**_Usnea antarctica_, an important Antarctic lichen, is vulnerable to aspects of regional environmental change**

*Running title: Lichen decline in the maritime Antarctic*

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## Abstract

Studies of cryptogam responses to climate change in the polar regions are scarce because these slow-growing organisms require long-term monitoring studies. Here we analyse the response of a lichen and moss community to 10 years of passive environmental manipulation using open-top chambers (OTCs) in the maritime Antarctic region. Cover of the dominant lichen *Usnea antarctica* declined by 71% in the OTCs. However, less dominant lichen species showed no significant responses except for an increase of *Ochrolechia frigida* which typically covered dying lichen and moss vegetation. There were no detectable responses in the moss or associated micro-arthropod communities to the influence of the OTCs. Based on calculated respiration rates we hypothesise that the decline of *U. antarctica* was most likely caused by increased net winter respiration rates (11%), driven by the higher temperatures and lower light levels experienced inside the OTCs as a result of greater snow accumulation. During summer *U. antarctica* appears unable to compensate for this increased carbon loss, leading to a negative carbon balance on an annual basis and the lichen therefore appears to be vulnerable to such climate change simulations. These findings indicate that *U. antarctica* dominated fell-fields may change dramatically if current environmental change trends continue in the maritime Antarctic, especially if associated with increases in winter snow depth or duration.

**Keywords:** $CO_2$; Gas fluxes; Micro-arthropods; Snow; *Usnea antarctica*; Winter.

## Introduction

The Antarctic Peninsula has been one of the regions of the world experiencing relatively fast regional climate warming over recent decades (Turner et al. 2009, 2013) and, due to its relatively simple ecosystems (Convey 2013), serves as an early warning system in understanding species and ecosystem responses to climate change. Terrestrial ecosystems in the Antarctic are dominated by mosses and lichens, with only two vascular plants present in localised areas of the maritime Antarctic (western Antarctic Peninsula region and associated outlying islands) (Convey 2013). The latter have undergone increases in population size over recent decades, and this spread is interpreted to be linked to the strong regional warming trend (Fowbert and Smith 1994; Grobe et al. 1997; Parnikoza et al. 2009; Torres-Mellado and Casanova-Katny 2011). However, the response of mosses and especially lichens to environmental change is often much harder to determine due to their slower growth rates (Lindsay 1973). Studies performed in the Arctic suggest that lichens are likely to decline in response to increased competition from vascular plants (Cornelissen et al. 2001), although winter climate change studies often show opposite patterns (Bjerke et al. 2011). Direct measurements of lichen and moss responses to climate warming without the confounding presence of vascular plants are sparse and often short term (Bokhorst et al. 2007a), and have not helped to clarify their predicted response under future climate scenarios (Lang et al. 2012). Mosses and lichens play a vital role in many ecosystems and in ecosystem service provision across the world, for instance as sinks for carbon in northern tundra regions (Cornelissen et al. 2007), suppliers of nitrogen to boreal forests (Lindo et al. 2013), food for vertebrates (Berg et al. 2011) and as a habitat and food source for many invertebrates (Gerson and Seaward 1977; Bokhorst et al. 2007b; Salmane and Brumelis 2008; Bokhorst et al. 2014; 2015). In the Antarctic context, the latter is particularly important, as soil invertebrates are the only macroscopic terrestrial faunal group (Convey 2013). Any changes in moss and lichen community composition and abundance are therefore likely to have major implications for the terrestrial fauna and food web of Antarctic ecosystems.

