Chapter 3: Effects of environmental manipulation of local climate on plant interaction.

Abstract:

Open Top Chambers (OTCs) were used as passive warming devices, to test whether an amelioration of harsh environmental conditions, simulating the effects of predicted climate change, would alter the balance between competition and facilitation in arctic/alpine plant communities.

The experiment was set up at an altitude of 1000 m a.s.l. in the Scottish Highlands, using *Carex bigelowii* and *Alchemilla alpina* as target plants. The target plants were transplanted into replicate environmental treatments, using OTCs, wind shelters and control treatments. Within each environmental treatment, the target plants were planted with as well as without neighbours. Measurements were taken of final above ground biomass of the target plants, as well as environmental variables (soil and air temperature, wind speed and direction, soil moisture and PAR).

The results showed that the changes in the measured environmental variables were not sufficient to alter the balance from competition and facilitation for either of the target species. This may be due to some variables counteracting each other, e.g. increased soil temperature and decreased wind speed versus decreased air temperature. The only significant changes in above ground biomass were seen between the with and without neighbours treatments for *A. alpina*. This was observed for all three environmental treatments. It is suggested that this was mainly due to cooling effects on the meristem, which resulted in the plants without neighbours being exposed to lower air temperatures and therefore reduced growth. Further work is needed.

3.1. Introduction

3.1.1. Competition and facilitation

Where plants are growing near each other, there is inevitably interaction between them. These interactions can be either negative or positive. Much emphasis has been placed on negative interaction in terms of competition for resources (Grime *et al.*1981, 2000, Grime & Hillier 2000, Tilman 1982, Campbell *et al.* 2003). However, in recent years, the importance of positive interactions within plant communities has also become a focus of research (Bertness and Callaway 1994, Callaway 1998).

Bertness and Callaway (1994) define positive interactions as "all non-consumer interactions among two or more species that positively affect at least one of the species involved". Positive interactions, or facilitation, between plants in harsh environments can affect recruitment success and establishment (Bertness & Callaway 1994, Brooker & Callaghan 1998) by ameliorating physical environmental stress. Bertness and Callaway (1994) give desiccation, low nutrient levels, osmotic stress, soil oxygen, soil moisture and disturbance as examples of contributors to physical stress. Callaway (1995) gives a comprehensive review of examples of facilitation. In physically severe conditions (heat, cold, etc.) the ability of plants to acquire basic resources is impaired, so if the presence of neighbours reduces severe stress, then this facilitation will out weigh any restriction caused by competition with that neighbour (Callaway 1995). Benefits of facilitation (Callaway *et al.* 2002) are, for instance, accumulation of nutrients, provision of shade, amelioration of disturbance, or protection from herbivores.

Positive interactions are not necessarily species-specific, however much of the early work concentrated on species-specific interactions (Callaway 1995, 1998). Such interactions can be important in determining the composition of plant communities (Callaway 1995, Choler *et al.* 2001). The strength of these interactions can be tested by using neighbour removal experiments, where plants are grown with and without neighbours. Where plants show greater growth in with-neighbours treatments, facilitation is more important as a driver than competition (Choler *et al*. 2001, Choler & Michalet 2002, Hobbie *et al*. 1999, Huckle *et al*. 2000, Huckle *et al*. 2002, Syndonia Bret-Harte *et al*. 2004).

The strength of species interaction changes along environmental gradients. Choler *et al*. (2001) found increased facilitation with increasing altitude in alpine plant communities in the French Alps, and Callaway *et al*. (2002) came to similar conclusions with experiments in mountain ranges in North and South America as well as Europe and the Caucasus. Facilitation may also be important in widening the distribution of plant species along environmental gradients (Choler *et al*. 2001). The changeover from competition to facilitation can be seen as the main driver along a gradient of increasing environmental severity and one which is often ignored or not fully taken into account in models (Callaway 1995).

3.1.2. Environmental manipulation - warming experiments

It is widely recognised that the global climate is changing, in part due to anthropogenic effects, and that this change will affect upland ecosystems (see Chapter 1). Previous studies have attempted to simulate the effects of climate change in the field, and a few have taken an active warming approach. At Great Dun Fell (845 m), in England, as part of an experiment investigating the effects of soil temperature on root growth, heating cables in a grid below the soil surface were used (Ineson *et al.* 1998, Fitter *et al.* 1999). The low voltage heating cables were buried at a depth of 2 cm, these were able to maintain a temperature of approximately 3°C above ambient. This led to a short term increase in nutrient availability and an increase in root turnover, but biomass was little affected (Fitter *et al.* 1999).

In another approach, suspended infrared heating lamps were used at a site in the Colorado Rocky Mountains, USA (Price & Waser 1998, Price & Waser 2000, Shaw & Harte 2001, Saavedra *et al.* 2003). This led to an increase in soil temperatures in the treatment plots of 5°C compared with the control plots (Shaw & Harte 2001). On this site there was also an increase in nutrient availability in the short term, but this declined over time (Shaw & Harte 2001). At the end of a four year period Price & Waser (2000) had found no evidence of a change in the plant community.

While these approaches give a great deal of control, they are costly and have obvious logistical limitations, i.e. requiring an electrical power supply. Many more studies have attempted to simulate climate change by the use of passive greenhouse type devices. A comprehensive review is given by Kennedy (1995a). He recommends that these devices be used with care and that the experimenter is aware of the environmental factors which are affected by the passive greenhouses. Most of the greenhouse type devices which Kennedy (1995a) reviews were closed; the use of open topped devices is less problematic. As Hollister & Webber (2000) have shown, Open Topped Chambers (OTC) can be used as an analogue of natural interannual temperature variation.

The International Tundra Experiment (ITEX) has developed a recommended standardised approach for the use of OTCs. These are shown to be effective at providing an analogue for climate warming (Kennedy 1995a,b, Marion 1996, Marion *et al*. 1997, Hollister & Webber 2000). ITEX chambers increase the temperature within the chambers by 1-3°C (Henry & Molau 1997), but at the same time reduce wind exposure experienced by the plants (Hollister & Webber 2000). The OTCs are designed to achieve a warming effect by reduction of wind speed and by acting as solar traps, in the same way as a greenhouse (Marion 1996).

3.1.3. Target plant species

Modelled simulations of the effects of climatic change on the distributions of several plants using a climate envelope model (Berry *et al*. 2002), have suggested that the altitudinal range of *Carex bigelowii* (Stiff sedge) and *Alchemilla alpina* (Alpine Lady's Mantle) may be affected by climate change. The predicted distribution maps show a marked reduction in the range of *A. alpina* and *C. bigelowii* in Britain by the 2080's (Berry pers com.).

C. bigelowii is a perennial clonal sedge with creeping rhizomatous growth (Brooker *et al*. 2001). *A. alpina* is a creeping herbaceous perennial, which occurs widely in upland Britain. Carlsson and Callaghan (1991) show that in Swedish Lapland *C. bigelowii* had greater above ground biomass where it was within *Racomitrium lanuginosum* or *Empetrum hermaphroditum* clumps than did plants growing without neighbours. A similar response could be achieved with the use of plywood shelters.

3.1.4. Aims

The main aim of the experiment described here was to determine if environmental manipulation can change the balance between facilitation and competition for the two target species on a Scottish mountain through the use of OTCs and wind shelters. The following hypotheses were tested:

- An increase in temperature may change the balance from facilitation to competition.
- Warming provided by small OTCs and wind shelters will be sufficient to increase levels of competition experienced by the target species.
- Temperature is a more important ecological factor than wind.

3.2. Methods

3.2.1 Site Description

This research was carried at 1000 m a.s.l. (NO048758), near the summit plateau of Glas Tulaichean (1051 m), in the Scottish Highlands to the north-west of the Spittal of Glenshee (Figure 3.1). The underlying geology is Caenlochan Schist with Lamprophyre and Felsite intrusions (BGS 1989), and the soil is acidic in nature. The area is designated as a Site of Special Scientific Interest (SSSI) of international importance and a provisional Special Area of Conservation. The SSSI citation states that the site has "a representative range of summit vegetation, including montane heaths" (SNH file Ref: NO07/2). The summit vegetation consists of an area of extensive *Carex – Racomitrium* heath, the vegetation below the summit is dominated by wind clipped *Vaccinium* and *Empetrum*. Permission was sought from and granted by the land owner and SNH before work was started. The site has a clear south westerly aspect and benefits from easy access by landrover along an existing track. The site slopes at an angle of 18.7 degrees and has a Topex score of 10 (Wilson 1984).

