the ratio of new tips to decayed tips and the ratio of rhizome dry mass to length (specific rhizome mass).

We separated clonal fragments into four live components: horizontal rhizomes, roots, short shoots with associated perennating buds, and aboveground parts (leaves and aboveground stems on sexual shoots). All plant tissues were oven-dried to a constant mass at 60°C and weighed to the nearest 0.01 mg.

Data manipulation and analysis

Age structure and demography of short shoots

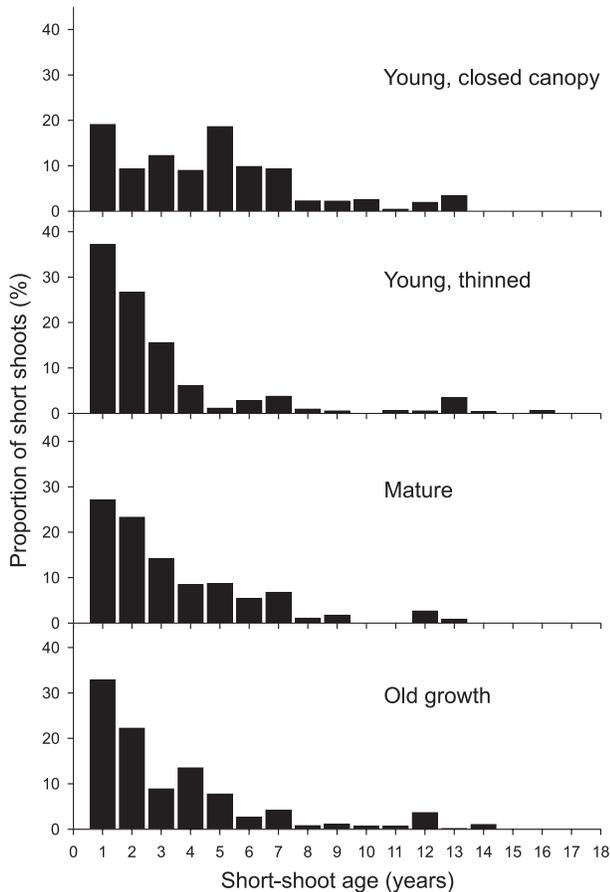
The proportion of short shoots in each annual age-class was determined for each clonal fragment. Proportions were averaged to produce an age distribution for each stand, then an aggregate age distribution for each forest type. Similar analyses of age structure have been used to reconstruct the formation and longevity of ramets of other clonal herbs (Silva et al. 1982; Whitman et al. 1998). Because of fragmentation of rhizomes, we did not attempt to assess the ages of *Maianthemum* genets, but used the maximum short-shoot age to represent the minimum age of each clonal fragment.

To test for differences among forest types in vegetative production of new ramets we conducted a one-way analysis of variance (ANOVA) on the proportion of clonal fragments with new (1- or 2-year-old) short shoots, followed by a Tukey HSD test to compare the means of individual forest types. Simple linear regressions were used to test for relationships between stand-level demographic traits and tree canopy cover or density ($n = 12$). Dependent variables (measured per clonal fragment and averaged per stand) included mean and maximum ages of short shoots, number of live short shoots, and ratio of dormant to leafy short shoots per clonal fragment.

Morphology and biomass

Nested ANOVAs (stands nested within forest types) were used to test whether the morphological and biomass traits of clonal fragments differed among the four forest types (main effect) (Sokal and Rohlf 1981). Analyses were performed using the MGLH (multivariate general linear hypothesis) module in Systat® 7.0, with the type III (sum of squares) model appropriate for unbalanced designs (SPSS 1996) and an F ratio calculated as MS forest types / MS stands within forest types. Where a significant main effect was shown, a Tukey HSD test was used to compare means among forest types. Log or exponential transformations of response variables were used to improve homogeneity of variances and normality of data. All statistical analyses were conducted with Systat® 7.0 (SPSS 1996).

Fig. 2. Frequency distribution of short-shoot ages per clonal fragment in the four forest types. Frequencies represent the average age of 9–15 clonal fragments per stand and 2–4 stands per forest type (see Methods).