Since 2003, a passive experimental environmental manipulation study has been operated in a moss-dominated and a lichen-dominated community on Signy Island in the northern maritime Antarctic (Bokhorst et al. 2007a). During the early years of this study no response to the experimental manipulation was observed in the moss community while, in the lichen community, some deterioration of the dominant lichen *Usnea antarctica* was reported (Bokhorst et al. 2007a, 2012), along with a decline in the abundance of micro-arthropods (Bokhorst et al. 2008). The lichen decline was suggested to be caused by the thicker snow pack that accumulates inside the manipulation chambers (open-top chambers, OTCs) in winter, which insulates the vegetation against the extremes of winter temperatures (Bokhorst et al. 2011, 2013). However, this 'protection' allows for more physiological activity during the winter period when it is hard for primary producers to acquire resources due to the low light levels. Therefore, respiration rates in the vegetation may increase during winter, using up stored resources, which may be hard to compensate for during the short periods of activity possible during the summer growing season when mosses and lichens are also often subject to considerable periods of desiccation stress (Schroeter et al. 1995; Kappen 2000). The decline in the micro-arthropod community was proposed to be directly linked to the decline in a potential food source (*U. antarctica*) (Bokhorst et al. 2007b, 2008). The lack of decline in the moss community was assumed to indicate the buffering capacity the thick moss layer has on water availability for its own growth and that of the micro-arthropods living among them. Therefore, if the moss vegetation and associated micro-arthropods are less affected by water stress during the summer months (Bokhorst et al. 2007a), they may be able to compensate for increased winter respiration rates, and even then increase in abundance due to the opportunities provided by the warmer summer temperatures generated by the OTCs. However, whether any of these changes hold in the longer term is unknown, as it is also recognised that such field manipulation approaches can generate more extreme responses and artefactual results in the shorter term (Kennedy 1995; Bokhorst et al. 2011, 2013).

After 10 years of year-round OTC manipulation at Signy Island, we here report on the impacts on the contained cryptogam and micro-arthropod communities. We hypothesized that: (1) based on the initially observed declines of lichens in OTCs (Bokhorst et al. 2007a), the lichen community will deteriorate further following longer term warming but that any impact on the moss community will be much less due to the larger water availability in the deeper moss turf ; (2) the lichen decline in the fell-field community is driven by a negative carbon balance caused by higher winter respiration rates due to warmer (and longer duration) sub-nivean temperatures inside OTCs; and (3) the micro-arthropod community will decline in tandem with the lichens, whereas the warming in the moss community is likely to increase their abundance by reducing temperature limitation on growth and reproduction.

## Materials and Methods

### *Study site*

The study site was located on Signy Island, in the northern maritime Antarctic South Orkney Islands (60°71'S 45°59'W), on the north facing 'back slope' area near the British Antarctic Survey (BAS) Signy Research Station. Signy Island has an annual mean temperature of around -2°C and receives about 400 mm $yr^{-1}$ of precipitation of which most falls as snow (Walton 1982; Royles et al. 2013). Two distinct vegetation types have developed on the back slope area: (1) a moss community dominated by *Polytrichum strictum* Brid. (63% cover) and *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth. in Engl. (76% cover), which has accumulated to a depth of approximately 20 cm, underlain by a base layer of quartz-mica-schist, and (2) a fell-field lichen community dominated by *Usnea antarctica* Du Rietz (> 50% cover) on the same rock type. The two study sites were c. 50 m apart (Bokhorst et al. 2007a).

*Environmental manipulation study*

During the austral summer of 2003 six Open Top Chambers (OTCs) (Bokhorst et al. 2013) were deployed in each vegetation type (moss and lichen), where they remained year-round until December 2013. The design of the hexagonal OTCs was based on the widely used ITEX chambers (Marion et al. 1997). Passive warming chambers, such as OTCs, tend to affect various micro-climatic conditions besides temperature (Bokhorst et al. 2013) but remain a widely used and most reliable tool in remote locations such as the Antarctic. To minimise confounding effects on other micro-climatic variables besides temperature, larger chambers are most suitable (Bokhorst et al. 2011). Therefore, we deployed relatively large-sized OTCs, measuring 1.8 m from opposite corners and 1.6 m from opposite sides at the top and 0.5 m high. Each OTC had a neighbouring control plot in a split plot design. The placement of OTC and control plots was randomized to avoid any possible consistent effects of OTCs on the neighbouring control plots, for instance by wind or snow. Temperatures (°C) in the air (+5 cm), at the soil surface and deeper in the soil (-5 cm) were recorded using copper-constantan thermocouples, and soil water content (Water Content Reflectometer CS616, Campbell Scientific UK) was measured at hourly intervals year-round in three paired plots of each vegetation type. In addition we measured Photosynthetically Active Radiation (PAR; µmol $m^{-2}s^{-1}$) at the soil surface in one OTC and control plot for each vegetation type (SKP215 Campbell Scientific UK). All data were recorded on a CR10X Storage module (Campbell Scientific UK). Precipitation was recorded with a self-registering heated precipitation gauge (PLUVIO, OTT Hydrometrie) that recorded weight increments at hourly intervals in the vicinity (50 m) of the experimental plots. Due to intermittent power shortages and damage to sensors, micro-climatic recordings are incomplete for many of the later years. Therefore, we focus here on microclimate differences for the years 2009-2011, regarded to be representative, as these had the most complete datasets available across entire years. OTC effects on the microclimate in the early years of the experiment (2003-2005) were reported by Bokhorst et al. (2007a).

