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The Use of Size as an Estimator of Age in the Subantarctic Cushion Plant, *Azorella selago* (Apiaceae)

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Abstract

Plant species with morphological features that enable the age of individuals to be estimated are potentially useful for understanding past environmental conditions. Here, the size and growth rate of the cushion plant, *Azorella selago* Hook. (Apiaceae), are examined to determine if an accurate and reliable age can be assigned to individual plants using the phytometric model detailed by Frenot et al. (1993). Plant size, growth rate, epiphyte load, nearest-neighbor characteristics, and spatial position (used as a surrogate, to encompass a range of abiotic conditions to which plants were exposed) were measured at three sites. Additionally, variation in some of these variables was quantified across three altitudinal transects. Relationships were examined using regression, trend surface and partial regression approaches. Growth rate was independent of plant size, differed between sites, and was related to abiotic as well as other biotic factors. As a result, the phytometric model's age estimates may be biased by environmental variables. The results of the phytometric model, albeit in the absence of support for one assumption, estimated mean plant age at 30 yr, with some plants estimated as older than 80 yr. Using a simulation model, the accuracy of age estimates was shown to vary with temporal variation in plant growth rate and plant size. Nonetheless, even a conservative approach suggested these estimates to be accurate to within 2 to 15 yr. While further development of the phytometric model would improve its reliability, the model remains a valuable tool for estimating plant ages in an environment where many related techniques can not be applied.

Introduction

Rising concern about the effects of current environmental change has led to increased interest in past environments (Bluemle et al., 1999; Trotter et al., 2002). However, the scarcity of historical records and information from long-term monitoring programs has necessitated the reconstruction of past environmental conditions from proxy records of climate and geomorphology (e.g., Bluemle et al., 1999; Mann, 2002). For example, dendrochronology, and in some cases lichenometry, has been used to reconstruct local temperature and precipitation levels (e.g., Vogel et al., 2001; Cook et al., 2002), glacial fluctuations, debris flow, and snow-avalanche frequencies (McCarroll, 1993; Winchester and Harrison, 1994; Winchester and Chaujar, 2002) and to estimate the age of landforms and surface features (Winchester and Harrison, 2000; Bradwell, 2001). Compared to methods such as the analysis of isotope ratios or pollen records, phytometric techniques (i.e. the use of plant growth or performance as a surrogate for an unmeasured variable) can potentially provide information on comparatively more recent environments and at finer spatial and temporal scales (Callaghan et al., 1989; Trotter et al., 2002).

Although most widely applied, dendrochronology and lichenometry are not the only phytometric methods that have proved useful for estimating the age of individual plants and the minimum time since substrate disturbance. For example, Callaghan et al. (1989) estimated the age of *Cassiope tetragona* (Ericaceae, evergreen dwarf shrub) in the Arctic from seasonal patterns in the sizes of leaves produced. Methods such as this are particularly useful because they extend the application of phytometric methods to higher latitudes, where trees and known-age sites may be absent (often precluding the use of traditional dendrochronology and lichenometry respectively; although see, e.g., Elvebakk and Spjelkavik, 1995; McCarthy, 2003). Indeed, it is in the

polar and subpolar regions where long-term environmental data are especially valuable, because the rate and magnitude of climate change is high in these areas, and is predicted to remain so (IPCC, 2001).

Previous studies have demonstrated the phytometric potential of cushion plants (dicotyledonous plants with a cushion-type growth form) (e.g., McCarthy, 1992; Molau, 1997), which are a conspicuous component of high-latitude vegetation (particularly in the southern hemisphere; Aleksandrova, 1980). In the Subantarctic (Kerguelen Island), Frenot et al. (1993) estimated the age of the cushion plant *Azorella selago* Hook. (Apiaceae) as the ratio of plant size to annual growth. *Azorella selago* is a long-lived species with a wide altitudinal range and broad geographic distribution in the Subantarctic. As a result, the species could potentially be used to estimate the age of landforms and contribute to the understanding of geomorphological processes across the region (see e.g., Winchester and Harrison, 2000; see Hall, 2002 for review of subantarctic periglacial landforms and processes).

The results of any phytometric analysis must, however, be interpreted cautiously. In dendrochronology, for example, missing annual growth rings, false rings, irregular growth patterns, and incorrect sampling height can lead to false age estimates (Vogel et al., 2001; Niklasson, 2002). Lichenometric analyses have similar problems and simplistic assumptions that disregard lichen biology, ignoring in particular the spatial and temporal variability of growth rates due to local differences in habitat, climate, and competition (McCarthy, 1999; Winchester and Chaujar, 2002), reduce the method's reliability. Therefore, researchers in the field have highlighted the importance of testing the assumptions of phytometric methods and of recognizing their limitations (McCarthy, 1997, 1999; Winchester and Harrison, 2000; Trotter et al., 2002).

The phytometric model outlined earlier implicitly assumes plant growth rate to be independent of space and time, and to vary randomly

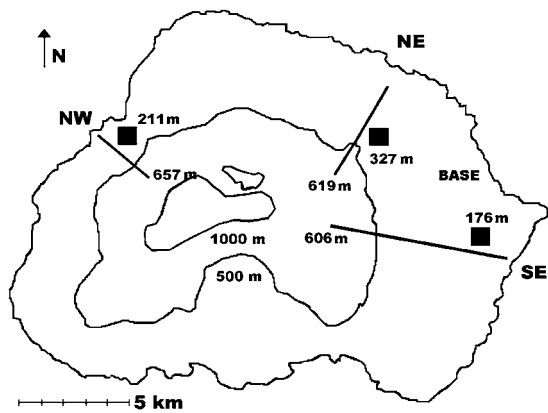


FIGURE 1. Schematic of Marion Island indicating the location of the study sites (transects – straight lines; quadrats – squares) and the 500 and 1000 m a.s.l. contour lines. The maximum altitude (in m a.s.l.) of each transect and the mean altitude of each quadrat are also indicated.

around a mean growth rate for the extent of the area examined. If growth rate varies in a nonrandom fashion (e.g., in response to competition or variation in local habitat suitability), then mean site growth rate will not be representative of the annual size increase of all plants at a site. This may greatly reduce the reliability of plant age estimates. However, the validity of these assumptions, and the effect of their likely violation on age estimates, can currently not be assessed because there are few published studies documenting the growth of *A. selago* (Huntley, 1972; Frenot et al., 1993, 1998).