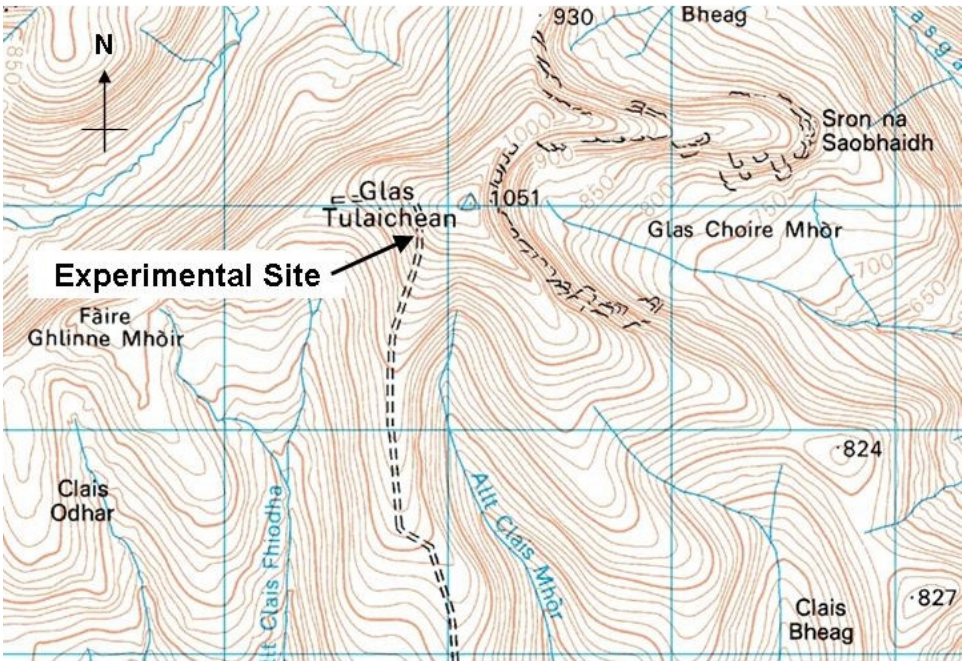

Figure 3.1. Map of the location of the experimental site on Glas Tulaichean at 1000 m a.s.l. (NO048758) in the Scottish Highlands. The site is situated next to a landrover track allowing

easy access and has a south westerly aspect. © Ordnance Survey (with permission). 1:50,000.

3.2.2. Experimental design

In order to test the effects of an increase in temperature on competition in plant communities, three different environmental treatments were used, OTCs, wind shelters, and controls. The OTCs, built to a design adapted from the protocol developed by ITEX for their programme of arctic and alpine climate change research (Molau & Mølgaard 1996), were used to manipulate the local climate. These OTCs have the advantage of being a robust, tried and tested design (Marion *et al.* 1997), and they are relatively cheap. The wind shelters (Shelter) are a simpler design, consisting of strips of 3 mm Plexiglas™ strapped to the side of wire cages, were used to provide shelter from the wind without causing the same level of heating as the chambers (Marion 1996). OTCs work by reducing the air flow inwith the chambers and the clear Plexiglas™ sides act in the same way as glass in a green house in allowing warming in side the chambers (Henry & Molau 1997, Marion 1996). The wind shelter can also have a warming effect, but to a far lesser extent. The control treatments were just wire cages. The same wire cages were used for both the Shelter and Control treatments to exclude large herbivores, i.e. mountain hares (*Lepus timidus*).

The three different environmental treatments were set out in a randomised block design. Each block consisted of one OTC, one wind shelter and a control, as shown in Figure 3.2. There were eight replicate blocks used in this experiment.

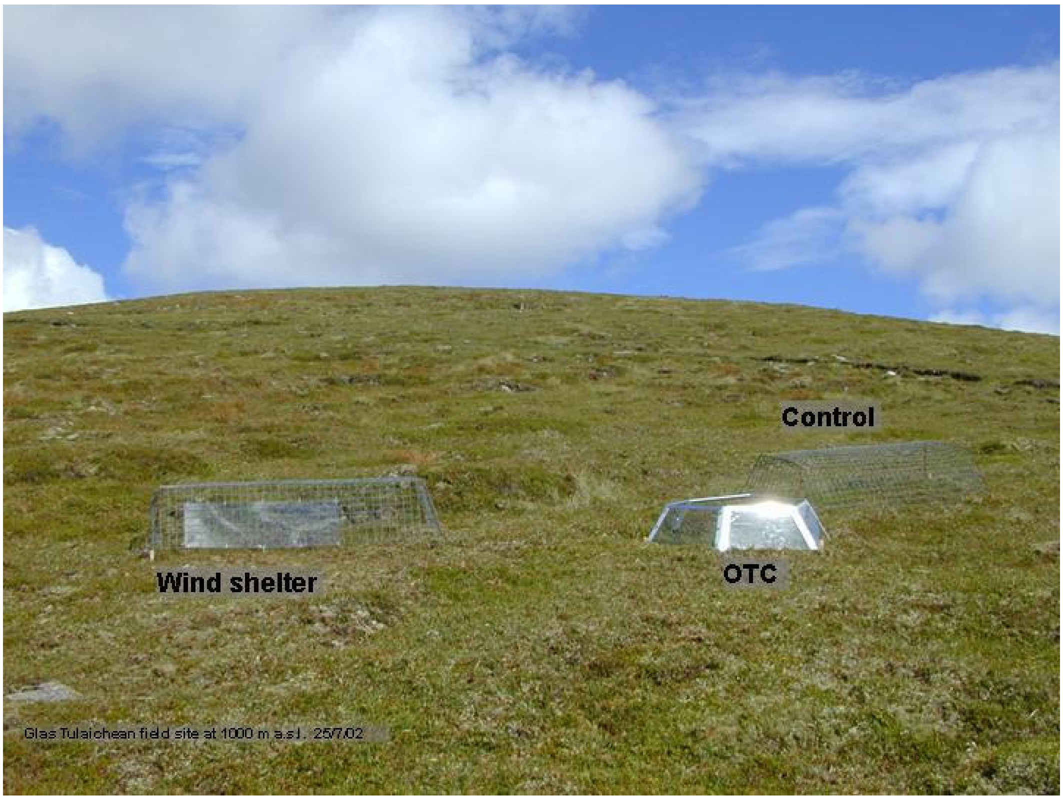

Figure 3.2. One replicate block consisting of an OTC, a wind shelter and control. The wind shelter and the control treatments used wire cages to exclude large herbivores.

Although the ITEX OTCs and Wind Shelters are relatively cheap, there was insufficient funding to build enough full sized chambers to the standard ITEX design, in order to provide sufficient replication for sound statistical analysis. Therefore it was decided that smaller chambers (half the recommended ITEX size) be used to allow an increased number of replicates.

The OTCs were adapted from a design used by the ITEX programme of arctic and alpine climate change research (Molau & Mølgaard 1996). Specifications for building a 25 cm tall, 75 cm open-top hexagon are shown in Figure 3.3. Fixing the 60° inclination of the panels, the height, and a diameter (basal or top) fixes all other dimensions through geometric relations. The panels were bolted to an aluminium corner brace bent at 120° to maintain the correct shape, and further aluminium braces were riveted to the top edge of each panel. The panels were made from 3 mm Plexiglas™, as recommended by Marion (1996).

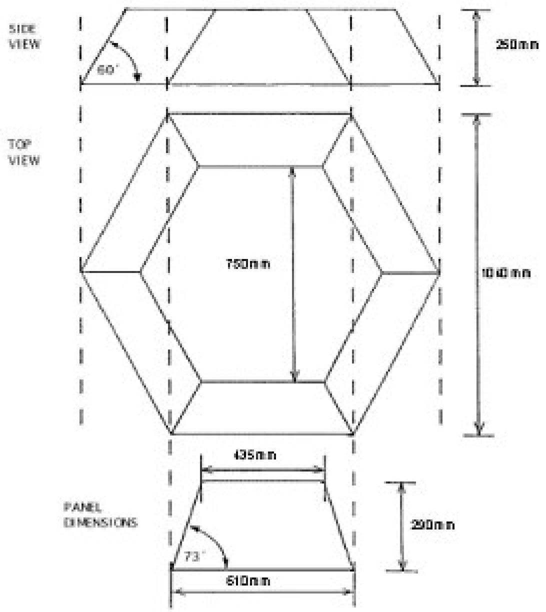

Figure 3.3. Schematics for building a 60°, 25 cm tall, 1.04 m basal diameter hexagon chamber (after Marion 1996).

The wind shelters used were 3 mm thick Plexiglas™ strips of 1 m length and 20 cm height, which were strapped to the windward side of the wire cages with cable ties. This is a simpler design than that recommended by ITEX (Molau & Mølgaard 1996).

The area within each environmental treatment was divided into four plots (north, south, east and west), with one plant in each plot. The treatments applied are shown in Table 3.1. Two plants of each target species were used, one with and one without-neighbours, respectively. This allowed for the position used for each treatment to be replicated twice, as a control for the effect of position within each treatment. These positions were randomly assigned to the eight blocks, and within each block the positions were kept the same in each treatment. An example of the plot design is shown in Figure 3.4.

Table 3.1. With and without neighbour treatments applied to the two target species planted into the different environmental treatments.