*Vegetation survey*

To quantify changes in the cryptogam communities in OTCs and control plots across time, we measured the percentage cover of each lichen and moss species through the point-intercept method in fixed 30 cm × 30 cm quadrats in each of the plots established in 2003. The presence/absence of each species was noted for 121 points at 2.5 cm intervals in the fixed quadrats. In one of the paired OTC-control plots of the fell-field vegetation the vegetation quadrat could not be accurately relocated in 2013 and therefore was not quantified.

Usnea antarctica *carbon balance*

To quantify potential changes in the carbon budget of *U. antarctica* - the most dominant of the lichen species in the fell-field community on Signy Island (Bokhorst et al. 2007a) and an abundant lichen throughout the maritime Antarctic (Øvstedal and Smith 2001) - due to OTC effects on the microclimate we calculated potential annual photosynthesis and respiration rates using the $CO_2$ response curves in relation to temperature and PAR described by Schroeter et al. (1995). For these calculations we used the hourly temperature data of individual plots (n=3 for both OTCs and control plots) and PAR values from one paired plot of OTC and control. We used five PAR categories (<5, 5-100, 100-300, 300-500 and >500 µmol $m^{-2}s^{-1}$) to calculate $CO_2$ fluxes. To achieve realistic calculations of annual $CO_2$ flux rates we set a number of restrictions: (1) The lower temperature limit was set to -10°C as the temperature response curves had a polynomial shape and lower temperatures would have resulted in increased respiration values, which is unrealistic considering the limited $CO_2$ efflux rates at very low sub-zero temperatures for lichens (Schroeter and Scheidegger 1995); (2) summer $CO_2$ flux rates were limited to periods with precipitation events, as drought is the main limiting factor for lichen physiological activity (Schroeter and Scheidegger 1995; Schroeter et al. 1997; Kappen 2000; Schroeter et al. 2010). If precipitation was recorded during a specific hour, irrespective of the amount, the corresponding $CO_2$ flux for that data point was included in the calculations; (3) during the snow cover period between April and September, we included all $CO_2$ flux values, as the sub-nivean microclimate provides high relative humidity allowing lichen physiological activity (Kappen et al. 1995); (4) these calculations were limited to 2004, 2005, 2009 and 2010, the years with the most complete micro-climatic recordings. Although there are clear limitations to these calculations they permit comparison of the potential carbon budget of *U. antarctica* between OTCs and control plots in a consistent manner and allow a test of hypothesis 2.

*Micro-arthropod abundance*

To quantify changes in the abundance and diversity of the micro-arthropod community in response to the warming treatment we collected vegetation and underlying soil using a PVC corer (7 cm diameter). In the moss community we collected the top 5 cm and in the lichen community all lichens and the first cm of soil and loose gravel in the lichen community of each plot. Micro-arthropods were extracted in a modified Tullgren extractor for 48 h. Collembola and Acari were identified to species level except for smaller Prostigmata, which were grouped together.

*Statistics*

Microclimate differences between OTCs and control plots were compared across seasons using monthly mean values to calculate a seasonal mean (summer: December-February, autumn: March-May, winter: June-August and spring: September-November). We used repeated-measures ANOVA with treatment (OTC vs. control plots) within a plot as a within-subject factor to test for significant differences between OTCs and control plots. As only minor, non-significant, differences were found in the soil moisture data we only present the summer mean values. To quantify changes in cryptogam species cover we used repeated measured ANOVA on the point-intercept data from 2003 and 2013. Differences in total and individual species abundances of micro-arthropods between OTCs and control plots were quantified through one-way ANOVA. Potential differences in the calculated values of photosynthesis, respiration and the net annual carbon budget between treatments were tested using repeated measures ANOVA. Log transformations were applied where necessary and homogeneity of variance was compared using Levene’s test. All analyses were carried out in SPSS 21.0 (SPSS Inc., Chicago, IL, USA).