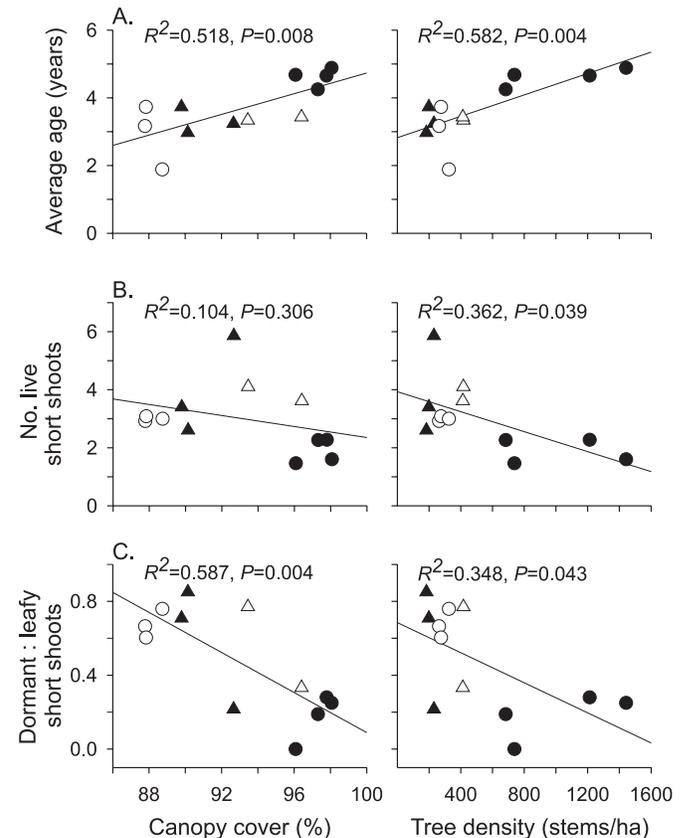
Results

Age structure and demography of shoots

We found little evidence of recent sexual reproduction in *Maianthemum*. Only 8 of the 140 clonal fragments excavated possessed intact primary roots; these had started from seed 1–7 years previously and occurred in all stand types except old growth. Although 23 prior flowering events were recorded as branched short shoots (4.7% of all short shoots examined), we found only three current sexual shoots and four buds containing preformed sexual shoots, all in young, thinned stands.

The age structure of short shoots was distinctive in young, closed-canopy (YCC) forests, with a fairly even distribution of 1- to 7-year-old shoots (Fig. 2). In the remaining forest types, the majority of short shoots were 1 or 2 years old with a gradual decline in the proportion of older shoots. The proportion of clonal fragments with new shoots was lowest in YCC forests (ANOVA on proportion with new shoots, $F_{[3,8]} = 8.74$, $P = 0.007$). Ramets persisted for at least 13 years in all forest types; 16 years was the maximum age observed (Fig. 2). Although the mean maximum short-shoot age per clonal fragment did not differ among forest types (data not shown), the mean average age was consistently highest in

Fig. 3. Stand-level demographic traits of *Maianthemum* clonal fragments versus canopy cover (on left) and tree density (on right) in the four forest types: ●, young, closed canopy; ○, young, thinned; △, mature; and ▲, old growth. Dependent variables are: (A) average age of short shoots; (B) number of live (dormant plus leafy) short shoots; and (C) ratio of dormant to leafy short shoots. R^2 and P values are from simple linear regressions of untransformed data.