Treatment	Neighbours
Warming and shelter (Chamber)	+
	-
Wind Shelter only (Shelter)	+
	-
No Warming or shelter (Control)	+
	-

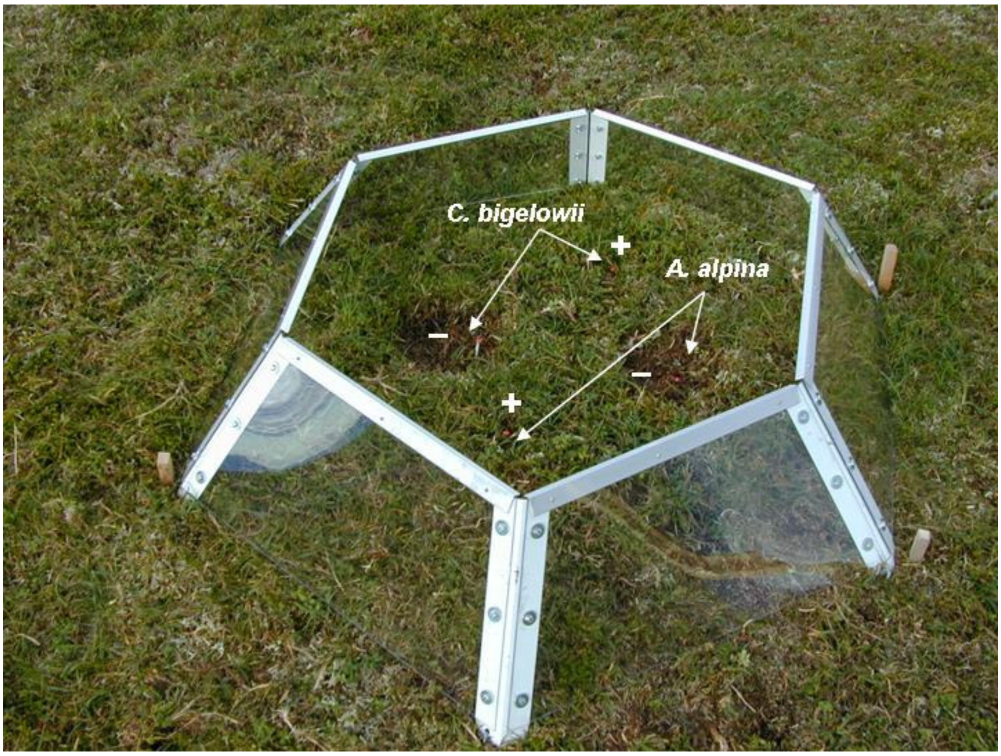

Figure 3.4. Example of the plot design showing planting positions within an OTC. The two target plants were planted either with (+) or without (-) neighbours, and the position of each plant was marked with a nail painted red.

Individuals of *C. bigelowii* and *A. alpina* were collected on the summit plateau area, and were transplanted into the experimental blocks. For *A. alpina*, 20-30 mm lengths of rhizome with a single growing apex were transplanted (Morecroft & Woodward 1996). For *C. bigelowii*, each plant consisted of two tillers, one storage tiller and one young growing tiller. All the young tillers that were chosen had a new tiller shoot on them (Figure 3.5).

Figure 3.5. Example of a *C. bigelowii* plant with two tillers and a new tiller shoot showing on the young tiller.

As far as possible the plants used for each replication were of a similar size (judged by eye) and age. The plants were marked with a nail painted red, so that they could be easily found and identified (see Figure 3.4). In the with neighbour treatments, the target plants were planted into the existing vegetation. For the without neighbour treatments, all plants within a 10 cm radius of the target plants were removed by manually clipping away all plants at ground level within the plot. The edges around these plots were cut straight downwards to sever roots or rhizomes from plants outwith the plot. The below ground parts of the plants were not removed, as this would have disturbed the root systems (Aarssen & Epp 1990). Removal of any plant re-growth, other than the target plant, was repeated as often as necessary throughout the growing season.

The experiment was set up in August 2002 and was run for two further growing seasons. The chambers and shelters were kept in situ for the whole experiment. The original plan had been for the chambers to be taken in for the winter period. However, as there was a early and heavy snow fall in October 2002, it was not possible to take the chambers in, and so they were left in situ and monitored to see how much they affected the snow cover inside the chambers. Both chambers and cages were seen to accumulate snow relative to the surroundings.

An attempt to record this was made, using a digital camera. Unfortunately, the photographs taken to show this were lost due the effects of cold on the digital camera, and no other measurements were taken due to the severe conditions on the mountain.

3.2.3. Growth of target plants

Measurements of growth were taken in May and August 2003, at the start and end of the growing season. The measurements taken for *C. bigelowii* were number of leaves and number of tillers. Measurements of culm height on flower stalks were intended to be taken, however no flower stalks were produced during 2003.

Measurements were also taken of the numbers of leaves (Kershaw 1960) and numbers of flowers of *A. alpina*. These measurements of were taken in May and August, as this represents the beginning and end of the growing season for this species (Peat *et al*. 2002).

In August 2004 (before the start of the main shooting season) all the target plants were removed and were air dried for two weeks. Then the above and below ground parts of the plants were separated. The above ground parts of the plants were weighed and recorded to determine the total above ground biomass of the plants. Below ground parts were not used, to avoid complications with soil, i.e. difficulties of separating fine roots from the soil and the resulting uncertainties.

3.2.4. Environmental monitoring

Measurements of air and soil temperature, soil moisture, and wind speed at ground level were taken in all environmental treatments. Irradiance was measured as Photosynthetically Active Radiation (PAR), and was recorded in the OTC and Control treatments only. Wind speed and direction were also measured at 1 m above ground level.

All temperature measurements were made using Campbell Scientific® 107 thermistors, wind speed at ground level was measured using modified Windtronic 2 (Kaindl Electronic®, Rohrbach, Germany) anemometers (Figure 3.6), wind speed and direction at 1 m was recorded with a three cup anemometer and a wind vane (Didcot Instruments, UK), irradiance was measured with a PAR meter (Didcot Instruments, UK), and soil moisture with ThetaProbe ML2x (Delta-T Devices, UK) soil moisture probes. All the instruments were calibrated and tested by technical services at the Macaulay Institute before be taken out into the field.

Figure 3.6. A modified Windtronic 2 anemometer as used to measure wind speed at ground level within the environmental treatments.

Temperature measurements were made next to two of the plants in each environmental treatment, one with and one without-neighbours. Air temperature was measured beneath vegetation cover, to shield the sensors from direct solar radiation in the with-neighbours treatments, as recommended by Marion (1996). In the without neighbour treatments the thermistors were angled to point north to avoid direct sunlight on the tip where temperature is measured. Soil temperature was measured at a depth of 1 cm below the soil surface in both treatments.

All measurements were made at 5 minute intervals, then averaged hourly and recorded with a Campbell Scientific® CR10 datalogger with an AM16 Multiplexer to increase the number of available channels. These measurements were taken during the growing seasons of 2003 and 2004. Due to a shortage of equipment, there were only enough instruments available to measure one block at a time (rather than all eight blocks being logged at the same time, which would have been ideal). Instruments were moved from block to block once a month in 2003 and once a week in 2004.

The logger and instruments were first installed at the site in the summer of 2003. At this time the battery was located inwith the logger housing, requiring the housing to be opened once a month to allow data to be downloaded and the battery to be changed. As a consequence of this, the weather sealing of the logger housing was poor and there were constant problems with water entering the housing. As a result there were frequent problems with the logger and little usable data were collected during the 2003 growing season. The logger eventually failed completely in September 2003.

Over the winter of 2003/2004 the logger was repaired and the housing modified, so that opening was no-longer required for data downloading and battery changing. The logger was returned to the site in May 2004, and this time there were fewer problems. For this reason the results given here are all taken from data recorded between 12th May and 28th July 2004.

There were, however, some problems with one of the thermistors recording in the Shelter treatments during the summer of 2004. There was also a loss of data in the final two weeks of the experiment, when the logger once again experienced problems with one of the data channels.

3.2.5. Analysis methods

Plant biomass

A two way Analysis of Variance (ANOVA) of the final dry weight of the above ground parts of the plants was carried out using GenStat V7.2 (Lawes Agricultural Trust, 2003). The difference in the numbers of leaves counted in May and August 2003, representing the previous years growth, was used as a covariate in the analysis using a log transformation.

Environmental measurements

Due to the lack of spatial replication of the environmental measurements, ANOVA could not be used as originally planned and a different statistical approach had to be found.

In order to explore the effects of the OTCs on the environmental variables (air temperature, soil temperature, wind speed, soil moisture and PAR), a number of charts were plotted. The temperature charts plotted the OTCs versus the Control treatments at three hourly intervals. A Least-square linear regression line was added and compared with a null hypothesis of there being no difference in temperature between treatments (1:1). A regression analysis was carried out to determine the significance of the difference between the regression and one (rather than zero as is conventional).

Differences in mean soil moisture were tested (under guidance from BioSS) using a one way ANOVA to exclude the variation due to block and to test the significance of the variation between blocks.

3.3. Results

3.3.1. Plant biomass

For the purposes of the analysis, it was assumed that the biomass of the target plants was the same within each species at the start of the experiment. The two target species in the experiment, *Alchemilla alpina* and *Carex bigelowii,* showed different responses to the neighbour removal treatment. Differences in the final dry weight of the above ground parts of the plants, harvested at the end of the experiment, were taken to represent the different total biomass of the plants.

Overall *C. bigelowii* had far greater above ground biomass than *A. alpina*, as the former plants tend to produce much larger leaves. In the with-neighbours treatments the *A. alpina* showed a greater above ground biomass than in the without-neighbours treatments, and this was seen across all three environmental treatments (Figure 3.7a). An ANOVA showed this difference in biomass to be statistically significant (Table 3.2). However, the biomass of *C. bigelowii* was less clearly affected by the neighbour removal treatment, as shown in Figure 3.7b, and this was found not to be statistically significant (Table 3.2). Neither of the target species showed a statistically significant interaction with the environmental treatment (Table 3.2).