The objective of this study was thus to test if the phytometric model (outlined by Frenot et al., 1993) can potentially provide unbiased and accurate age estimates for *A. selago* on Subantarctic Marion Island (Prince Edward Islands: 46°55'S, 37°45'E). We quantify the spatial variability in *A. selago* and evaluate the effect of this variability on the accuracy of the phytometric model. The relationships between plant growth rate, plant size, and a suite of spatial (altitude and position on the island which are used as surrogates for abiotic environmental variation) and biotic (nearest-neighbor characteristics and epiphyte load) variables were examined (1) to test the phytometric model's assumption that growth rate varies independently of plant size, and (2) to identify the relative influence of spatial location and selected biotic variables on plant size and growth rate. A simulation model is used to evaluate the sensitivity of the phytometric model's age estimates to the variability around mean site growth rate found. These results are then used to evaluate the efficiency of *A. selago* as a phytometer.

Methods

AZORELLA SELAGO AND THE PHYTOMETRIC MODEL

Azorella selago is a cushion-forming perennial that grows in a variety of habitats, and is able to colonize recently deglaciated and high-altitude areas (Huntley, 1972; Frenot et al., 1993). It often dominates the vegetation of these habitats (Huntley, 1972), and is widespread across the Subantarctic (Moore, 1968; Frenot et al., 1993).

Azorella selago cushions are commonly hemispherical on Marion Island, with short stems carrying simple leaves and growing radially from the center of each plant (Orchard, 1989). At the plant's surface both the leaves and the stems grow tightly against each other, creating a hard and compact surface. *Azorella selago* leaves turn brown at the start of the austral winter, and discontinuities in the color of leaves retained on the stem allow up to the past 5 yr of growth to be determined (a method requiring destructive sampling; used by Frenot et al., 1993). Alternatively, the growth rate of *A. selago* plants can be measured by quantifying annual increases in the size of each plant (a nondestructive

method facilitated by the plants' compact surfaces; used by Huntley, 1972). In this study, Huntley's (1972) nondestructive method was considered more appropriate for use within a conservation area.

Frenot et al.'s (1993) model estimated plant age as

$$\text{Age (yr)} = \frac{\text{Size (mm)}}{\text{Growth rate (mm/yr)}}, \quad (1)$$

where size was measured by plant diameter and growth rate as the annual increase in plant diameter. On Marion Island, growth rate was measured as the annual increase in plant height, and accordingly plant size was measured as plant height. In this study we used vertical growth rather than radial growth (following Huntley, 1972), because vertical growth markers were considered to be less damaging to the plant and less susceptible to disturbance. The assumptions and rationale of Frenot et al.'s (1993) model are identical regardless of the measure of plant size (and its associated measure of growth rate) used.

STUDY SITES

Marion Island (46°55'S, 37°45'E; the larger of the two Prince Edward Islands) experiences an oceanic climate, characterized by low (mean temperature in warmest month 7.3°C, and in coldest month 3.2°C) but stable temperatures (mean diurnal variation 1.9°C), high relative humidity (on average 83%), cloud cover, and rainfall (approximately 2500 mm yr⁻¹, distributed evenly throughout the year), and strong winds (dominated by prevailing westerly winds; exceeding gale force on more than 100 d yr⁻¹; Schulze, 1971). Marion Island is of volcanic origin and has a dome-like profile, rising to 1230 m a.s.l. (Verwoerd, 1971). Three transects and three quadrats of *A. selago* were sampled between April 2001 and April 2002 (Fig. 1). Transects were orientated along the altitudinal gradient on the island and each comprised 100 plants (although the length of transects differed due to topographical differences between the eastern and western sides of the island; Fig. 1). Transects began at the highest altitude plant in the area, and successive plants were sampled every 4 to 6 m decline in elevation thereafter. Plants were selected to be representative of surrounding plants, although only plants >0.15 m in diameter were considered. The transects included both gray (older and undulating due to glacial erosion) and black (younger and more irregular) lava (Verwoerd, 1971). Although detailed mesoclimatic data are not available for the island, higher altitude sites are colder, windier, and cloudier than lower altitudes, and rainfall is maximal at intermediate elevations (Blake, 1996). A quadrat of 200 plants (>0.15 m diameter) was surveyed adjacent to each transect (Fig. 1). All plants within the demarcated 200-plant area, including those <0.15 m diameter, were measured. Only the size, and not the growth rate and relative position, of small plants (i.e. <0.15 m diameter) were determined, because of the risk of measurement-related damage resulting in their mortality.