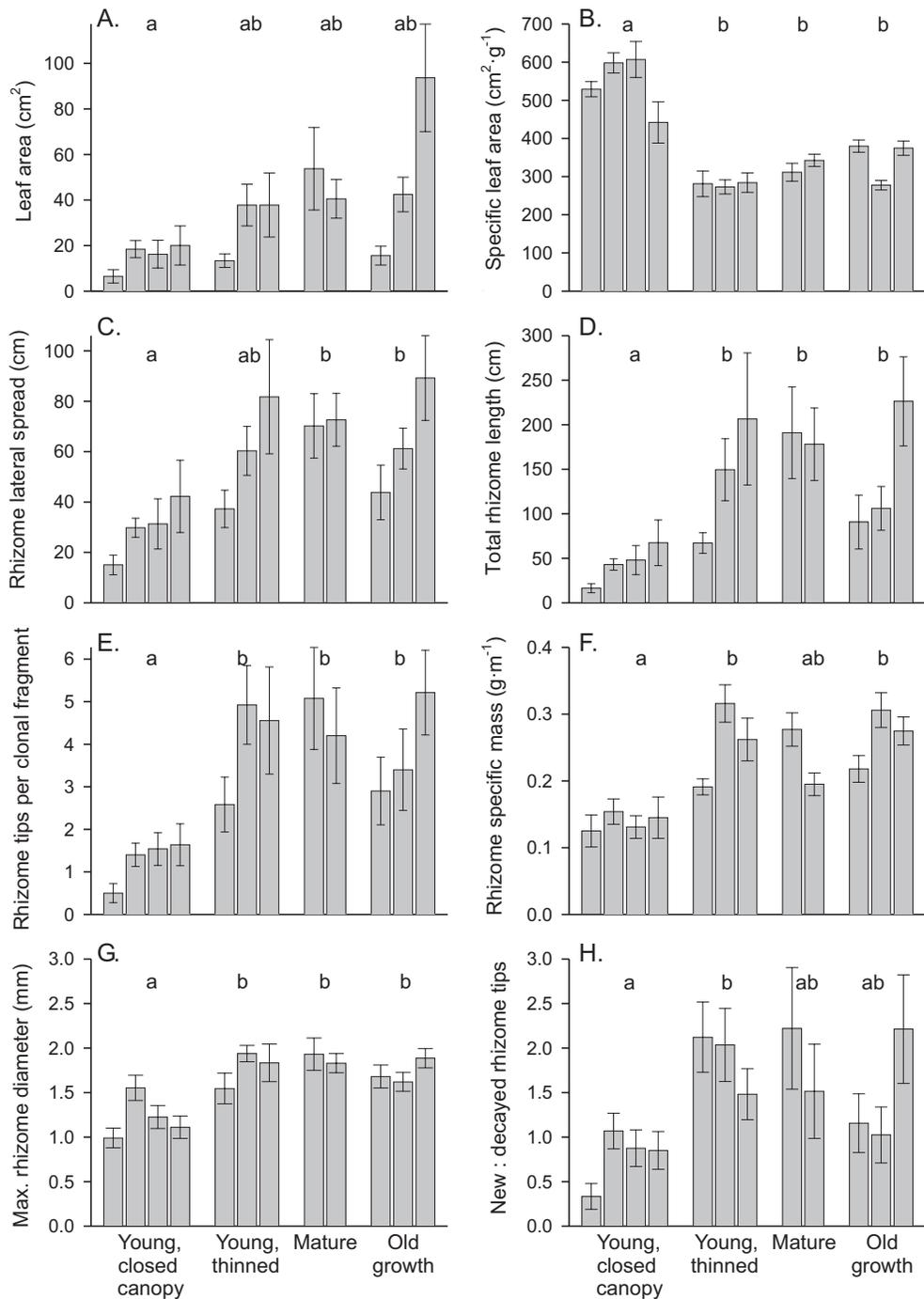


YCC stands and was positively correlated with canopy cover and tree density (Fig. 3A).

The number of live (aerial plus dormant) short shoots per clonal fragment was consistently lowest in YCC stands and decreased significantly with tree density (Fig. 3B). In YCC stands, 36–60% of clonal fragments consisted of a single live ramet, significantly more than in the remaining forest types, where <34% consisted of a single ramet (ANOVA on proportion with a single ramet, $F_{[3,8]} = 11.83$, $P = 0.003$). Clonal fragments never had more than six short shoots in YCC stands, but we found as many as 17 shoots per clonal fragment in older stands (up to nine in thinned stands).