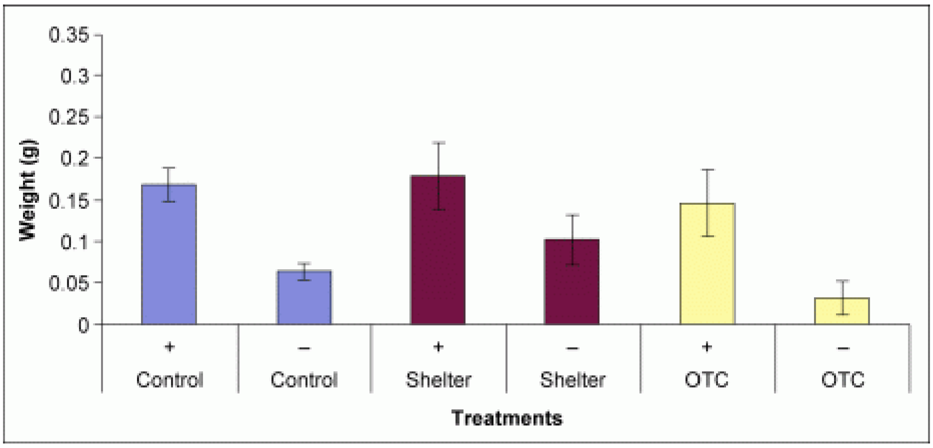

Fig 3.7a. Comparison of the mean dry weights of the above ground parts of *Alchemilla alpina* under the three different environmental treatments. The + sign signifies that the plants were grown with-neighbours and the – sign shows plants grown without neighbours. The error bars show the Standard Error of the eight replicates.

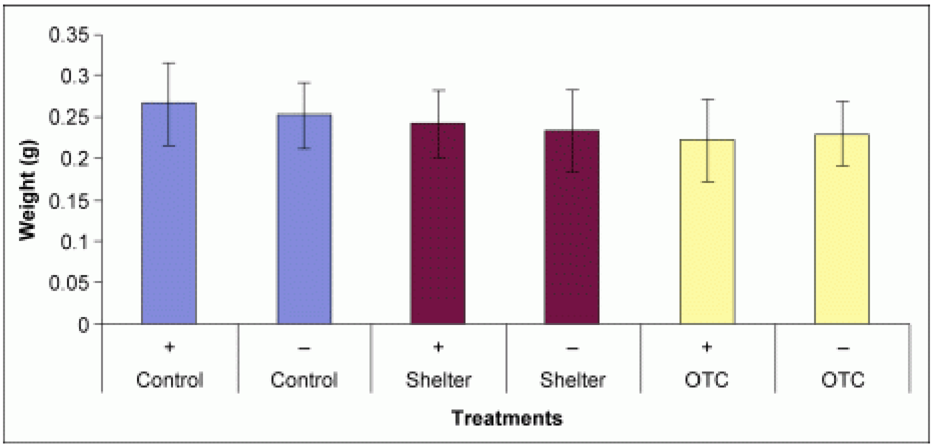

Fig 3.7b. Comparison of the mean dry weights of the above ground parts of *Carex bigelowii* under the three different environmental treatments. The + sign signifies that the plants were grown with-neighbours and the – sign shows plants grown without neighbours. The error bars show the Standard Error of the eight replicates.

Table 3.2. Results of an ANOVA of the mean dry weights (shown in Figure 3.7a. and 3.7b) of the above ground parts of plants grown with or without-neighbours in three different environmental treatments, using number of leaves in the previous year as a covariate. Significant values are given in bold.

Alchemilla alpina (Fig. 3.7a)	d.f.	s.s.	m.s.	v.r.	cov.ef	P value
Neighbours	1	0.116	0.116	25.71	0.95	**<0.001**
Environmental Treat	2	0.005	0.002	0.54	0.95	0.593
Neighbours						
Covariate	1	<0.001	<0.001	0.17		0.685
Carex bigelowii (Fig 3.7b)						
Neighbours	1	0.001	0.001	0.11	0.96	0.749
Environmental Treat	2	0.001	<0.001	0.04	0.97	0.964
Neighbours						
Covariate	1	0.006	0.006	0.61		0.445

3.3.2. Environmental variables

Wind Speed and direction

Wind speed recorded at ground level was slower than at 1 m (Figure 3.8) due to the effects of surface roughness of the vegetation causing drag. Within the environmental treatments wind speed was significantly slower in the OTC than it was in the Shelter or Control. The difference in wind speed between the Shelter or Control was not significant.

The wind shelter environmental treatments were set up based on the assumption that the prevailing wind direction would be south westerly. However, as Figure 3.9 shows the prevailing direction during the period recorded was south easterly.

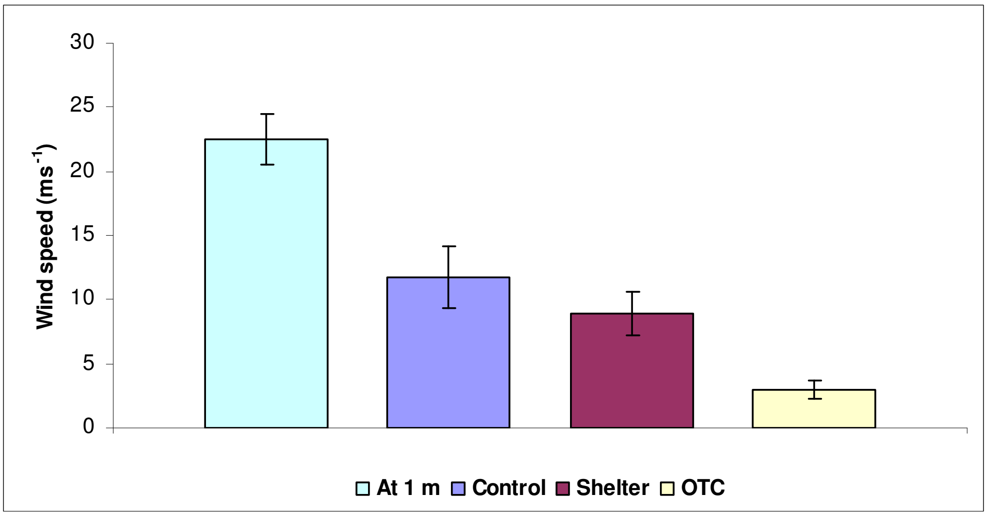

Figure 3.8. Comparison of the mean hourly wind speeds at 1m above ground and mean wind speeds recorded at the ground level inwith the three environmental treatments. The error bars show standard error calculated from the combined means of the data recorded by treatment block.

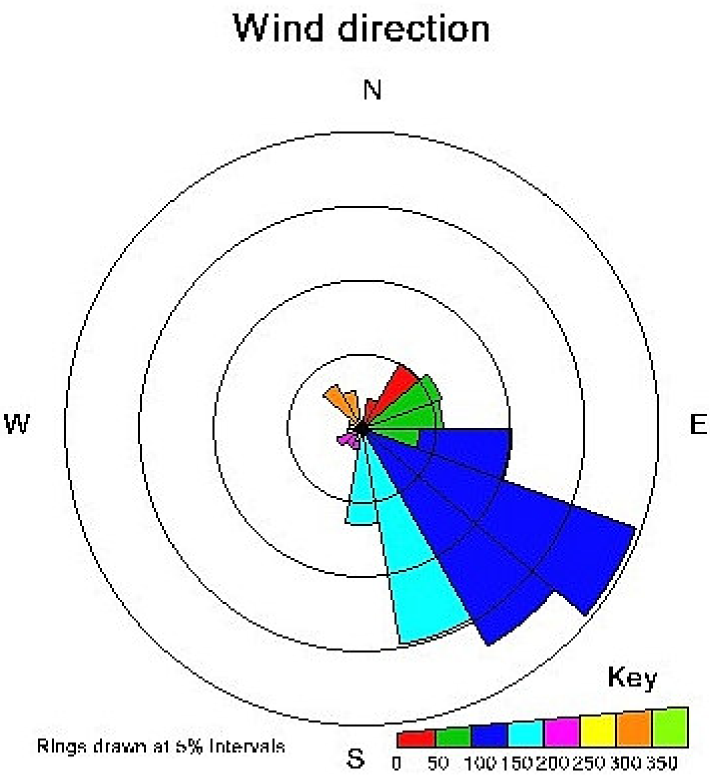

Figure 3.9. Wind rose showing the frequency of wind directions recorded between 12th May and 28th July 2004. The key shows the direction from which the wind was blowing in 50^{o} intervals, and the bars the percentage of time from that direction, i.e. the longer the bar, the greater the time the wind was blowing from the given direction.

Temperature

Temperature was recorded in all blocks between 12th May and 28th July 2004. However, partial logger failure resulted in the loss of temperature records in blocks three and four. For the with-neighbours treatments, mean air temperatures were higher in the Control blocks than in either the wind shelters or OTCs. These differences in air temperature are shown in Table 3.3. Air temperatures shown are for the with-neighbours treatments only, as there were too many errors in the measurement of the without neighbours treatment due to direct solar radiation on the tip of the thermistor.

Table 3.3. Mean of hourly differences in temperature between environmental treatments recorded between 12th May and 28th July 2004 (78 days). Overall the air temperatures in the Control treatments were higher than in either the OTC or shelter treatments. However, soil temperatures in the OTC treatments were higher than in the Control treatments. Soil temperatures for the Shelter treatments are not available due instrument failure.