PLANT MEASUREMENTS

Each plant was marked with an aluminum tag. A thin (≤10 mm diameter) wooden rod (growth-rate marker) was carefully inserted vertically into each plant and into the underlying soil. Growth-rate markers were inserted approximately halfway between the center of a plant and its perimeter. By marking the height of the plant against the marker immediately after insertion and again before removal one year later, annual vertical growth (hereafter growth rate; mm.yr⁻¹) was determined for each individual (following Huntley, 1972). These growth-rate markers were inserted as deeply as possible into the soil underlying the plant to limit any potential movement by frost-heave. Depth of freeze-thaw on Marion Island is shallow, reaching a maximum depth of 0.2 m at high altitudes in open soils (Boelhouwers et al., 2003). Thus, because our growth-rate markers were inserted approximately

0.15 m into the soil underneath plants, and because cushion plants buffer the temperature of underlying soil (see e.g., Arroyo et al., 2003), frost-heave did not affect the plant vertical growth measurements taken in this study. Nonetheless, growth-rate markers that showed any signs of dislodging as a result of any disturbance (approximately 12% of the 900 growth-rate markers) were excluded from analyses.

Three size measurements were taken for each plant, i.e. maximum diameter, diameter perpendicular to the maximum diameter (hereafter perpendicular diameter), and height of the plant. Height was determined by measuring the vertical distance between the highest point of the plant surface and the ground beneath it using a stadia rod. The relative position of each individual (>15cm diameter) within a quadrat or transect was determined using a Nikon Total Station DTM350 Theodolite, with an accuracy of 10 mm (Anonymous, 2001). The altitude of the highest plant in each transect was determined using a Garmin 12MAP GPS, because no suitable known-points were available on the island to determine the exact altitude and geographic position using the theodolite (readings were cross-checked against a topographical map of the island: Langenegger and Verwoerd, 1971).

The influence of biotic and abiotic environmental conditions on plant growth rate and size were considered by examining the relationship between plant characteristics and selected variables. Our intention was not to identify mechanistic explanations for variability observed in *A. selago*, but rather to quantify variability in plant characteristics and evaluate the effect of this variability on the accuracy of the phytometric model. This study was designed to encompass plants from as broad a geographic and altitudinal range on the island as possible, and in addition to measure those biotic variables thought to have the greatest likely impact on plant growth rate. First, the spatial position of the plants (i.e. locality coordinates of each plant within the quadrats and altitude of plants along the transects) was used as a surrogate for abiotic environmental variation (on the rationale that plants on different parts of the island and at different altitudes are exposed to different abiotic environmental conditions; see also Koenig, 2002). Thus, hereafter, the net influence of abiotic factors on plant characteristics are considered in analyses by inclusion of these spatial variables. Second, nearest neighbor characteristics and epiphyte load were measured directly, because these were the two biotic factors thought most likely to affect plant growth rate. The number of *Agrostis magellanica* (Lam.) Vahl (Poaceae) individuals growing epiphytically on each plant was counted as a measure of epiphyte load. This grass is the dominant epiphyte on *A. selago* on Marion Island, and at mid-altitudes may cover up to 61% of the surface of plants (le Roux and McGeoch, unpublished). Within quadrats, the distance between each plant and its ten nearest-neighbors was calculated. Preliminary analyses showed that data for the two nearest neighbors explained the most variation in plant size and growth rate (hereafter 2NN distance). Therefore, the mean maximum diameter, perpendicular diameter, height, and growth rate of the two-closest plants were also calculated (hereafter 2NN maximum diameter, 2NN perpendicular diameter, etc.). To ensure that nearest-neighbor distances were not overestimated for plants at the edge of the sampled quadrat, progressively more outer plants were excluded from analyses until the nearest-neighbor distances of the outermost plants were approximately similar to those of the central plants. This required the exclusion of the outermost 35 to 40% of plants.

ANALYSES

Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference tests for Unequal *N* were used to identify which sites differed from each other in terms of plant size and growth rate. Logarithmic or square-root transformations were used to achieve normal distributions for all variables where necessary (normality assessed using Shapiro-Wilk's *W* test). Data from each site were

analyzed separately, except where calculating mean plant size and growth rate across the island. Analyses were repeated with and without the inclusion of those plants that showed no vertical growth during the study period (approximately 15% of all plants measured; the size and epiphyte load of these plants did not differ significantly from those for which growth was recorded).

To test if variability in plant growth rate increased with plant size, the coefficient of variation (CV) of growth rate was determined for different plant size classes. The number of size classes used for these analyses was determined using Sturge's rule (Legendre and Legendre, 1998). The relationship between plant size class and its CV of growth rate (arcsine transformed) was then examined using simple linear regression (Collet, 1991).

Partial Regression Analyses

Potential biases in the model, and resulting biases in age estimates (i.e. any systematic deviation of the ages estimated by the phytometric model from the real ages of the plants sampled), were examined by considering the influence of spatial and biotic factors on plant size and growth rate. To identify the proportion of variability in plant size and growth rate explained by spatial (i.e. using geographic coordinates and altitude as a surrogate for environmental variation, see above) and biotic (i.e. nearest-neighbor characteristics, epiphyte load) variables, trend surface analysis and partial regression approaches to the analysis of spatially explicit data were used (Legendre and Legendre, 1998). This is currently one of the approaches adopted to incorporate spatial position into explanatory models, i.e. modeling the spatial variation in plant size or growth rate as a linear combination of biotic variables and geographic coordinates of each plant (see e.g., Brewer and Gaston, 2002; Lobo et al., 2002). This method also accounts for biases that may occur as a result of the spatial nonindependence of data points (Legendre and Legendre, 1998). Trend surface analysis was thus performed on growth rate and plant size measures to test for spatial structure in these variables across the quadrats (transect data were analyzed differently; see below). A third-order polynomial combining the geographic coordinates, *X* and *Y*, for each plant was fitted to each dependent variable using general linear models. The least significant term in each model was identified and excluded, and the model refitted to the data. Following the method described by Legendre and Legendre (1998), this process (backwards elimination) continued until all remaining spatial terms contributed significantly to the model. The final model thus describes the broad-scale spatial trends (if any) of the variable modeled across the quadrat (Legendre and Legendre, 1998).

