Measurement of moss growth in continental Antarctica

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Abstract Using steel pins inserted into growing moss colonies near Casey Station, Wilkes Land, continental Antarctica, we have measured the growth rate of three moss species: *Bryum pseudotriquetrum* and *Schistidium antarctici* over 20 years and *Ceratodon purpureus* over 10 years. This has provided the first long-term growth measurements for plants in Antarctica, confirming that moss shoots grow extremely slowly in Antarctica, elongating between 1 and 5 mm per year. Moss growth rates are dependent on availability of water. Antheridia were observed on some stems of *B. pseudotriquetrum*; no archegonia or sporophytes were observed. Stems bearing antheridia elongated much more slowly than vegetative stems in the same habitat. Two other methods of growth rate measurement were tested, and gave similar rates of elongation over shorter periods of time. However, for long-term measurements, the steel pin measurements proved remarkably reproducible and reliable.

Introduction

In continental Antarctica, terrestrial plants grow in conditions close to the limits for their survival. Vegeta-

tion is sparse and discontinuous in most of the ice-free areas, but a few areas are noteworthy for their relatively lush plant growth including some small areas of continuous plant cover. The Bailey and Clark Peninsulas (66°S, 110°E) near Casey Station in Wilkes Land are two areas notable for their abundant vegetation including some areas of continuous plant cover (Lewis Smith 1986; Selkirk and Seppelt 1987). The vegetation in each of these locations has been recognised as the basis for their protection in Bailey Peninsula Antarctic Specially Protected Area ASPA 135 (formerly Site of Special Scientific Interest 16) and Clark Peninsula ASPA 136 (formerly SSI 17; SCAR 2004).

Low-growing bryophytes, lichens and terrestrial algae form the vegetation with lichens dominating the drier areas and mosses the wetter areas. Only a few species are found in any given area. From the vicinity of Casey Station five species of bryophytes and about 36 species of lichens have been recorded (Lewis Smith 1986; Melick et al. 1994).

In the inhospitable continental Antarctic environment, liquid water for active plant growth is available only for a few weeks in summer (Wilson 1990; Lewis Smith 1999). Here plants are subjected to the stress of continuous light in summer (Adamson and Adamson 1992; Kappen et al. 1989) and in winter to the combined stresses of low temperatures, lack of water and very low irradiance. The growing season is very short, and overall rates of plant growth are generally regarded as low (Lewis Smith 1984).

Standing crop and annual production data have been used as a basis for the calculation of moss growth rate, including rate of elongation of shoots (Lewis Smith 1984). Russell (1984) reviewed a range of direct methods for measuring growth rates in temperate

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mosses including (1) measurements between innate markers presumed to be annual, (2) measurements against cranked wires (or pins) inserted into the moss turf, (3) measurements of growth above tags tied to stems, (4) measurement of growth above nets placed over the surface of the moss turf, (5) measurement of growth above a stain applied to the surface of the moss turf, (6) measurements of stems cut from a turf, bagged or tied into bundles, replaced and remeasured, (7) measuring the later remeasuring the length of stems above a marked reference layer parallel to the ground surface within a moss turf, and (8) photographing and later rephotographing the outlines of discrete moss colonies.

We report here the first long-term study of Antarctic moss growth rates, measured over 20 years, including measurements made by techniques (2), (5) and (6) above.

Materials and methods

Measurement sites were established in 1982, in an area of abundant moss growth near Casey Station on the shore of Vincennes Bay, Wilkes Land, Antarctica. The study sites are within the area that has since been designated ASPA 135 (SCAR 2004). The study area was roughly level, with higher ground to the south from which a small drainage line carried melt water. Beyond a low ridge to the east was a small lake with a rocky margin. The area was scattered with rocks, and three species of moss, *Bryum pseudotriquetrum* (Hedw.) Schwaegr., *Ceratodon purpureus* (Hedw.) Brid. and *Schistidium antarctici* (Card.) L.I. Savicz and Smirnova, formed continuous turfs amongst the rocks in parts of the study area. Plants growing on the higher ground to the south and east formed discontinuous cover, often polsters, in drier habitats than those along the drainage line or at the lake margin. The level of available moisture at a site influenced the occurrence of species at the site (Selkirk and Seppelt 1987), and morphology of the mosses. Morphology of *B. pseudotriquetrum* and *S. antarctici* was strikingly different at wet and dry sites (Seppelt and Selkirk 1984; Wilson 1990).