Difference between Treatments	Mean Difference °C
Control and OTC Air Temperature (with-neighbours)	-0.8
Control and Shelter Air Temperature (with-neighbours)	-0.3
Control and OTC Soil Temperature (with-neighbours)	1.3
Control and OTC Soil Temperature (without-neighbours)	0.9

In order to explore the effects of the OTCs on air temperature, a number of charts were produced (Figure 3.10). These charts plotted the mean temperatures recorded at different times of day. Where the best fit line is below the 1:1 line (red), the OTCs where cooler than the controls and where it is above, the OTCs were warmer than the controls (Table 3.4).

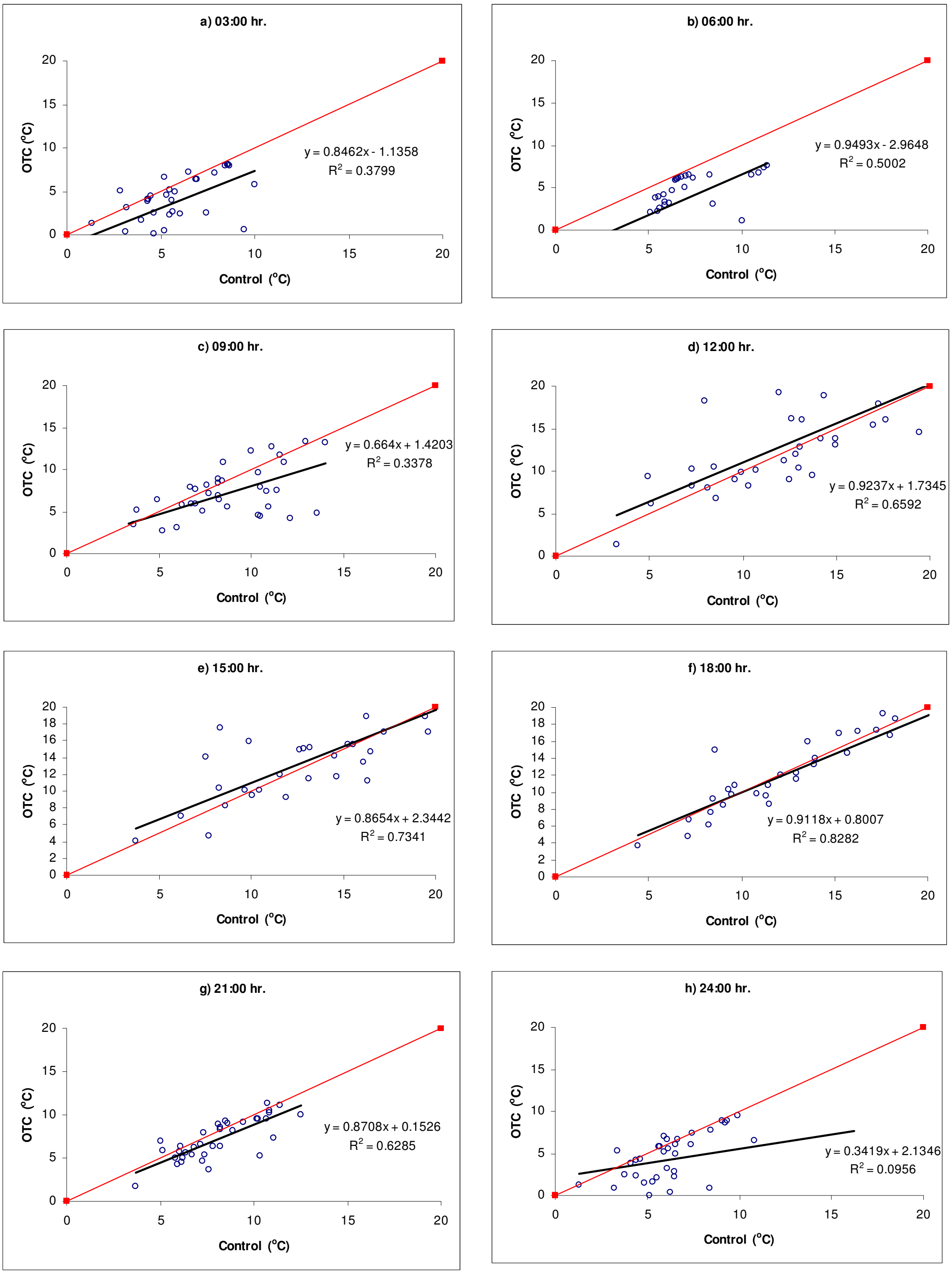

Figure 3.10. Mean air temperatures recorded in the with-neighbours treatments within the OTC and Control environmental treatments. The red line shows the null hypothesis, i.e. that there is no difference in temperature between OTC and Control treatments.

Overnight cooling of air in the OTCs is clearly shown at 03:00 hr (Chart a) and 06:00 hr (Chart b) in Figure 3.10. Cooling is at its greatest at 06:00 hr, when the mean difference in temperature is 3°C and this is statistically significant (Table 3.4). At midnight (Chart h) the slope is significantly different from the 1:1 line.

Table 3.4. The results of the regression analysis to determine if the differences observed in mean air temperatures in the with-neighbours treatments in the charts shown in Figure 3.10 (above) are significant. The null hypothesis being tested is that the deviation is different from one (not zero, as is conventional). Significant values are given in bold.

Time (chart)	d.f.		Coefficients	Standard Error	t Stat	P-value
03:00 (a)	34	Intercept	-1.136	1.086	-1.046	0.303
		Slope	0.846	0.185	0.829	0.413
06:00 (b)	34	Intercept	-2.965	1.105	-2.682	0.011
		Slope	0.949	0.162	0.312	0.757
09:00 (c)	34	Intercept	1.42	1.458	0.974	0.337
		Slope	0.664	0.159	4.165	0.337
12:00 (d)	34	Intercept	1.734	1.572	1.103	0.277
		Slope	0.924	0.113	0.669	0.507
15:00 (e)	34	Intercept	2.334	1.4	1.674	0.103
		Slope	0.865	0.089	1.507	0.141
18:00 (f)	34	Intercept	0.801	1.038	0.771	0.445
		Slope	0.912	0.071	1.238	0.224
21:00 (g)	34	Intercept	0.153	0.96	0.159	0.875
		Slope	0.871	0.115	1.125	0.268
24:00 (h)	34	Intercept	2.135	1.248	1.711	0.096
		Slope	0.342	0.18	3.649	**<0.001**

The same approach was also used to look at mean soil temperatures. Mean soil temperatures were higher in the OTC treatments than in the Controls (Figure 3.11). These differences, with the exception of midday (Chart d), were significant (Table 3.5). They showed more buffering and therefore have less temperature fluctuation than is seen in the air temperatures.

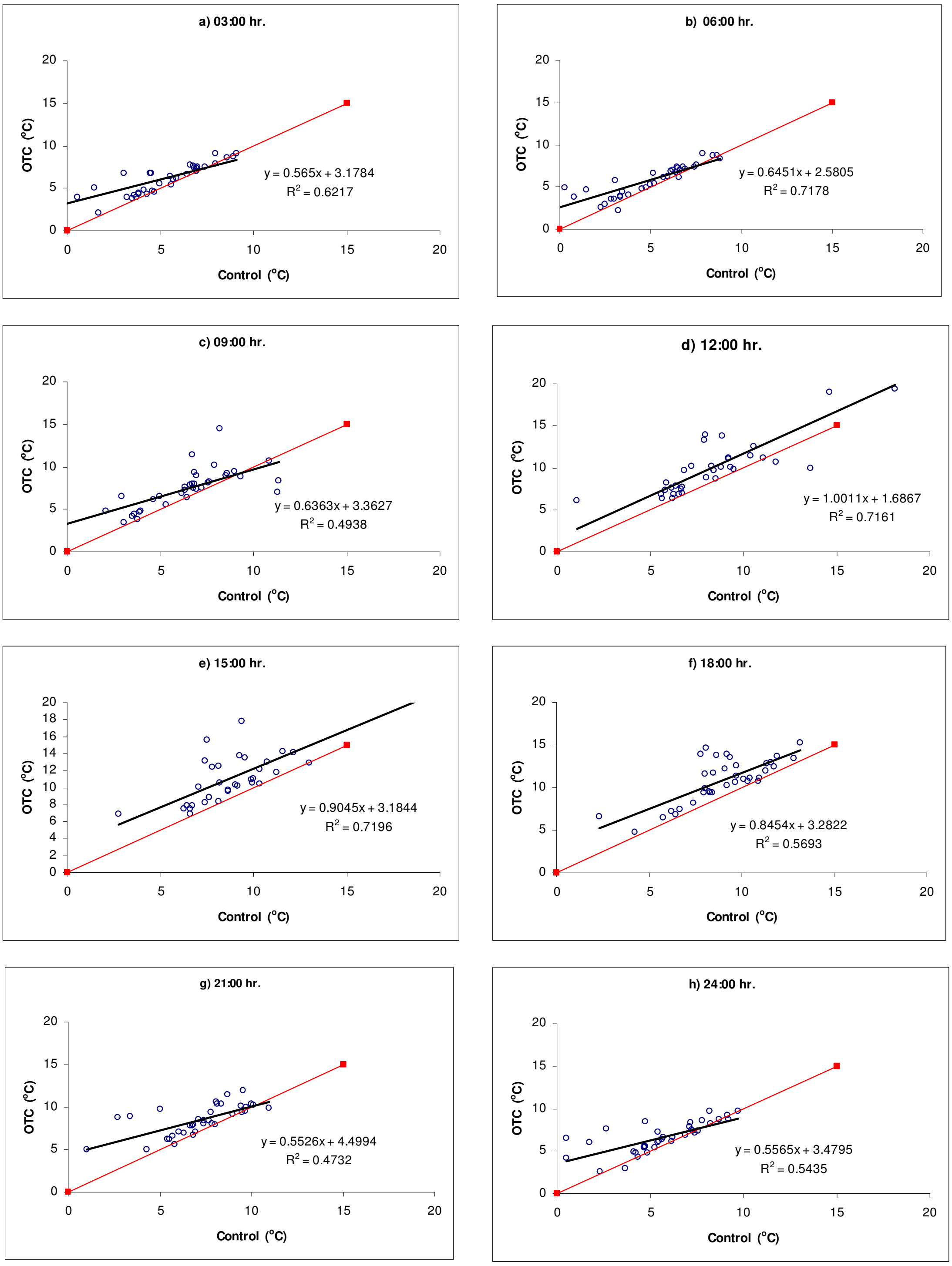

Figure 3.11. Mean soil temperatures recorded in the with-neighbours treatments within the OTC and Control environmental treatments. The red line shows the null hypothesis, i.e. that there is no difference in temperature between OTC and Control treatments.