Biotic variables that contributed significantly to explaining variation in plant size and growth rate were then determined for each quadrat. Models of plant size and growth rate were again constructed by backwards elimination, with all environmental variables initially included (Growth rate = Plant size + 2NN distance + 2NN size + 2NN growth rate + Epiphyte load; Plant size = Growth rate + 2NN distance + 2NN size + 2NN growth rate). Epiphyte load was not included in plant size models because there is a significant relationship between plant size and epiphyte load (data pooled over quadrats; maximum diameter: $R^2 = 0.40$, $F_{1, 456} = 309.44$, $P < 0.01$; height: $R^2 = 0.09$, $F_{1, 456} = 45.42$, $P < 0.01$), and plant size places a limit on epiphyte load (see Lyons et al., 2000). Thereafter, partial linear regression analyses were conducted in which independent variables included the best-fit trend surface model variables (abiotic variables; *sensu* "spatial component": Legendre and Legendre, 1998), nearest-neighbor characteristics and epiphyte load (biotic variables; *sensu* "environmental component": Legendre and Legendre, 1998). In these partial regression analyses the variation in plant size or growth rate was divided into fractions representing the proportion explained by the biotic variables (A), either biotic variables or spatial (abiotic) terms (B: spatially

structured biotic effect), the spatial terms (C), and remaining unexplained variation (D: Legendre and Legendre, 1998). This method identifies the relative contribution of the biotic and abiotic variables to the variation explained by a model, although it does not specifically quantify the importance of individual variables (Legendre and Legendre, 1998; see also Brewer and Gaston, 2002; Lobo et al., 2002 for application of this approach). Full models were considered statistically significant if they exceeded the Bonferroni-corrected, table-wide significance level ($\alpha = 0.05/18 = 0.0028$) (Rice, 1989).

The same method was then modified and applied to the plant size and growth rate data for each transect. Because plants in the transects were distributed across an altitudinal gradient, altitude (rather than geographic coordinates) was used as a surrogate for abiotic variation (i.e. included as the spatial component during variance partitioning), enabling the proportion of explained variability attributable to altitude to be calculated. The environmental component included in variance partitioning for the transects was then also calculated (i.e. Growth rate = Plant size + Epiphyte load; Plant size = Growth rate).

Simulation Model

Simulation models of plant ages were constructed to investigate the influence of variability in growth rate and plant size on plant age estimates. In the absence of temporal data, the observed spatial (between-plant) variability in growth rate was used as a surrogate for temporal variation in the growth rate of individual *A. selago* plants. Although the validity of this surrogacy approach cannot currently be assessed, the objective here was merely to demonstrate how the accuracy of age estimates is affected by variability in growth rate and plant size. Nine idealized plant sizes (heights) were selected to represent a range of plant sizes documented on Marion Island, i.e. 75, 150, 225, . . . and 675 mm (while the greatest plant height sampled was 600 mm, larger plants were also observed on the island). These heights were each successively reduced by subtracting randomly-selected (with replacement) growth rate values chosen from a “set of observed values” (described below), until plant height was reduced to, or less than, zero. Thus,

$$H - \sum_{j=1}^x y_j = h_j \quad (\text{until } h_j \leq 0), \quad (2)$$

where H = plant height (mm), y_j = growth rate (mm.yr^{-1}) value randomly chosen from the set of observed values used for the simulation, h_j = plant height j years ago, and x = plant age (years).

The number of times height was required to be reduced was then recorded as one simulated age for a plant of that size. This process was repeated 10^4 times to generate distributions of simulated plant ages for each plant size. The mean and one standard deviation around the mean (i.e. $\pm 68\%$ of simulated ages closest to the mean) were calculated for each distribution (two standard deviations around the mean, i.e. $\pm 95\%$ of simulated ages closest to the mean, were also calculated and are reported). This standard deviation (1 S.D.) provided a measure of the accuracy of the phytometric model's (eq. 1) age estimates, assuming that accuracy is inversely proportional to the range of plant ages simulated for a plant of a given size.

The “set of observed values” from which growth rate values (y_j) were selected comprised either (i) all the growth rate values measured at a site, or (ii) three sets of randomly generated values with normal distributions. These randomly generated growth rate distributions had identical means (4.26 mm.yr^{-1} = mean plant growth rate measured across Marion Island), but different standard deviations (2.9 [=observed S.D. of growth rate across Marion Island], 0.29 , 0.029). Randomly generated growth rate distributions (ii) were used in addition to measured site growth rates (i), because the range of variability in growth rate in the measured data was low, and a greater

range of variability was necessary to determine if variability in growth rate influenced the S.D. of age estimates. The relationship between variability in growth rate (measured as CV) and the S.D. of the age estimates was examined for both the measured (i) and generated (ii) data sets using simple linear regression. Changes in the S.D. of age estimates with plant size were similarly examined. Annual growth increments were selected ignoring possible temporal autocorrelation in growth rates. However, in the presence of temporal autocorrelation standard deviations are likely to be reduced, and the approach taken here is the more conservative. Moreover, the results of the simulation model are likely to underestimate the phytometric model's accuracy, because the range of growth rate values used are wide relative to those expected for an individual plant over time (ranges of growth rate values used varied between 1.4 – 11.0 and 1.0 – 16.0 mm.yr^{-1} , which are ranges double that previously recorded for *A. selago*: Huntley, 1972; Frenot et al., 1993).