On average, clonal fragments supported more aerial shoots (i.e., vegetative and sexual shoots) than dormant short shoots (means \pm SE of 2.17 ± 0.14 and 0.87 ± 0.12 , respectively). However, the ratio of dormant short shoots to aerial shoots within a clonal fragment was typically lowest in YCC stands (Fig. 3C). A significantly smaller proportion of clonal fragments had dormant short shoots in YCC stands (21%) than in mature (71%) or old-growth (52%) stands (ANOVA on proportion with dormant shoots, $F_{[3,8]} = 6.28$, $P = 0.017$).

Fig. 4. Morphological traits of *Maianthemum* clonal fragments (stand mean \pm 1 SE) in the four forest types. Different letters above groups of replicate stands indicate significant differences among forest types (Tukey HSD) at $P \leq 0.05$ following a significant ANOVA.



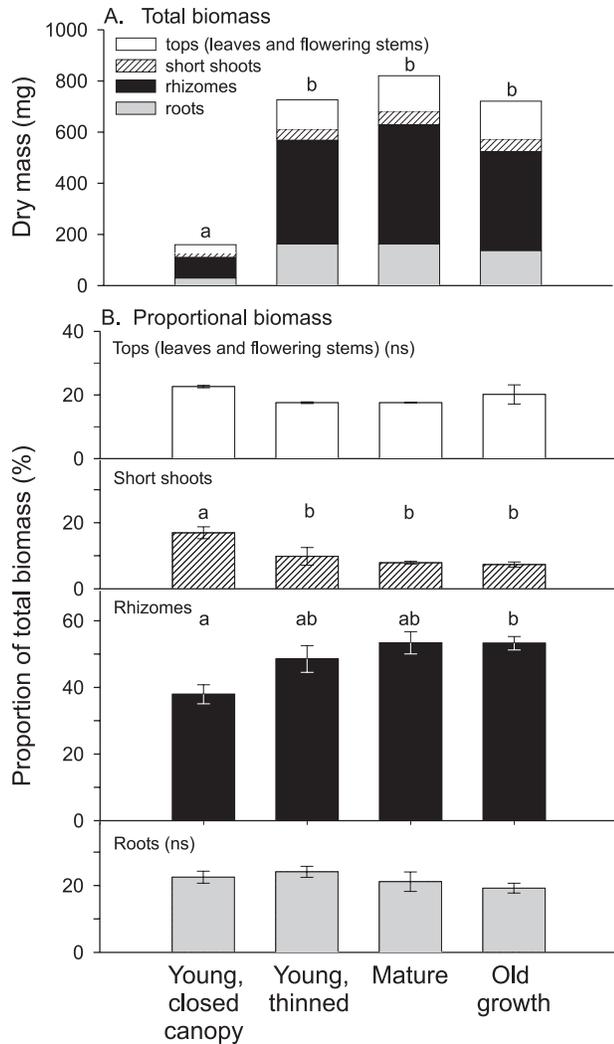
Above- and below-ground morphology

Total leaf area per clonal fragment tended to be smallest in YCC stands, but this trend was not statistically significant because of high variation among stands (Fig. 4A; $F_{[3,8]} = 3.53, P = 0.068$). However, clonal fragments in YCC stands exhibited the highest specific leaf area (Fig. 4B; $F_{[3,8]} = 15.70, P = 0.001$).

Rhizome systems tended to be smaller and less robust in YCC stands than in the other forest types. Lateral spread of

clonal fragments averaged less than half of that found in older or thinned stands (Fig. 4C; $F_{[3,8]} = 6.13, P = 0.018$) (maximum spread observed among all stands was 2.45 m). Total rhizome length (Fig. 4D; $F_{[3,8]} = 8.44, P = 0.007$) and number of new rhizome tips per clonal fragment (Fig. 4E; $F_{[3,8]} = 9.23, P = 0.006$) were lowest in YCC stands; up to 60% of the fragments in YCC stands lacked a growing rhizome tip. Rhizome specific mass (Fig. 4F; $F_{[3,8]} = 8.73, P = 0.007$), maximum diameter (Fig. 4G; $F_{[3,8]} = 7.17, P =$

Fig. 5. Mean clonal fragment biomass and proportional biomass of plant parts in the four forest types. (A) Mean dry mass of leaves, short shoots, rhizomes, and roots. (B) Mean proportion of total dry weight (± 1 SE) for above- and below-ground organs. Different letters above bars indicate significant differences among forest types (Tukey HSD) at $P \leq 0.05$ following a significant ANOVA.