Table 3.5. The results of the regression analysis of the mean soil temperatures in the with-neighbours treatments to determine if the differences observed in the charts shown in Figure 3.11 (above) are significant. The null hypothesis being tested is that the deviation is different from one (not zero, as is conventional). Significant values are given in bold.

Time (chart)	d.f.		Coefficients	Standard Error	t Stat	P-value
03:00 (a)	34	Intercept	3.178	0.416	7.639	**<0.001**
		Slope	0.565	0.074	5.84	**<0.001**
06:00 (b)	34	Intercept	2.58	0.378	6.82	**<0.001**
		Slope	0.645	0.069	5.116	**<0.001**
09:00 (c)	34	Intercept	3.363	0.756	4.448	**<0.001**
		Slope	0.636	0.11	3.292	**0.002**
12:00 (d)	34	Intercept	1.687	0.991	1.701	0.098
		Slope	1.001	0.108	0.01	0.992
15:00 (e)	34	Intercept	3.184	1.052	3.026	**0.005**
		Slope	0.905	0.097	0.986	0.331
18:00 (f)	34	Intercept	3.282	1.169	2.807	0.008
		Slope	0.845	0.126	1.226	0.229
21:00 (g)	34	Intercept	4.499	0.753	5.978	**<0.001**
		Slope	0.553	0.099	4.475	**<0.001**
24:00 (h)	34	Intercept	3.479	0.537	6.481	**<0.001**
		Slope	0.556	0.087	5.072	**<0.001**

Differences in soil temperature in the without neighbours treatments between the OTC and Control environmental treatments are shown in Figure 3.12. These show a difference in day time soil temperatures, with the OTCs being warmer. At night soil temperatures recorded in the OTCs were slightly lower. Due to instrument problems there were fewer measurements for all time points except Chart (g) 21:00 hr. This time point showed the only significant difference between the OTCs and Controls (Table 3.6).

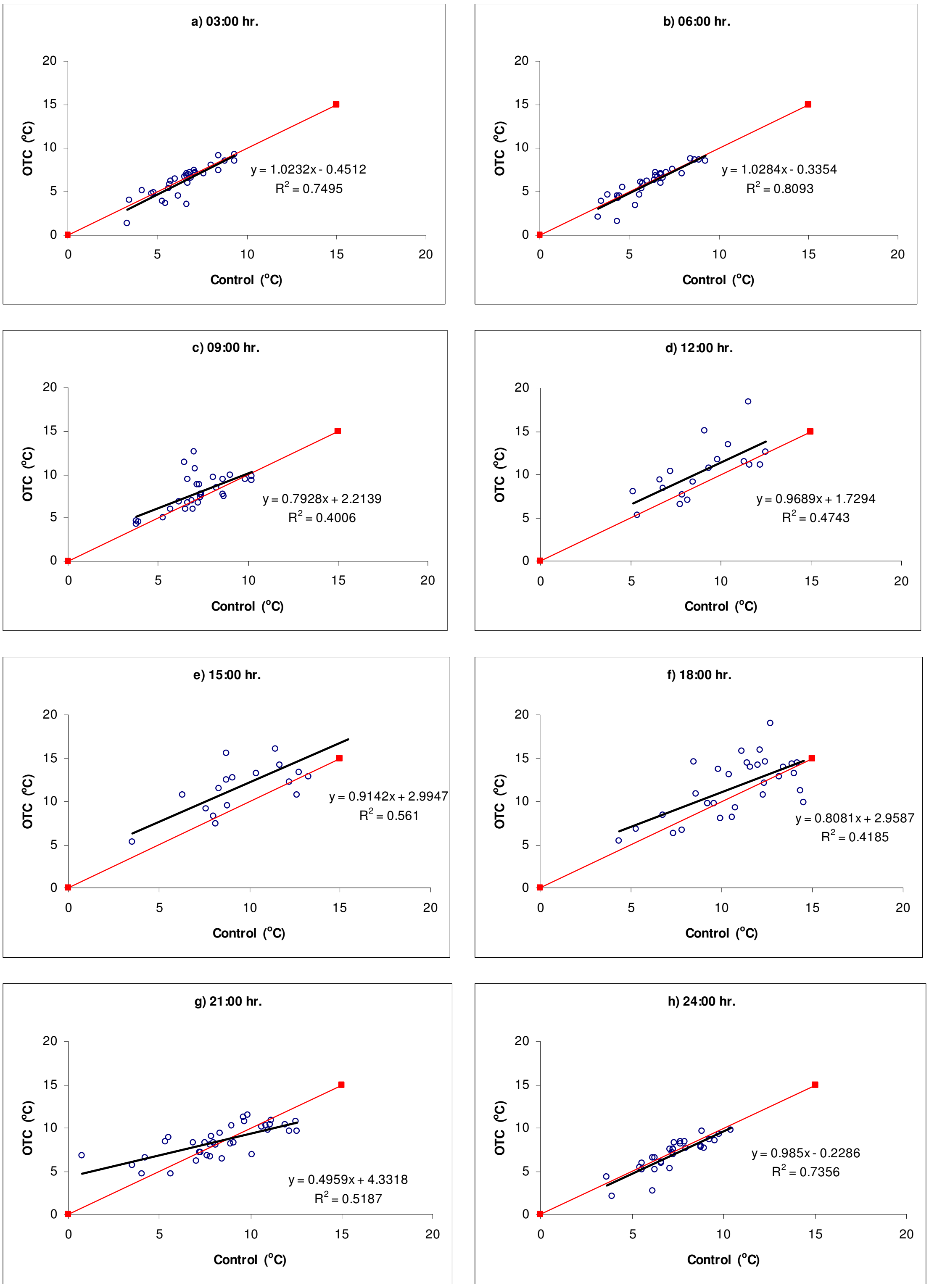

Figure 3.12. Mean soil temperatures recorded in the without neighbours treatments within the OTC and Control environmental treatments. The red line shows the null hypothesis, i.e. that there is no difference in temperature between OTC and Control treatments.

Table 3.6. The results of the regression analysis of the mean soil temperatures in the without neighbours treatments to determine if the differences observed in the charts shown in Figure 3.12 (above) are significant. The null hypothesis being tested is that the deviation is different from one (not zero, as is conventional). Significant values are given in bold.

Time (chart)	d.f.		Coefficients	Standard Error	t Stat	P-value
03:00 (a)	28	Intercept	-0.451	0.748	-0.604	0.551
		Slope	0.023	0.112	0.207	0.837
06:00 (b)	28	Intercept	-0.335	0.598	-0.561	0.579
		Slope	0.028	0.094	0.301	0.766
09:00 (c)	28	Intercept	2.214	1.351	1.639	0.112
		Slope	0.207	0.183	1.13	0.268
12:00 (d)	16	Intercept	1.729	2.355	0.735	0.473
		Slope	0.031	0.255	0.122	0.904
15:00 (e)	16	Intercept	2.995	2.069	1.447	0.167
		Slope	0.086	0.202	0.425	0.677
18:00 (f)	28	Intercept	2.959	2.006	1.475	0.151
		Slope	0.192	0.18	1.066	0.295
21:00 (g)	34	Intercept	4.332	0.714	6.068	**<0.001**
		Slope	0.504	0.082	6.153	**<0.001**
24:00 (h)	28	Intercept	-0.229	0.83	-0.275	0.785
		Slope	0.015	0.112	0.135	0.894

Differences in air temperature between the Shelter and Control treatments are shown in Figure 3.13. In the Shelter treatments mean air temperatures were closer to the 1:1 line than in the OTC treatments. Due to instrument problems there were fewer measurements for Chart (d) 12:00 hr and Chart (e) 15:00 hr time points (Table 3.7). At midnight the intercept is shown to be significantly different but not the slope, suggesting there was some seasonal variation.