Results

PLANT SIZE, GROWTH RATE, AND AGE

The distribution of *A. selago* plant size and growth rate at each site were right-skewed, with the majority of plants ranging from 0.40 to 1.15 m in diameter (mean \pm S.E. (m): maximum diameter = 0.59 ± 0.01 , perpendicular diameter = 0.36 ± 0.01 , height = 0.13 ± 0.01 , $n = 1038$) (Fig. 2). The growth rate of plants ranged between 0.7 and 21.0 mm.yr^{-1} (mean \pm S.E. [mm] = 4.26 ± 0.11 , excluding plants not showing growth). The three plant size measurements were significantly positively related to each other (maximum diameter – height: $R^2 = 0.16$, $F_{1, 1036} = 202.24$, $P < 0.001$; perpendicular diameter – height: $R^2 = 0.21$, $F_{1, 1036} = 275.74$, $P < 0.001$), most strongly so for maximum and perpendicular diameter ($R^2 = 0.58$, $F_{1, 1036} = 1432.92$, $P < 0.001$). As a result, only maximum diameter and height were used as plant size measures in subsequent analyses. Similar results were obtained when analyses were performed using growth rate data excluding or including plants showing zero growth and only results from analyses excluding zero growth plants are reported.

Growth rate was not related to plant height (all sites $P > 0.05$). In addition, there was no clear relationship between variability in growth rate and plant size (Table 1). The coefficient of variation in growth rate across plant size classes was high (between 50 and 65% ; Table 1). Plant size and growth rate differed significantly between sites on Marion Island (Fig. 3). Among the sites, the Northeast Transect had the largest plants, and plant growth rates were highest in the Northeast and Northwest Transects (Fig. 3).

Age estimates (from the phytometric model; eq. 1), were found to be non-normally distributed ($P > 0.05$ for all sites) with right-skewed distributions (Fig. 2d). Mean plant age estimated for the six study sites ranged between 26 and 41 yr (Table 1). The tallest plants in the Northwest and Southeast Transects were estimated to be the oldest sampled; 84 and 97 yr old, respectively (Table 1).

PARTIAL REGRESSION ANALYSES

Plant size and growth rate were weakly related to the explanatory variables measured in this study; less than 36% of the variation observed in either size or growth rate was explained (Table 2). Variance partitioning, nonetheless, generally attributed most (3 – 16%) of the explained variation to biotic factors (‘A’; Table 2). Spatially structured biotic factors (‘B’; Table 2) accounted for an additional 0 to 19% of the variability in plant characteristics (the small negative value merely indicates that the biotic and abiotic variables have effects of an opposite direction on plant growth rate in the Northeast Quadrant; Legendre and Legendre, 1998). Therefore, in the full regression models

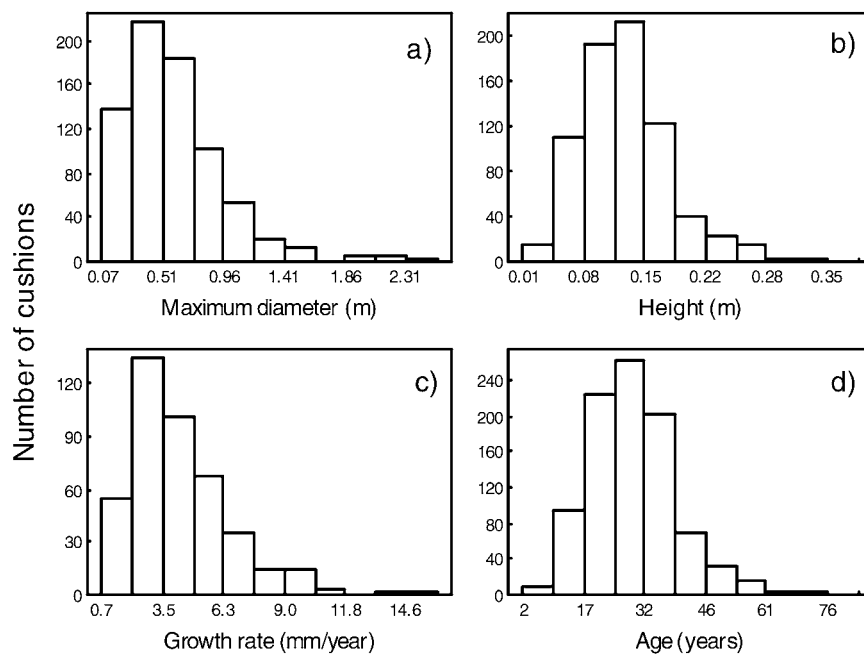


FIGURE 2. Frequency distributions for *Azorella selago* cushion plants across all quadrats of a) maximum diameter ($n = 738$), b) height ($n = 738$), c) growth rate ($n = 527$), d) estimated plant age ($n = 738$, using mean growth rate for each quadrat to estimate age).

up to an additional 19% of variability in plant size and growth rate could possibly be attributed to the biotic variables recorded in the study. However, this variability may equally be a result of some abiotic variable sharing a common spatial structure with the biotic variables (i.e. this proportion of explained variation cannot be confidently attributed to either category; Legendre and Legendre, 1998). Finally, abiotic variables ('C'; Table 2) accounted for between 0 to 27% of observed variability in plant size and growth rate.

BIOTIC VARIABLES

Among the biotic variables, plant size (height and diameter) in the quadrats was consistently significantly related to the distance and size of nearest neighbors (Table 2). The mean maximum diameter of the two nearest neighbors (2NN) was always significantly positively related to plant maximum diameter (Table 2, Fig. 4). Similarly 2NN distance and 2NN height were significantly positively related to plant diameter and height, respectively (Table 2). While the strength of these relationships varied, nearest-neighbor characteristics were the most consistent predictors of plant size in the quadrats.