## Results

*Impact of OTCs on microclimate*

Mean summer air temperature warming achieved by OTCs was 0.3°C and 0.7°C in the lichen and moss communities respectively (Table 1). The strongest warming took place during winter reaching on average 1.0°C higher in the OTCs compared to controls, most likely as result of snow accumulation inside OTCs. At the soil surface, summer warming reached 0.7°C and 0.2°C in the lichen and moss communities, respectively, and strongest warming also occurred during winter, 0.9°C and 0.2°C. Deeper in the soil, summer warming by OTCs was 0.6°C and 0.3°C in the lichen and moss communities, respectively, while during winter, warming effects of 0.7°C and 1.5°C were recorded. Soil moisture was reduced, but not always significantly so, during the summer months, with 6-20% lower mean values recorded in OTCs compared to control plots (Table 1). PAR showed small non-significant changes between OTCs and control plots, ranging between 10% lower and 5% higher mean values during summer (Table 1). Larger differences (up to -84%) were recorded between OTCs (2.5 µmol $m^{-2}$ $s^{-1}$) and control plots (11.0 µmol $m^{-2}$ $s^{-1}$) in winter, again indicating snow accumulation inside OTCs. In addition, freeze-thaw cycles were often reduced during late winter inside the OTCs (see Online Resource 1) indicating that OTCs were accumulating more snow than the surrounding non-manipulated habitats.

*Response of the lichen community to warming*

There were strong responses by parts of the lichen community to the OTC manipulation (Table 2, Fig. 1). The cover of the dominant lichen species *Usnea antarctica* declined by 71% in the OTCs following 10 years' of warming, while reducing by only 16% in the control plots (Fig. 2a). The percentage cover of the lichen *Ochrolechia frigida* increased (Tukey HSD $P < 0.01$) from 1.3% (SE: ±0.9) to 14.3% (±2.2) in the OTCs between 2003 and 2013 while showing no significant change in the control plots (4.1±1.7% to 4.6±1.9%) (Fig. 2b). The other lichen and moss species, which have a low cover in this ecosystem, showed no significant changes in response to the OTC manipulation (Table 2, Online Resource 2). On average, photosynthetic rates of *U. antarctica* were lower (6%) in the OTCs compared to control plots while respiration increased (11%) (Table 3, Fig. 3). The changes in photosynthetic and respiration rates resulted in a decreased net carbon budget for *U. antarctica* in the OTCs compared to control plots, and in overall carbon loss during 2005 and 2009 (Fig. 3c) and this may have been the underlying cause for the cover declines observed in the OTCs.

Total Collembola and Acari abundance was not affected by the warming treatment (Table 4). However the abundance of the less common collembolan *Folsomotoma octooculata* decreased by 71% ($P < 0.05$) in the OTCs compared to control plots.

*Response of the moss community to warming*

There were no species-specific changes in the bryophyte community in response to the OTC treatment (Table 2). However, there were overall declines of 68±7% and 51±11% in *Polytrichum strictum* cover in the control plots and OTCs, respectively (Fig. 4, Online Resource 2). The liverwort *Cephaloziella varians* had invaded two of the OTC plots replacing *P. strictum*, covering up to 9% of the surface (Fig. 4), while this was not observed in the control plots. There were no abundance differences for Collembola and Acari between control plots and OTCs in the moss community (Table 4).

## Discussion

We found a clear contrast between Antarctic moss and lichen communities in their response to 10 years of experimental field environmental manipulation mimicking long-term climate change scenarios. The currently widespread and common lichen *Usnea antarctica* was very vulnerable to the applied manipulation, while none of the moss species showed detectable responses. The response of the lichen community is in line with reports from the Arctic (Wahren et al. 2005) but also provides a clear account of lichen responses to climate change without confounding effects from vascular plants (Cornelissen et al. 2001) thereby highlighting the vulnerability of lichens to future environmental change. The very limited response detected in the micro-arthropod community is likewise consistent with results obtained in a three year manipulation experiment on High Arctic Svalbard (Webb et al. 1998), indicating that these organisms are resistant or resilient to the magnitude of micro-climatic changes induced by the OTC methodology on this experimental timescale.