Method 1; measurements against cranked wires (or pins)

Stainless steel marker pins, purpose-made following Clymo's (1970) design for cranked wires, were installed in December 1982. The pins were 0.2 cm in diameter and a total of 21 cm long: 10 cm from base to a right-angled bend (or crank), 1 cm to a second right-angled

bend, 10 cm to top of the pin. A 1 cm diameter, 0.5 cm thick disc was slipped onto the upper section of the pin, and could be fixed in position by tightening a small screw in the rim of the disc which extended to the central pin.

Fifty measuring pins were initially installed. For each, the pin was pressed into the moss turf as far as it would go, until the base of the pin "grounded" on rock. If the grounding was on ice (which could subsequently melt) the baseline for future measurements would be upset. If the turf was deep enough, the crank or bend in the wire was within the turf, helping stabilise its position and minimising the likelihood of subsequent movement of the pin with freeze-thaw action. The disc was positioned on the upper section of the pin, resting on the surface of the moss turf. If the turf was not deep enough for the crank to be within the turf, the crank formed the measuring base for moss height.

The distance from the surface of the moss turf to the under surface of the crank or the disc (as appropriate) was measured and recorded. A small sample of the moss forming the turf was collected to allow laboratory identification. The site of each measuring pin was photographed and the location mapped, to facilitate their relocation at a later date. The measurements were repeated (at irregular intervals as logistics and collaboration with colleagues permitted) in 1984 by I. Stone, February 1986 by R. Hancock, February 1987 by M. Wilson, December 1991 by P. Selkirk, December 2001 by M. Skotnicki.

In December 1991, and again in December 2001, 49 of the original 50 pins were found. In 2001 loose or dislodged pins (presumably due to freeze-thaw action) were removed and omitted from subsequent searches and measurements. Some of the remaining pins were bent, but this did not affect the measurements.

Groups of pins were installed in patches of substantial moss cover within two areas of approximately 250 m², 150 m apart, and densely scattered with rocks. The substrate was rocky and very uneven. The pins were not installed on a grid or other regular pattern, but rather at locations where they could be inserted into the moss turf deeply enough to be secure.

The measuring pins were designed and manufactured in Sydney in 1981 without the benefit of a preliminary examination of the Antarctic field site. At the time of their installation in 1982 it was not known whether this method of moss growth rate measurement, designed for use in temperate *Sphagnum* mires (Clymo 1970) would be successful in Antarctic moss turfs. When the pins were installed in 1982 it was envisaged that monitoring pin security and measuring moss growth would be continued for a modest time period of

1–2 years only. It was not possible at that time to predict future visits to the site. However, by arrangements with colleagues visiting the vicinity for other purposes it has been possible to monitor the site and remeasure moss growth against the pins over 20 years.

In December 2001, an additional 21 measuring pins were installed at nearby sites, and initial measurements were recorded. At this time the locations of all measuring pins were also surveyed by GPS, facilitating future measurements of both old and new pins.

Method 2; measurement of stems cut from a turf, bagged or tied into bundles, replaced and remeasured

In November 1985, at sites in the vicinity of the measurement pins near the meltwater drainage channel, stems of all three species of moss were cut below the level to which green leaves were attached, measured, tied in bundles with cotton thread, and reinserted into the hole in the moss turf from which they had been taken. After 4 months the bundles were retrieved and the lengths remeasured (R. Hancock personal communication, who conducted this portion of the study)

Method 3; measurement of growth above a stain applied to stems

In December 1982, in isolated pockets amongst rocks on the eastern margin of the study site, an aqueous solution of the optical brightener Calcafluor White ST, 0.01% (Hughes and McCully 1975; Waaland and Waaland 1975) was poured over the surface of moss turfs, left for 5 min, then rinsed off with water from the nearby meltlake. The sites selected were higher than, and drained away from the rest of the study site, so that any runoff containing Calcafluor did not enter the rest of the study site. Samples of moss stems were collected after 1 month, and after a further 4 years. The samples were kept frozen until their examination at Macquarie University in Sydney. Individual stems were teased out, the apical segments cut in half longitudinally, mounted cut surface upwards in water, and examined using an Olympus Vanox microscope, UV light and L420 filter. Using an ocular micrometer the length of unstained stem at the apex was measured.

Results

Method 1; measurements against pins

Of the 50 measuring pins established in 1982, 27 were monitored for 10 years and 18 for 20 years. Although

all but one of the original 50 pins were located in subsequent visits to the site, measurements from those that had fallen over or become loose in the moss turf were disregarded, as it was felt that freeze-thaw action or interference by curious south polar skuas (*Catharacta maccormicki*) may have moved the pins relative to the moss turf. Where the moss had grown over the disc or the crank in the pin, or where the base of the pin was resting on a rock beneath the moss, the pin appeared secure as a measurement datum. In Fig. 1a discs can be seen on many of the pins but in Fig. 1(b) 10 years' moss growth has enveloped many of the discs. The mean rate of stem elongation in the turfs adjacent to the pins is shown in Table 1.