Both epiphyte load and altitude contributed significantly to

explaining plant size and growth rate, although these relationships were neither strong nor consistent. Epiphyte load was significantly negatively related to plant growth rate in two of the models and positively in one (Table 2). Altitude contributed significantly to explaining plant height or growth rate in three of the transect models

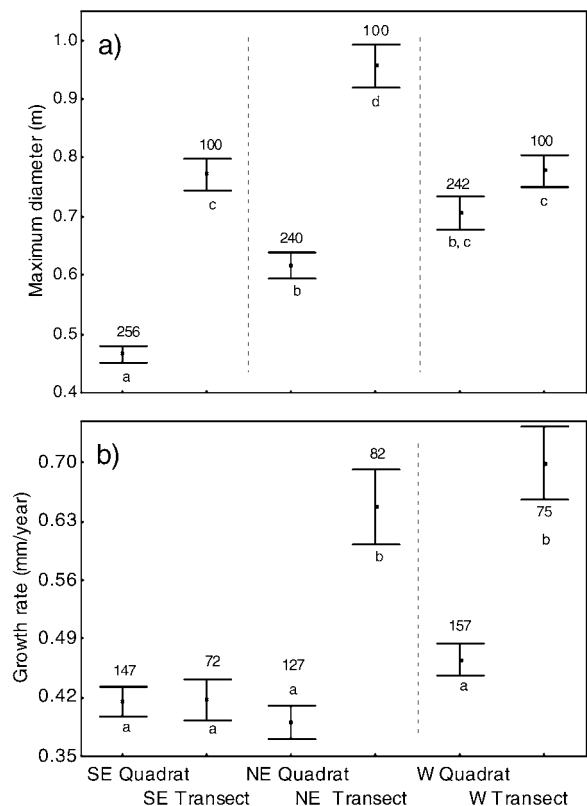


FIGURE 3. Mean (\pm S.E.) a) maximum diameter and b) growth rate of *Azorella selago* plants sampled at each site. Number above whiskers indicates sample size. Sites not sharing a letter (below whiskers) were significantly different at $P < 0.05$.

TABLE 1

Coefficient of variation of growth rate (% CV) (across all size classes), and the results of the regression of CV against plant height classes for each site. Age (years) estimates for plants at each site also provided. Minimum ages not estimated for plants within transects

Site	Coefficient of variation					Estimated plant age			
	CV %	n ¹	R ²	d.f.	F	Mean (\pm S.E.)	n ¹	Min.	Max.
SE Quadrat	51.7	147	0	1, 6	0.21	26.7 \pm 0.6	256	6.9	55.0
NE Quadrat	58.8	127	0.15	1, 6	2.25	26.3 \pm 0.6	240	5.3	64.4
NW Quadrat	53.1	157	0	1, 6	0.01	33.4 \pm 0.8	242	2.1	83.0
SE Transect	50.3	72	0.83	1, 5	26.11*	41.0 \pm 1.3	100	—	96.6
NE Transect	64.7	82	0	1, 5	0.02	29.2 \pm 1.4	100	—	71.4
NW Transect	53.7	75	0	1, 5	0.83	26.3 \pm 1.3	100	—	83.5

¹ number of plants, * significant at $P < 0.05$.

TABLE 2

Proportion of variation in plant diameter, height and growth rate attributable to biotic and spatial variables. Standardized coefficient estimates are provided for the biotic variables and altitude to indicate the direction and magnitude of effects

Variable	Quadrat	Independent variables ¹ (coefficient estimate)	Spatial terms	Proportion of variation explained (%)				<i>P</i> <	
				Total	Biotic; A ²	Biotic × Spatial; B ³	Spatial; C ⁴		
Diameter	SE	2NN Diam. ⁵ (0.36)	y, xy ² , y ³	24.04	9.93	12.65	1.46	F _{4, 114} = 10.34	0.001
	NE	2NN Diam. (0.21), 2NN Dist. (0.28)	⁶	13.78	13.78	—	—	F _{2, 90} = 8.35	0.001
	NW	2NN Diam. (0.06), 2NN Dist. (0.38)	y, y ² , y ³ , x ² , x ³	35.62	11.96	19.35	4.31	F _{7, 110} = 10.25	0.001
Height	SE	2NN Height (0.43)	y, x ² , x ² y, x ³	25.82	16.26	6.62	2.94	F _{5, 113} = 9.21	0.001
	NE	2NN Height (0.25)	—	5.42	5.42	—	—	F _{1, 91} = 6.27	0.014 ⁷
	NW	2NN Height (0.28)	x ² , xy, x ² y	21.29	5.14	12.39	3.76	F _{4, 113} = 8.91	0.001
Growth rate	SE	—	—	—	—	—	—		
	NE	Diam. (−0.25), Epiphyte load (0.28)	x ² y, xy ²	10.96	3.55	−0.02	7.41	F _{4, 89} = 3.86	0.006 ⁷
	NW	—	y, y ² , y ³	4.99	—	—	4.99	F _{3, 114} = 3.05	0.032 ⁷
Transect									
Diameter	SE	—	—	—	—	—	—		
	NE	—	—	—	—	—	—		
	NW	Growth rate (0.28)	—	6.63	6.63	—	—	F _{1, 73} = 6.25	0.015 ⁷
Height	SE	—	Altitude (−0.47)	21.14	—	—	21.14	F _{1, 70} = 20.04	0.001
	NE	—	—	—	—	—	—		
	NW	—	Altitude (−0.53)	27.43	—	—	27.43	F _{1, 73} = 28.96	0.001
Growth rate	SE	Diam. (0.20), Epiphyte load (−0.22)	Altitude (0.29)	18.47	3.52	9.58	5.37	F _{3, 68} = 6.36	0.001
	NE	Epiphyte load (−0.38)	—	13.48	13.48	—	—	F _{1, 80} = 13.62	0.001
	NW	Diam. (0.25)	—	5.19	5.19	—	—	F _{1, 73} = 5.05	0.028 ⁷

¹ Independent variables contributing significantly in final model ($P < 0.05$).