### *Cryptogam response to climate warming*

In support of Hypothesis 1, the dominant lichen *U. antarctica* declined under the climate change simulation while the moss community was unchanged. The limited response by the moss vegetation to warming indicates that this community is relatively resistant to climate change, probably as a result of the larger water availability in the deeper moss turf. The large decline of the moss *P. strictum* over time was unrelated to the influence of OTCs, indicating either that there was a natural turn-over in the moss community (Collins 1976) or that local environmental conditions in this part of Signy Island are becoming less favourable for this moss species. Large changes in precipitation regime are predicted for the Antarctic Peninsula region (Thomas et al. 2008; Turner et al. 2009, 2013) and have already been implicated in affecting moss growth in the South Orkney Islands (Royles et al. 2012, 2013). Together with invasion of non-native or expansion of native vascular plants these changes may well lead to outcompeting of these moss communities in the near future if regional climate warming becomes more intense (Day et al. 2009; Hill et al. 2011).

The lichen decline was driven by that of the dominant species *U. antarctica*, while many other sub-dominant crustose lichens in this community did not respond significantly to the OTC treatment (Online Resource 2) indicating that not all lichens were vulnerable to these climate change scenarios. In addition, the initially less common *O. frigida* increased, as has also been reported in a long-term warming study in the Arctic (Wahren et al. 2005). *O. frigida* typically can be found overgrowing dead mosses and lichens and its increase may at least in part be in response to the high mortality of *U. antarctica*. The experimental manipulation remained in place year-round, typically resulting on average in temperature increases of less than 1.0°C. These changes are well within the current annual temperature variation for these Antarctic lichens and should therefore not provide a problem for their survival. However, maximum short-term temperatures (i.e. extreme events) have been reported to increase in OTCs (Bokhorst et al. 2011) which could have negatively affected the physiology of lichens (Schroeter et al. 1995). Furthermore, some drying of the soil was also measured inside the OTCs which, although often not reaching significance, could have placed additional restrictions upon the already limited water supply for their contained terrestrial communities (Kennedy 1993; Convey et al. 2014). In addition, the 16% decline of *U. antarctica* observed in the control plots may indicate that conditions are already becoming unfavourable for this lichen on Signy Island.

Although the warming achieved with the OTCs was on average not particularly high, it was most apparent during winter due to thicker snow insulation inside the OTCs (as confirmed by the much lower PAR values during this period), reduction in freeze-thaw cycles and the loss of deep freezing temperatures (Bokhorst et al. 2011). Therefore, changes in the winter temperature and light regime due to snow accumulation were the most likely cause underlying the observed lichen decline inside the OTCs. Similar lichen declines have been reported in several Arctic studies, particularly in those that led to alterations in snow regimes (Benedict 1990, 1991; Wahren et al. 2005). The assumed underlying cause of these declines is the depletion of stored carbon through increased winter respiration (Benedict 1991; Kappen 2000), itself resulting from the increased insulation and higher temperatures provided by the deeper snow pack (Kappen 1993). Therefore, it is possible that the same mechanism, carbon depletion due to increased winter respiration, also affected *U. antarctica* inside the OTCs, a proposition which is supported by the $CO_2$ calculations.

*Carbon budget of* Usnea antarctica *under climate warming*

In support of hypothesis 2, there was a potential negative carbon balance for *U. antarctica* based on the calculated $CO_2$ flux rates. The differences in carbon balance of *U. antarctica* between OTCs and control plots were primarily driven by increased winter respiration rates (11%), themselves most likely a direct result of the higher winter temperatures in combination with lower light levels (Schroeter et al. 1995) due to the build-up of a thicker snow pack inside OTCs (Bokhorst et al. 2013). In addition, the decrease in growing season photosynthetic rates, although small, reduced the total carbon uptake. These combined effects resulted in a lower net carbon uptake and for some years a negative carbon balance for *U. antarctica* inside the OTCs. Furthermore, the lower photosynthetic rates may have been a consequence of the lichen mycobiont parasitizing the photobiont as stored carbon became depleted, as suggested by Gannutz (1970). Some evidence for deterioration of the photobiont was observed in 2005 when *U. antarctica* thalli showed a reduction (42%) in chlorophyll content inside the OTCs compared to control plots (Bokhorst et al. 2012) indicating that it was performing poorly, as would be consistent with parasitization by the mycobiont. The calculated $CO_2$ flux rates here were much lower compared to the maximum potential rate identified by Schroeter et al. (1995) (323 mg $CO_2$ $g^{-1}$ dw $y^{-1}$) and reflect the limitation of carbon uptake by the infrequent occurrence of precipitation for lichen hydration in our calculations. Although Antarctic lichens can withstand particularly harsh climatic conditions the OTC treatment appears to greatly affect the performance of *U. antarctica* through relative minor changes in temperature, light availability and water availability during different parts of the year, indicating that some Antarctic lichens may be very vulnerable to season-specific climatic changes.