0.012), and ratio of new to decayed rhizome tips (Fig. 4H; $F_{[3,8]} = 4.48$, $P = 0.040$) were also smallest in YCC stands.

Biomass allocation

Total biomass and biomass allocation patterns of *Maianthemum* were also distinctive in YCC stands. Clonal fragment dry mass averaged <22% of that in thinned or older stands (Fig. 5A; $F_{[3,8]} = 9.73$, $P = 0.005$). Dry masses of all plant components were consistently lowest in YCC stands (Fig. 5A).

Among all samples, ca. 80% of plant biomass was in belowground organs (rhizomes, short shoots, roots) (Fig. 5A). Biomass was distributed as follows: rhizomes (47%), short shoots (11%), roots (22%), and leaves plus flowering stems (20%). The proportion of biomass in foraging organs was similar among forest types (Fig. 5B; leaves: $F_{[3,8]} = 3.04$, $P = 0.093$; roots: $F_{[3,8]} = 1.18$, $P = 0.376$). However, allocation to short shoots was highest and allocation to rhizomes

tended to be lowest in YCC stands (Fig. 5B; short shoots: $F_{[3,8]} = 9.31$, $P = 0.005$; rhizomes: $F_{[3,8]} = 4.83$, $P = 0.033$).

Discussion

Age structure and demography

Our first prediction that turnover of short shoots of *Maianthemum* would be lowest in young, closed-canopy stands was supported by the comparative age structures of ramets among forest types. Although short shoots survived to similar maximum ages in all forest types, the greater average age of ramets in young, closed-canopy stands is consistent with longer average survival and decreased production per ramet. Greater persistence and reduced initiation of ramets support the generalization that in environments with very low resource availability, as in the understory of our young, closed-canopy stands, survival of existing structures takes precedence over formation of new modules. Reduced ramet formation in clonal herbs frequently results from low light (Ashmun and Pitelka 1984; Pitelka et al. 1985; Navas and Garnier 1990; Salonen 1994; Whitman et al. 1998), but more generally reflects the small size and poor vigor of plants (Ashmun and Pitelka 1985; Cain and Damman 1997; Wijesinghe and Whigham 1997) that could result from limitation by one or more resources in young, closed-canopy stands. Within each of the more open forest types, short-shoot frequencies declined markedly with age, suggesting fairly rapid turnover. Similar age structures dominated by young ramets have been found for other clonal forest herbs growing in favorable environments (Silva et al. 1982; Navas and Garnier 1990; Whitman et al. 1998). In the closely related species, *Maianthemum bifolium* (L.) F.W. Schmidt, rhizomes generally are not as long lived as those of *M. dilatatum*. Where *M. bifolium* occurs, growing conditions may be more favorable, as indicated by high herb cover (Czarnecka 1996), and selection for longer lived rhizomes or ramets may be reduced.

Clonal fragments of *Maianthemum* in young, closed-canopy forests rarely had dormant short shoots, which are a drain on photosynthate reserves. Old, leafless, belowground ramets with dormant buds and viable roots contribute to resource uptake in some forest herbs (Pitelka et al. 1985; D'Hertefeldt and Jónsdóttir 1994; Jónsdóttir and Watson 1997). However, their function in *Maianthemum* is uncertain: they may represent a protracted or delayed process of bud development, an early stage of short-shoot senescence, or a type of "recovery" ramet, one that develops preformed shoots late in the growing season in response to damage of nearby rhizomes or apical buds (sensu Jónsdóttir and Watson 1997).

As with other clonal species under extremely low levels of light, new rhizome growth of *Maianthemum* may be temporarily suspended, so that survival depends on continual releasing of long-lived, perennial shoots (Ashmun and Pitelka 1984; Huffman et al. 1994; Whitman et al. 1998). Annual replacement of aerial shoots on ramets should be less costly than vegetative formation of new ramets, which requires the production of new rhizomes. However, persistent short shoots alone cannot account for the survival of *Maianthemum* through the dense canopy stage of forest development, which typically lasts much longer (>20 years) than the maximum age of ramets observed. Long-term persistence thus depends on

occasional vegetative formation of new ramets or recruitment of seedlings.