The pin measurements over 4 years (Table 2), all from moist sites within the study area, yielded greater elongation rates for *Bryum pseudotriquetrum* (4.6 mm year^{-1}) and *Ceratodon purpureus* (2.9 mm year^{-1}) than the average over the longer periods of

Fig. 1 One of the moss measuring sites established in 1982 in ASPA 135 at Casey, photographed in 1991 (a) and 2001 (b) showing 10 cranked wires (measuring pins) inserted in a turf of *Schistidium antarctici* and *Bryum pseudotriquetrum*. Shadows cast by the pins help to locate them. Note the discs present on some pins, although others have been lost and some pins are bent, due to the strong winds which occur frequently and to the weight of snow cover. In 2001, most discs were located within the moss turf due to elongation of the shoots over them. The area of each photograph is approximately $60 \times 40 \text{ cm}$

Table 1 Rate of stem elongation (mm year^{-1}) in moss turfs adjacent to stainless steel measuring pins at Casey Station, Wilkes Land continental Antarctica, measured over 10 and 20 years

<i>Bryum pseudotriquetrum</i>			<i>Ceratodon purpureus</i>			<i>Schistidium antarctici</i>		
Pin no	10 years	20 years	Pin no	10 years	20 years	Pin no	10 years	20 years
11	0.4		9	2.6		10	0.7	
12	1.5		37	1		13	2.7	3
14	1.4	1.1	39	5.6		15	1.9	1.9
19	2.2	1.4				17	1.5	1.4
20	1.8	1.3				21	0.6	0.3
33		0.9				22		0.7
43	1.5					23	0.1	
46	0.2					24	0.4	1.6
47		0.1				25	0.5	0.4
48	3.1	1.9				26	0.1	0.1
						27	0.8	0.8
						28	0.7	0.6
						29	1	0.5
						30	0.8	0.6
Mean	1.5	1.1		3.1			0.9	1
SD	0.9	0.6		2.3			0.7	0.8

time. For *Schistidium antarctici* the rate of 1 mm year^{-1} was comparable to the 10 and 20-year rates.

Method 2; measurement of stems cut from a turf and tied into bundles

Although measured for only a short time, the annual elongation rates for all species measured by the “cut bundles” method was comparable to the same species measured against measuring pins (Table 2). The sites for these measurements were adjacent and the plants were growing in comparable habitats.

Method 3; measurement of growth above a stain

Stems of all three species collected 1 month after application of the solution of optical brightener fluoresced white to the apex, confirming that cellulose in existing cell walls was stained. Stems examined with 4 years

growth after staining had an unstained apical segment, while the lower portion of the stem continued to fluoresce white. The observations are consistent with Calcafluor acting as a vital stain, remaining immobile in the stained walls, while the walls of cells newly formed by division of the apical cell were unstained. The length of the unstained portion thus satisfactorily gives a measure of new growth between the staining event and harvest.

The need for longitudinal sectioning of the stems followed by microscopic examination meant that only a small number of stems was measured, but also resulted in the observation of reproductive structures that would otherwise have gone unnoticed. Antheridia and paraphyses were observed in some apices, however no archegonia or sporophytes were observed. Table 2 shows that *B. pseudotriquetrum* stems which had developed antheridia and paraphyses had elongated considerably less than stems with vegetative growth only.

Table 2 Rate of stem elongation (mm year^{-1}) at Casey Station, Wilkes Land continental Antarctica

	<i>Bryum pseudotriquetrum</i>			<i>Ceratodon purpureus</i>			<i>Schistidium antarctici</i>		
	Moist Pins	Moist Bundles	Dry Stain	Moist Pins	Moist Bundles	Dry Stain	Moist Pins	Moist Bundles	Dry Stain
Rate of stem elongation mm year^{-1}	4.6	4.3	0.09 ^a , 0.02 ^b	2.9	2.4	0.15 ^a	1	1.3	0.15 ^a
<i>n</i>	13	116	7 ^a , 7 ^b	4	38	5	7	64	4

Moist site pins: elongation measured over 4 years in moss turfs adjacent to stainless steel measuring pins. Moist site bundles: elongation of cut bundles of stems measured over 4 months (data of R. Hancock, personal communication). Dry site Calcafluor stain: elongation of stems beyond chemical marker, measured over 4 years

n = number of stems or pin sites measured

^a Stems produced vegetative leaves only

^b Stems produced antheridia

The sites at which the Calcafluor measurements were made were on higher ground receiving no overland flow of melt water, providing drier habitats than those at which the measurement pin and cut bundles measurements were made. For all three species the rate of elongation of vegetative stems at these drier sites was considerably lower than at the wetter sites (Table 2).