² Variation in plant characteristics explained by biotic variables.

³ Variation in plant characteristics explained by biotic and spatial variables, but which cannot be split between the two components.

⁴ Variation in plant characteristics explained by spatial variables.

⁵ 2NN Diam. = mean maximum diameter of two nearest neighbors, 2NN Dist. = mean distance to two nearest neighbors, 2NN Height = mean height of two nearest neighbors, Diam. = maximum diameter.

⁶ No significant contribution by variables.

⁷ Models no longer significant after significance levels adjusted using the Bonferroni table-wide $\alpha = 0.003$.

(Table 2). Plant height declined significantly with increasing altitude in two cases, whereas plant growth rate increased with altitude in one of the models (Table 2). Therefore, in addition to nearest-neighbor

characteristics, in some cases plant size and growth rate were related to altitude and epiphyte load.

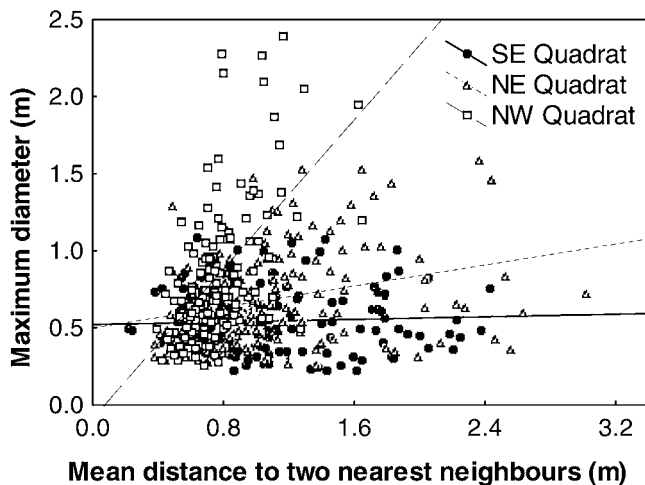


FIGURE 4. Relationships between *Azorella selago* plant maximum diameter and distance to its two nearest neighbors for each quadrat (simple linear regression lines fitted for illustration, see Table 2 for full model results).

SIMULATION MODEL

Simulation model results showed that the magnitude of one S.D. around the mean plant age estimate is influenced by the size of the plant being aged, as well as the variability in site growth rate. Variability in growth rate and the standard deviation around mean age were significantly positively related in the three randomly generated data sets (generated with low, medium and high variability in growth rate; for all plant sizes: slope estimates > 0.65 , $R^2 > 0.9$, $F_{1, 1} > 100.0$, $P < 0.05$). However, no significant relationships were found between the accuracy of age estimates and the variability in growth rate for the measured data sets (for all plant sizes: $F_{1, 4} < 0.27$, $P > 0.5$). Using both measured and generated growth rate distributions (i and ii in Methods), the standard deviation around the mean estimated age increased significantly with plant size (all data sets: slope estimates between 0.001 and 0.008, $R^2 > 0.9$, $F_{1, 7} > 64.0$, $P < 0.01$, except for the generated data set with the least variation in growth rate, since S.D. of simulated ages was zero for some size classes; Table 3). Therefore, within any particular site, small plants (i.e. 75 mm tall) could be aged more accurately (S.D. = 1.8–2.6 yr) than large plants (600 mm tall: S.D. = 4.9–6.0 yr; using the observed growth rate data, Table 3). Averaged over all plant sizes, the mean accuracy of age estimates (i.e.

TABLE 3

Simulated ages (mean simulated age and three measures of variability around that mean age, i.e. estimate of accuracy) for three idealized plant heights using measured growth rate data from the six study sites

Plant height	Variable (yr)	Quadrat			Transect		
		SE	NE	NW	SE	NE	NW
75 mm	Mean age	18.6	19.9	16.7	11.2	12.1	18.6
	1 S.D. around mean ¹	2.2	2.6	2.1	2.1	2.2	1.8
	2 S.D. around mean ²	4.4	5.2	4.2	4.2	4.4	3.6
	Min.–Max.	10–27	11–30	9–24	4–18	6–23	11–27
300 mm	Mean age	72.6	77.6	64.9	42.7	45.6	72.3
	1 S.D. around mean	4.3	5.2	4.2	4.2	4.3	3.5
	2 S.D. around mean	8.6	10.4	8.4	8.4	8.6	7.0
	Min. – Max	57–89	54–97	50–82	30–56	30–65	57–92
600 mm	Mean age	144.7	154.6	123.2	84.8	91.1	144.5
	1 S.D. around mean	6.2	7.3	6.0	6.0	6.0	4.9
	2 S.D. around mean	12.4	14.6	12.0	12.0	12.0	9.8
	Min. – Max.	121–172	129–182	106–150	65–104	70–116	124–168

¹ Approximately 68% of simulated plant ages fall within the mean age \pm 1 S.D.

² Approximately 95% of simulated plant ages fall within the mean age \pm 2 S.D.

averaged across the second row of all plant heights in Table 3) was approximately 4.5 yr.

Discussion

The results of this study confirm the potential of *A. selago* as a phytometer for estimating minimum landscape age. The first assumption important for the use of Frenot et al.'s (1993) phytometric model to estimate the age of *A. selago* was supported, i.e. that plant growth rate is independent of plant size. However, the second assumption was not supported, because plant characteristics were related to biotic and abiotic factors, and differed across the island. As expected, plant characteristics were not independent of site-specific habitat or environmental characteristics and age estimates could, as a consequence, be biased. In addition, variability in growth rate was high across all plant size classes, and was shown to reduce the accuracy of plant age estimates. Although these findings highlight limitations for the application of *A. selago* as a phytometer, they also suggest possible avenues for improving the reliability of the phytometric model.