We found occasional clonal fragments that originated as seedlings, as shown by the presence of a primary root which can persist for at least 7 years. Thus, low levels of seedling establishment appear to contribute to perpetuation of *Maianthemum*, even in young, closed-canopy stands. Nonetheless, flowering and seed production are very limited in this forest type: in a survey of 20 stands in the study area, only 1 of 25 plots in young, closed-canopy forests contained flowering individuals of *Maianthemum* (compared with 39–56% of plots in old-growth and thinned forest). Ultimately, the establishment of new genets may depend on the proximity of sexually reproducing plants in more open forests.

Above- and below-ground morphology

Our second prediction that clonal fragment size will be smallest in young, closed-canopy stands was also supported. Both reduced growth and increased fragmentation may contribute to the smaller size of fragments in these stands. The relatively low ratio of new rhizome tips to decayed rhizome ends in young, closed-canopy stands could indicate reduced initiation of rhizome branches, or accelerated mortality of rhizomes. Reduced rhizome branching is consistent with the low resource levels and low rates of short-shoot initiation in these stands. However, increased fragmentation of rhizomes is also likely and may reflect a decline in the physiological function of rhizome connections among ramets. Carbon-14 labeling experiments with the related *M. bifolium* showed less extensive integration among ramets in a nutrient- and light-limited forest than in a resource-rich forest (D'Hertefeldt and Jónsdóttir 1994). Maintenance and production of structural connections require resources (Carlsson et al. 1990; Stuefer et al. 1996; Jónsdóttir and Watson 1997) and may be of limited value where resources are uniformly low. Although we cannot quantify the relative importance of reduced growth vs. fragmentation in young closed-canopy forests, our observations are consistent with declines in rhizome development of *Maianthemum* under dense *Tsuga diversifolia* (Maxim.) M.T. Mast. canopies (Kawano et al. 1968), with smaller rhizome systems of *M. bifolium* on sites with lower levels of soil nutrients (Czarnecka 1986, 1996), and with similar declines in clonal forest herbs and shrubs under reduced light or canopy openness (Ashmun and Pitelka 1984; Tappeiner and Alaback 1989; Huffman et al. 1994).

Clonal fragments of *M. dilatatum* tended to be smaller (in number of ramets and total rhizome length) than those of *M. bifolium* (Czarnecka 1996), suggesting that growing conditions may be less favorable or that a tradeoff exists between persistence and lateral growth. Although *M. bifolium* is found to be more shade tolerant than *M. dilatatum* in Japan, both species form much reduced populations under hemlock canopies, but large clones in favorable environments (Kawano et al. 1968; Oinonen 1971). Thus the ability to spread effectively by rhizomes and to produce large numbers of ramets is likely to be a critical advantage of clonal growth when resource levels increase in the forest understory.

Although larger foraging organs may be expected to form as an adaptive response to shading (Lovett Doust 1987; Menges 1987), *Maianthemum* tended to have smaller leaves under low light, as has been observed with other shade-

tolerant, clonal herbs (Dahlem and Boerner 1987; Menges 1987; Marino et al. 1997). However, other traits, such as delayed leaf senescence (Watson and Lu 1999), can improve carbon assimilation. Persistence of *Maianthemum* under low light may be a consequence of a low compensation point (Koyama and Kawano 1973), greater specific leaf area, and longer retention of green leaves in young, closed-canopy stands compared with other forest types.