Figure 1 illustrates another observation we have made but not been able to quantify in the vicinity of the measuring pins. The 10 pins (arrowed) and the pale grey rocks in upper and lower right hand corners of the photographs provide fixed points that allow comparison of the extent of *B. pseudotriquetrum* cover compared with *S. antarctici* cover in 1991 (a) and 2001 (b). Comparison of the photographs makes it clear that over the 10-year period, *B. pseudotriquetrum* (pale colour, coarse-textured appearance) has expanded its cover at this site, encroaching on the area covered by *S. antarctici* (darker colour, fine-textured appearance) and the rock in the lower right hand corner. This is consistent with our findings that stems of *B. pseudotriquetrum* grow faster than those of *S. antarctici* in this location. Although we have observed and photographically documented such changes in cover and distribution of the three moss species at a few sites, since we did not establish fixed points for repeated quadrat studies we are not able to quantify or document the changes on a large scale.

Discussion

Although lichens are capable of photosynthesis at substantially sub-freezing temperatures in Antarctica (*Umbilicaria aprina* down to -17°C , Schroeter et al. 1997), the mosses that have been studied cease photosynthesis at close to freezing point (Green et al 2000; Schlensog and Schroeter 2000). Like lichens, mosses are poikilohydric, hence are metabolically active only when moisture is available (Wilson 1990; Schlensog and Schroeter 2000). It is likely that low temperatures through the winter have little effect on moss photosynthesis since the plants are effectively freeze-dried, and hence metabolically inactive.

At continental sites, adequate liquid water for plant growth is available for only a few weeks in the summer. The precise length of the growing season varies from place to place, depending upon latitude, aspect and nature of the substrate. At Casey, Wilson (1990) reported a growing season for mosses of eight weeks in summer 1986–1987, while Lewis Smith (1999) reported conditions favourable for growth for only a few weeks

in 1996 at Edmonson Point, Victoria Land ($74^{\circ}20'\text{S}$, $165^{\circ}08'\text{E}$). Conditions also vary from year to year. Melick and Seppelt (1997) calculated a growing season for *S. antarctici* as a percentage of the years 1991, 1992, 1993, and 1994, equivalent to 15, 11, 6 and 5 weeks. As the length of the growing season can vary significantly between years, it is also likely that growth rates will also be variable between seasons.

The growth rates reported here show variation between methods, between sites and over time. In addition, slightly different things have been measured by the three methods. Measurements against the pins have measured the rate of upward growth of the general surface of the moss turf, so have estimated the rate of elongation of the population of moss stems immediately surrounding the pin. The cut bundle method has measured the rate of elongation of individual stems. The staining method has similarly measured the rate of elongation of individual stems by observing the length of stem and leaf tissue produced subsequent to staining.

The pin measurements over 10 and 20 years (Table 1) were over periods long enough to include years with both long and short growing seasons. The measurement pins were spread widely within the study site, and the calculated elongation rates are averages over a range of microhabitat and variations in microclimate. There is good agreement in rates over 10 and 20 years for both *B. pseudotriquetrum* and *S. antarctici*: for each, the growth rate was close to 1 mm year^{-1} . *Ceratodon purpureus*, for which measurements were obtained over only 10 years, elongated at almost 3 mm year^{-1} .

For *S. antarctici*, the rates calculated by both pin and bundle methods are close to the 1.3 mm year^{-1} that Melick and Seppelt (1997) quote for a nearby site, using tagged individual stems over 3.3 years, and vastly different from the $10\text{--}20\text{ mm year}^{-1}$ quite erroneously ascribed to *P. Selkirk* by Melick and Seppelt (1997). For *B. pseudotriquetrum*, we calculate 0.9 mm y^{-1} from Melick and Seppelt's (1997) figures, comparable with our pin measurements over 20 years for this species.