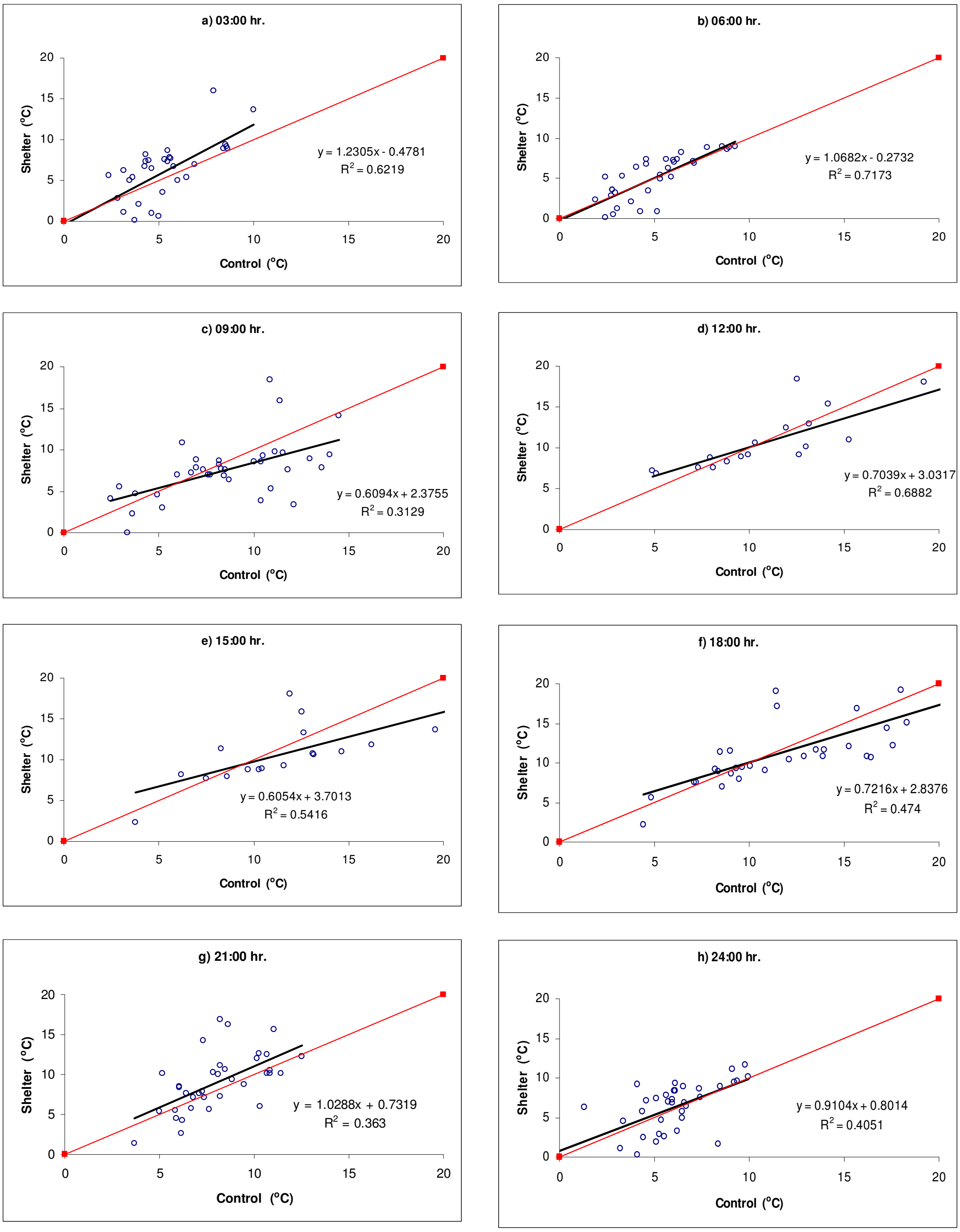

Figure 3.13. Mean air temperatures recorded in the with-neighbours treatments within the Shelter and Control environmental treatments. The red line shows the null hypothesis, i.e. that there is no difference in temperature between Shelter and Control treatments.

Table 3.7. The results of the regression analysis of the mean air temperatures to determine if the differences observed in the charts shown in Figure 3.13 (above) are significant. The null hypothesis being tested is that the deviation is different from one (not zero, as is conventional). Significant values are shown in bold.

Time (chart)	d.f.		Coefficients	Standard Error	t Stat	P-value
03:00 (a)	34	Intercept	-0.478	0.892	-0.536	0.595
	34	Slope	1.231	0.165	-1.401	0.17
06:00 (b)	34	Intercept	-0.273	0.609	-0.449	0.657
	34	Slope	1.068	0.115	-0.593	0.557
09:00 (c)	34	Intercept	2.375	1.416	1.677	0.103
	34	Slope	0.609	0.155	2.522	0.017
12:00 (d)	16	Intercept	3.032	1.455	2.084	0.054
	16	Slope	0.704	0.118	2.5	0.024
15:00 (e)	16	Intercept	3.701	1.765	2.097	0.052
	16	Slope	0.605	0.139	2.834	0.012
18:00 (f)	34	Intercept	2.838	1.79	1.585	0.122
	34	Slope	0.722	0.13	2.136	0.04
21:00 (g)	34	Intercept	0.732	1.954	0.374	0.71
	34	Slope	1.029	0.234	0.123	0.903
24:00 (h)	34	Intercept	0.801	0.189	4.812	**<0.001**
	34	Slope	0.91	0	0.474	0.639

Due to instrument failure soil temperatures for the Shelter treatments were not recorded. In all of the without neighbour treatments air temperature measurements proved to be unreliable and are not shown here.

Soil moisture

There was little difference between the OTC and Shelter treatments, however both these treatments were drier, with regard to means, than the Control treatment (Figure 3.14).

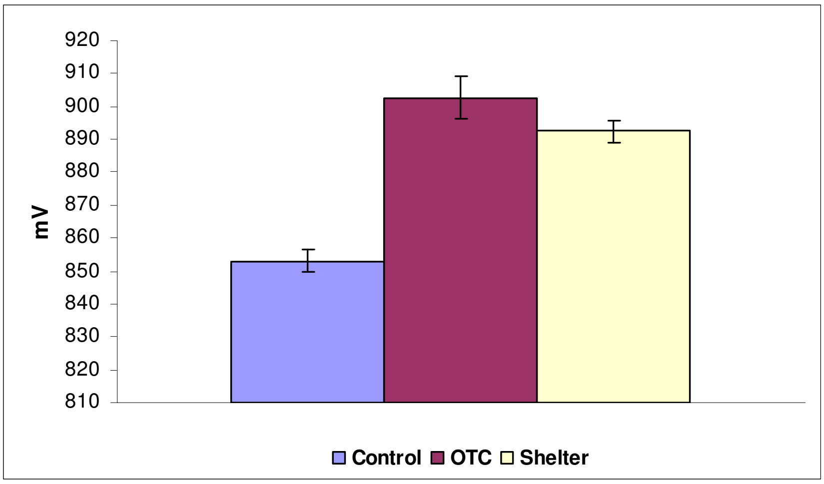

Figure 3.14. Mean soil moisture in the three environmental treatments (given in mV of resistance where the higher the value, the lower the level of soil moisture). The error bars show standard error calculated from the means of the data.

The differences in mean soil moisture due to the different environmental treatments were assessed using an ANOVA and the results are shown in Table 3.8. While the difference between the treatments is shown to significant, it should be noted that the variance is greater between the blocks.

Table 3.8 Results of ANOVA showing the differences in soil moisture between treatments. Significant values are shown in bold.

Source of variation	d.f.	s.s.	m.s.	v.r.	P-value
Block	7	624485	89212	11.95	
Treatment	2	128266	7467	8.59	**<0.001**

Photosynthetically Active Radiation (PAR)

Only two PAR meters were available for use with the logger, therefore only the Control and OTC treatments were logged. The cages used for the Control and Shelter environmental treatments were considered to cast the same level of shadow. The measurements were taken to determine whether there was any difference in PAR between the caged treatments and the OTCs.

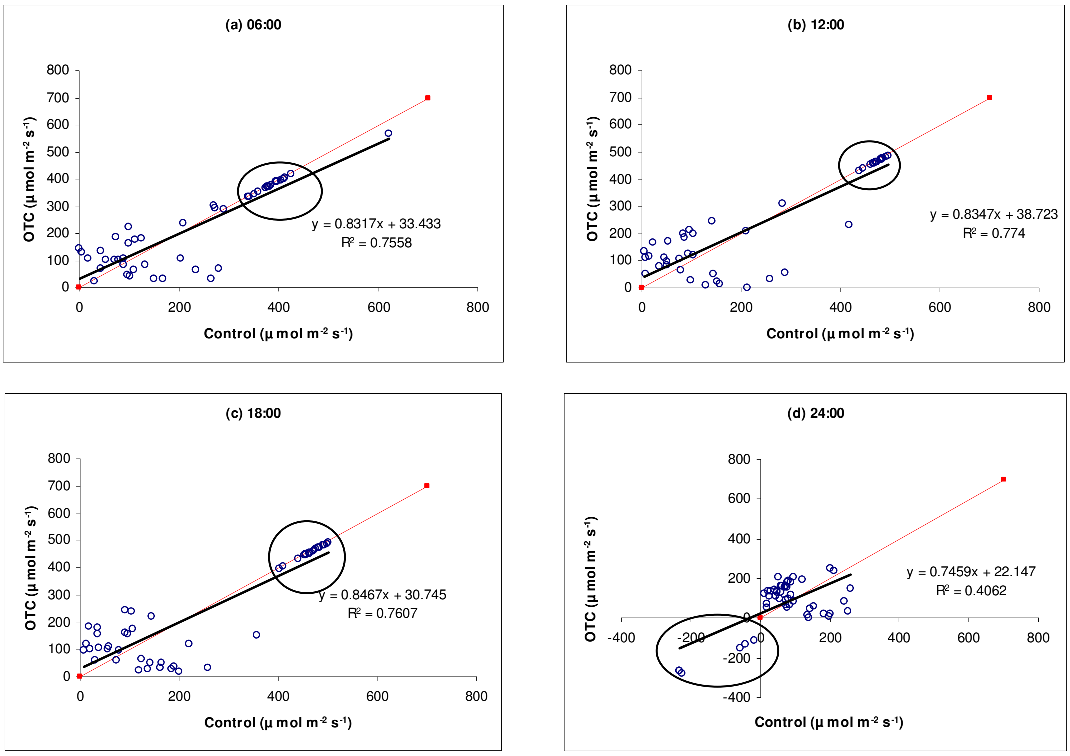

Figure 3.15 Mean PAR levels recorded in the with-neighbours treatments within the OTC and Control environmental treatments. The red line shows the null hypothesis that there is no difference in temperature between OTC and Control treatments. The points circled were recorded between 12th May to 2nd June 2004 during a period clear weather.