*Micro-arthropod response to OTC manipulation*

The micro-arthropod communities were little affected by our climate manipulations. Neither the most dominant springtail in this ecosystem, *C. antarcticus* (Bokhorst et al. 2008), nor any of the mite species, showed any detectable response to the 10 year manipulation. However, the significant decline in numbers of the less common springtail *F. octooculata* in the lichen OTCs may provide some support for Hypothesis 3. These findings are inconsistent with the previously reported declines of *C. antarcticus* in various passive warming treatments as a result of desiccation (Convey et al. 2002) or the increased abundance observed under summer warming with water additions (Convey et al. 2002; Day et al. 2009). The limited response in our OTCs used on Signy Island indicates that the climate manipulations were not strong enough to have an impact on the micro-arthropod community, indicating that this group of invertebrates appears relatively resistant. Initial declines in *C. antarcticus* abundance following two years of warming in these OTCs (Bokhorst et al. 2008) may therefore be an example of an artefactual response, or there may be inter-annual variation in the micro-arthropod response depending on the ambient temperature and moisture conditions experienced. The latter explanation would suggest that the microclimate of the OTCs was only capable of affecting these organisms during unfavourable ambient weather conditions, resulting in abundance declines from which the population could recover during better years. The lack of response by the micro-arthropod community to the massive decline in *U. antarctica* suggests that the species involved either do not depend on this lichen for food (Bokhorst et al. 2007b), or were not limited by food availability despite the decline (Davis 1981). It may also be possible that micro-arthropods could benefit from the increase of the lichen *O. frigida*. Overall, the minimal responses identified here in either the moss community or the micro-arthropods of both vegetation communities suggest that both these important elements of Antarctic terrestrial ecosystems have considerable resistance to changes in abiotic and biotic conditions under current change scenarios.

In conclusion, the regionally important lichen *U. antarctica* appears very sensitive to changes in winter snow depth and associated alterations in light levels and temperature regime. As climate change is likely to affect the precipitation patterns along the Antarctic Peninsula, *U. antarctica* dominated fell-field communities may drastically change in floristic composition during the coming decades.

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## Figures

Figure 1. Cover of the fruticose lichen *Usnea antarctica* inside an Open Top Chamber on Signy Island at the start of the environmental manipulation in 2003 (left) and after 10 yearsof the study (right). Distance between metal pegs is 30 cm.

Figure 2. Lichen cover changes following 10 years of manipulation using OTCs on Signy Island. a % cover of the lichens *Usnea antarctica* and b *Ochrolechia frigida* in control plots (C) and Open Top Chambers (OTC) from surveys taken in 2003 and 2013. Bars are mean of n = 5 with SE as error bars. * indicate significant ($P < 0.05$) differences between years.

Figure 3. Annual $CO_2$ gas fluxes of *Usnea antarctica* in control plots (C) and Open Top Chambers (OTC). Values are based on calculations of $CO_2$ exchange using hourly temperature and photosynthetically active radiation data from six experimental plots on Signy Island and $CO_2$ response curves of *U. antarctica* quantified by Schroeter et al. (1995). Bars are mean of n = 3 with SE as error bars. * indicate significant ($P < 0.05$) differences between years.

Figure 4. Shifts in the moss community on Signy Island between 2003 and 2013. The top photograph shows the decline of *P. strictum* while *C. aciphyllum* remains dominant in the control plots. The lower pictures show the invasion of the liverwort *Cephaloziella varians* (white square of the lower right figure) in an OTC where previously *P. strictum* was growing. Although this only occurred in one OTC it indicates the start of a community shift. The distance between the wooden pegs is 30 cm.