Azorella selago sizes and growth rates observed in this study were within the ranges reported from previous studies in the Subantarctic (Moore, 1968; Huntley, 1972; Frenot et al., 1993; Frenot and Gloaguen, 1994; Frenot et al., 1998). For example, the results of the phytometric model (albeit in the absence of support for one of its two assumptions) confirm that *A. selago* plants are long-lived. The age of the oldest individuals sampled in this study ranged from 55 to 96 yr. This is comparable to plants on Kerguelen Island (Frenot et al., 1993). Some between-island and between-study differences in plant characteristics were, however, apparent. For example, an extremely tight link between plant diameter and height was quantified for Kerguelen Island ($R^2 = 0.93$; Frenot et al., 1993), whereas the same was not true on Marion Island ($R^2 = 0.16$, this study). Frenot et al.'s (1993) radial growth rate estimates were lower than the mean vertical growth rate observed here ($t = 5.63$, d.f. = 590, $P < 0.01$). Similarly, Huntley's (1972) estimates of vertical growth rate on Marion Island were also lower than those observed in this study. However, because *A. selago* has not been extensively surveyed on these islands, and because we show within-island variability to be high for Marion Island, between-island comparisons remain premature.

Plant size and growth rate have to date not been found to be related in *A. selago* (Frenot et al., 1993; this study). Therefore, despite

the high spatial variability observed in growth rate, the use of a linear function to model the relationship between size and age for the species is justified. The phytometric model's second assumption was, however, violated by the demonstration that plant size and growth rate on Marion Island differed between sites, and that these variables were, at least partly, related to biotic and abiotic variables. Much stronger relationships were found between plant size, rather than growth rate, and environmental characteristics. Plant size is, nonetheless, a cumulative product of growth rate over time and thus also contributes to the violation of this assumption. Therefore, the dependence of plant characteristics on environmental variables will result in biased plant estimates.

These between-site differences versus within-site variability in plant characteristics have different implications for the application of the phytometric model. First, between-site differences in plant growth rate highlight the importance of site-specific growth rate estimates. It is therefore not possible to extrapolate growth rate estimates from one site on the island to another. Furthermore, the assumption that larger plants are older than smaller individuals is not necessarily true, especially when comparing plants from different sites. Second, the implication of within-site relationships between plant characteristics and environmental variables is that age estimates will be biased. One or more unmeasured variables are clearly also important determinants of plant characteristics, because more than 65% of the variation in these characteristics was not explained. To reduce environmental bias in age estimates, the determinants of *A. selago* growth rate need to be identified. Variability in soil moisture and nutrients, wind exposure and snow cover, due to topographical and microclimatic variation, are known to be important determinants of plant performance in arctic and alpine communities (Callaghan et al., 1997; Jumpponen et al., 1999), and are likely to be equally important in the Subantarctic (both at fine scales and between areas on single islands) (Frenot et al., 1993). A more complete understanding of the determinants of plant growth rate may enable the incorporation of these variables into the phytometric model, reducing the effect of environmental bias on age estimates.

The usefulness of the phytometric model clearly depends on both the biases in, and the accuracy of, its results. For example, very accurate age estimates are of little worth if the model's answers are strongly biased by the effect of unaccounted for environmental variation. Similarly, unbiased age estimates are of limited value if their accuracy is very poor. While it is theoretically possible to remove bias

from the model (e.g., by including major variables that influence *A. selago* growth rate), the accuracy of age estimates is determined by temporal variability in growth rate. Despite the importance of such variation, it has not been explicitly quantified for *A. selago* (although Frenot et al., 1993 noted no significant difference in mean plant growth rate over five successive years). If growth rate varied nonrandomly over time, this would contribute to bias in plant age estimates. For example, if soil quality or climate (i.e. factors showing long-term trends) strongly influence plant growth rate, current short-term measures of growth rate may not be representative of historical growth rates (Trotter et al., 2002). By contrast, the effect of random temporal variation is a reduction in the accuracy of age estimates. This was demonstrated by the simulation model that showed that (1) age estimates for young plants are likely to be more accurate than those of old plants (see also Molau, 1997; Campana, 2001), and (2) with increasing temporal variability in growth rate there is a decline in accuracy of age estimates. Under a simulated scenario of high temporal variability in growth rate (incorporated using the extent of between-plant variability in growth rates as a surrogate), a plant of 300 mm could, for example, be estimated with 68% probability as being between 68 and 77 yr old. Generally, under this high temporal variability scenario plants could be aged to within 2 to 7 yr with 68% probability, and to within 4 to 15 yr with 95% probability. Therefore, except where high-resolution age estimates are required, the usefulness of the phytometric model may not be limited by the level of accuracy it provides. This would be particularly true were temporal variation in growth rate lower than that used in the simulation model here.

Phytometry using *A. selago* in the Subantarctic, like other phytometric techniques, must therefore necessarily rely on fairly detailed information on the spatial and temporal variability in the species and its environment (McCarthy, 1997). Data on the temporal variation in growth rate is required to quantify the accuracy of the model's age estimates, although even the wide range of growth rates used in the simulation model produced age estimates accurate to within 2 to 15 yr. Bias in the model may be reduced by developing a more complete understanding of the ecology of the plant species, identifying determinants of its growth rate and using site-specific growth rate estimates. Explicit inclusion of such information into the phytometric model for *A. selago* will improve its reliability and value as a tool for reconstructing past environmental conditions in the sub-Antarctic.

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