The rates of elongation of vegetative stems measured after staining with Calcafluor were an order of magnitude lower than those measured against pins, or using cut bundles, or Melick and Seppelt's (1997) tagged shoots. We interpret this as indicating the low frequency of hydration to full turgor and hence low rate of metabolic activity and growth in the extremely dry sites at which these measurements were made, as described by Wilson (1990) for *S. antarctici*. However, another possible explanation is that application of the stain reduced the rate of stem elongation. No experiments have been

conducted to examine for possible deleterious effects of Calcafluor pulse-staining on moss stem elongation under Antarctic conditions. However growth and development of red algal tissues after pulse-staining with 0.01% Calcafluor were unaffected (Waaland and Waaland 1975). Roots of corn seedlings elongated normally in the presence of 0.001 and 0.01% Calcafluor, but elongation was restricted in the presence of 0.1% (Hughes and McCully 1975). At a site in the maritime Antarctic, optical brightener was virtually undetectable in moss stems after only 15 months, presumably because of the much wetter conditions than at Casey (R.I. Lewis Smith, personal communication).

Few measurements of moss stem elongation have been made in other Antarctic locations besides the Wilkes Land location of these studies. Lewis Smith's (1999) study of *Bryum argenteum*, *B. pseudotriquetrum* and *C. purpureus* at Edmonson Point in Victoria Land recorded the distance between the change in colour and size of leaves that appear to mark the start of two successive year's growth. For all three species, measured along a moisture gradient, the growth increments for the growing season of 1994–1995 were significantly greater in moist than dry sites. For *B. pseudotriquetrum* and *C. purpureus*, the annual growth increments were comparable with those measured in this study in Wilkes Land (*B. pseudotriquetrum* wet 3.2, moist 4.6, dry 1.2 mm year⁻¹; *C. purpureus* moist 3.5, dry 1.4 mm year⁻¹).

Russell's (1984) study on subantarctic Marion Island provides a very useful critique of the range of methods available. As it was conducted in the much moister subantarctic environment, and on different taxa from the present study, no comparisons of rates can be made. Whinam et al.'s (2004) measurements of moss stems on buildings of known age were made in the subantarctic climate of Heard Island, but in the frequently dry habitat of wind-exposed walls of wooden buildings. For *B. pseudotriquetrum* and *C. purpureus* rates of 0.19 and 0.29 mm year⁻¹ respectively were calculated, rates that are of the same order of magnitude as and approximately twice the value of those obtained in the present study for extremely dry sites. Lewis Smith's (1982) study of growth and production of *Chorisodontium aciphyllum* on moss banks on subantarctic South Georgia showed local variation in the rate of elongation, resulting from differences in moisture regime and wind exposure. Over a few centimetres distance he recorded a threefold variation in rate of elongation, depending on exposure.

The long-term studies presented here confirm the conventional wisdom that mosses in continental

Antarctica indeed do grow slowly, and have documented the considerable variation in growth rate between sites and over time as measured by gametophyte stem elongation. For the three species studied, *B. pseudotriquetrum*, *C. purpureus* and *S. antarctici*, there is broad agreement in stem elongation rates calculated by different methods and by different authors for plants growing under comparable environmental conditions. It is clear that environmental conditions such as length of growing season and frequency of available moisture at the site strongly influence elongation rate. Measurements made over long periods of time will 'even out' temporal variations in growth rate of a given species at a given site, but measurements made over even relatively short periods of time are able to give reasonable estimates of stem elongation rates. At relatively moist sites, vegetative stems of *B. pseudotriquetrum*, *C. purpureus* and *S. antarctici* all appear to elongate at between 1 and 5 mm year⁻¹, but at extremely dry sites where plants would infrequently experience hydration adequate for carbon gain (Schlensog and Schroeter 2000), elongation rates are up to an order of magnitude lower.

Although sporophytes have not been observed on mosses in the vicinity of Casey, microscopic examination of apices of *B. pseudotriquetrum* revealed antheridia and paraphyses. Stems bearing gametangia elongated much more slowly than vegetative stems in the same habitat, suggesting that the limitations of the Antarctic growing season cannot support both elongation and differentiation of gametangia.

At the outset, we had no idea whether any of the three methods would be practicable under Antarctic conditions, and no real idea of how long it would be necessary to continue measurements in order to have generate useful data. We had no idea how often it would be possible to arrange revisits to the site and remeasurements. With hindsight, the experimental setup could have been different, with a larger number of measuring pins, systematic arrangement of the pins, the cut-bundle sites and Calcafluor stain sites, and collection of environmental and microclimatic data at measurement sites. However, this project, despite its small number of surviving pins and limited replication, by continuing over 20 years has generated the first useful long-term direct measurements of Antarctic moss growth by stem elongation. It has confirmed three methods of directly measuring moss growth in Antarctica over varying lengths of time, and has shown the potential for using such measurements in the exploration of a variety of environmental influences on the rate of moss growth in continental Antarctica.

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