Plasticity in biomass allocation

We found no evidence of increased allocation to leaves in the low-light environment of young, closed-canopy stands; thus, our third prediction was not supported. Soil resources, as well as light, may be limiting understory plants in these stands, as is typical of many forests (Coomes and Grubb 2000). However, we did not observe increased allocation to roots or rhizomes, which would be expected if plants were actively “foraging” for microsites with greater resource levels. Thus, our observations are more consistent with a model of “passive growth response”, in which growth or production show a simple relationship to resource availability, than with a model of “active foraging”, in which lateral growth increases in locally unfavorable microsites (Cain 1994; Cain et al. 1996; Stoll et al. 1998). Although allocation to foraging organs did not increase in young, closed-canopy forests, allocation related to clonal growth and storage was affected. Consistent with our first two predictions, a shift in biomass distribution from rhizomes to short shoots suggests that, in young, closed-canopy forests, short shoots are maintained at the expense of horizontal rhizomes, conserving the potential to resprout leafy shoots while minimizing costs of rhizome growth or maintenance. Rhizomes, which store carbon and nitrogen (LaFrankie 1986; Nordin and Näsholm 1997), had the smallest specific masses where light was most limiting. This is consistent with the observation that defoliation can reduce rhizome specific mass in *M. bifolium* (D'Hertefeldt and Jónsdóttir 1994). Although reserves should be exploited when overstory conditions limit carbon gain (Chapin et al. 1990; Dong and de Kroon 1994; Hutchings 1997), as demonstrated for clonal shrubs in closed-canopy, coniferous forests (Messier et al. 1989; Tappeiner et al. 1991; Huffman et al. 1994), *Maianthemum* may compensate for reduced storage in horizontal rhizomes by increased storage in short shoots.

Forest development and clonal growth

Clonal development and growth of *Maianthemum*, as expressed by a diversity of demographic, morphological, and biomass traits, were consistently poorest in young, closed-canopy forests, but were similar among mature, old-growth, and young, recently thinned forests despite marked differences in their canopy cover, overstory density, and age. Why did we not detect progressive changes in clonal development with overstory conditions or successional stage? There may be several explanations. First, variation among the relatively few stands sampled per forest type may mask more subtle differences among types. Second, clonal fragment characteristics may not reflect local canopy conditions very well if these have changed recently. Third, clonal growth may not increase with canopy openness if photoinhibition occurs (sensu Ashmun and Pitelka 1985; Pfitsch and Pearcy 1992) or if there are coincident increases in water stress or in the abun-

dance of competing vegetation. For example, taller understory plants could negate the effects of increased light for species of smaller stature like *Maianthemum* (Givnish 1982). Relatively high understory cover in thinned and old-growth stands could explain why clonal fragments of *Maianthemum* were no larger than those in mature stands. However, there is little direct support for this explanation, as we observed no increase in cover of competing plants directly adjacent to measured clonal fragments (data not shown). Fourth, the age and structural criteria used to distinguish these forest types may be too coarse to capture smaller scale variation in resource availability or other potentially important factors (e.g., fungal pathogens or herbivory; Kana 1982; Rooney 1997). Finally, *Maianthemum*, like other herbaceous species of deep shade, may be physiologically adapted to tolerate low light (Koyama and Kawano 1973; Grime 1979; Henry and Aarssen 1997), such that only extreme environmental conditions limit growth enough to affect clonal performance. Once tree canopies rise, canopy gaps form, or young stands are thinned, a critical threshold may be surpassed, allowing clonal expansion of *Maianthemum* through the formation of new ramets and the production and maintenance of larger rhizome systems.

Ultimately, clonality alone may not be the trait that promotes survival of *Maianthemum* through the dense canopy stage of forest succession. During this period, resources are often consistently low. Investment in lateral growth of rhizomes or maintenance of inter-ramet connections are unlikely to be offset by access to more resources. Thus, light limitation might be expected to favor clonal herbs with connections that disintegrate annually (Kelly 1995; van Groenendael et al. 1996; Kudoh et al. 1999), or nonclonal herbs that maintain large belowground reserves and form leaves in the same location for many years (Lezberg et al. 1999). However, extensively spreading clonal species with long-lived ramets frequently persist in forest understories with low light (Silva et al. 1982; Antos and Zobel 1984; Whitman et al. 1998; Lezberg et al. 1999). For *Maianthemum* and these species, clonal growth is an efficient means of increasing ramet density and spread once resource conditions become more favorable. However, storage in persistent belowground structures (short shoots), ability to produce leaves in the same location for many years, and limited investment in "movement" could be key factors for survival through prolonged periods with low light.

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