As is shown in Figure 3.15, the differences in PAR were small, and similar patterns were found across the day light hours. The slopes in all four charts are not significantly different from the null hypothesis (see Table 3.9), i.e. there was no significant difference in PAR between the OTCs and the caged treatments.

The points in circled in Figure 3.15 were recorded in the first three weeks (12th May to 2nd June 2004) during a period of clear weather. Chart (d) in Figure 3.15 shows a seasonal trend with increasing PAR at midnight around the solstice. The reason for the negative values is unclear, it possible that it instrument error, however calibration test before and after show no errors. The lower PAR shown in Chart (a) at 06:00 hr show the effects of shadow due to the south westerly aspect of the site.

Table 3.9. The results of the regression analysis of mean PAR to determine if the differences observed in the charts shown in Figure 3.15 (above) are significant. The null hypothesis being tested is that the deviation is different from one (not zero, as is conventional). Significant values are shown in bold.

Time (chart)	d.f.		Coefficients	Standard Error	t Stat	P-value
06:00 (a)	46	Intercept	33.433	19.134	1.747	0.087
	46	Slope	0.832	0.07	2.415	0.02
12:00 (b)	46	Intercept	38.723	20.879	1.855	0.07
	46	Slope	0.835	0.067	2.486	0.017
18:00 (c)	46	Intercept	30.745	21.456	1.433	0.159
	46	Slope	0.847	0.07	2.19	0.034
24:00 (d)	46	Intercept	22.147	16.883	1.312	0.196
	46	Slope	0.746	0.133	1.911	0.062

3.4. Discussion

There did not appear to be any support for the central hypothesis, i.e. that an increase in temperature changes the balance from facilitation to competition. While the different environmental treatments did not have a significant effect on the final above ground biomass of the target species, there were significant differences in some of the environmental variables measured. The only treatment that had significant effects on plant biomass was the with and without neighbours treatment.

The environmental variables showed contrasting patterns in the Shelter and Control treatments compared with the OTCs. In the Shelters and Controls, higher wind speeds, mean air temperatures and soil moisture were observed, as well as lower mean soil temperatures. The Shelter treatments were intended to assist in separating the influences of temperature and wind speed. Abnormal weather conditions in the summer of 2004, i.e. the prevailing wind direction being south easterly (Figure 3.9), rather than the expected south westerly winds resulted in this not being testable with the data collected.

A. alpina showed a statistically significant greater above ground biomass in all the with-neighbours treatments (Table 3.2) than in the without neighbours treatments. This suggests that facilitation is relatively more important than competition. This difference in biomass was seen across all environmental treatments (Figure 3.7a). The balance between competition and facilitation is as strong in the OTC as in the Control treatments, although final biomass appears to be slightly lower in the OTCs than in the Controls. A 0.4℃ difference in mean soil temperatures in the OTCs between the with and without neighbour treatments (Table 3.3) may have had some effect on the growth of *A. alpina.* This is discussed further below.

In contrast to *A. alpina*, the results for *C. bigelowii* (Figure 3.xx7b) showed no evidence for facilitation or competition in any of the environmental treatments, and there was no significant difference in biomass between the with and without neighbours treatments. These results are in contrast to Brooker & van der Wal (2003), who took soil cores of arctic vegetation which they warmed in water baths of different temperatures, whilst maintaining the same ambient air temperature. Their results showed that raised soil temperature relative to air temperature increased the growth of sedges (including *C. bigelowii*) to a greater extent than non-graminoids.

In a warming study similar to the current experiment, Gugerli & Bauert (2001) had comparable results using standard ITEX OTCs, finding that night time air temperatures were reduced and soil temperatures were increased. They reported small increases in above ground biomass of their target species *Polygonum viviparum* in their OTCs relative to the controls. While Gugerli & Bauert (2001) showed a slight (but not significant) increase in biomass in their OTCs, the biomass of *A. alpina* in the current experiment was slightly (but again not significantly) lower in the OTCs than in the controls.

In contrast to other experiments (e.g. Brooker & van der Wal 2003, Gugerli & Bauert 2001), plants of both target species were individually transplanted (i.e. bare-rooted) into the experimental treatments, rather than using plants growing in situ or using soil cores. This may have had some effect on the

difference in performance of the target species in this experiment. While *C. bigelowii* was planted with the new tiller entirely below ground (Figure 3.5), *A. alpina* was planted with the shoots of the rhizomes slightly exposed.
As most alpine and arctic plants grow close to the ground, with the meristem below ground to avoid the extremes of temperature (Körner 1999), this unintentional bias in the planting may have resulted in *A. alpina* in all without neighbours treatments being more exposed to the effects of air temperature than *C. bigelowii*.

While no measured differences in air temperature between with and without neighbour treatments are available, due to difficulties in the measurements (Section 3.3.2), it is suggested here that the exposed meristems of *A. alpina* were subject to lower temperatures and greater temperature fluctuation in the without neighbour treatments. This may have resulted in their above ground biomass being lower, compared with the with neighbours treatment, where the plants would gain shelter from their neighbours (Figure 3.7a).

Increases in soil temperature can lead to an increase in short term nutrient availability (Brooker & van der Wal 2003, Fitter *et al*. 1999). However it is unlikely that the difference in soil temperature of 0.4℃ between the with and without neighbour treatments resulted in a great increase in nutrient availability, as the difference in soil temperature between the OTC and Control treatments did not produce an equivalent increase in above ground biomass.

Effects of the environmental treatments

As with any experimental simulation of climate, this warming experiment has its limitations. The measurement results of the individual environmental variables are discussed below.

Wind

Of all the data recorded for the environmental variables, as expected, the clearest difference between treatments was in the wind strength at ground level (Figure 3.8). There is also a clear difference in the mean wind speeds recorded at 1 m and those recorded at ground level. This is because there is greater turbulence due the surface roughness of the vegetation (Vangardingen & Grace 1991). The Control and OTC treatments are also clearly significantly different, with there being far higher wind speeds recorded in the Controls. However the differences between the Control and Shelter treatments were far smaller, the error bars overlap and do not appear to be significantly different. The Shelter treatments were set up to provide shelter from the expected prevailing south westerly wind. However, during the period when logging was successful the predominant wind direction was from the south east. For this reason the data from the Shelter treatments were not analysed further.

Temperature

The OTCs showed a mean increase of 1.3°C in soil temperature compared with the control treatment, but there was also a decrease in mean air temperature of -0.8°C in the OTC and -0.3°C in the Shelter treatments (Table 3.3). These decreases in mean air temperature were unexpected, as most studies using OTCs have reported an increase in air temperature (Kennedy 1995a, Marion 1996, Henry & Molau 1997, Welker *et al.* 1997, Marion *et al.* 1997, Totland & Nyléhn 1998, Walker *et al.* 1999, Hollister & Webber 2000, Richards *et al.* 2002, Kudo & Suzuki 2003, Sandvik *et al.* 2004). Although Gugerli & Bauert (2001) did report night time cooling, unlike the results reported in the current experiment, their overall mean temperature rise was 1°C above their control. Interestingly, Walker *et al.* (1999), working on a long term (ongoing) project at two different sites, one arctic tundra and one alpine, have reported differences in the levels of warming in their OTCs, with slightly higher mean air temperature increases at the alpine site and greater diurnal variation. Soil temperatures within the OTCs at the two sites also show a difference, with increases recorded at the alpine site, but not at the arctic tundra site. This suggests latitudinal differences, with performance of the

OTCs at the Glas Tulaichean site showing alpine rather than arctic characteristics. Another explanation for the differences in temperature would be differences in the instrument, however all instruments were cross calibrated before being used in the field, so this is less likely.

The greatest decreases in air temperature were recorded at night in the OTCs (Figure 3.10). The most likely reason for this would be that the OTCs formed frost pockets as cold air descended at night. Figure 3.10 does show day time warming particularly between mid day and mid afternoon (Charts (d) and (e) in Figure 3.10). The level of cooling at 03:00 hr and 06:00 hr is fairly constant over the recording period, as shown by the parallel lines in Charts (a) and (b) (Figure 3.10). Later in the day the lines tend to cross, suggesting a seasonal effect. Towards the solstice (21st June) there can be up to 18 hours of daylight in this part of Scotland. The change in the temperature range in the evenings is due to the south westerly aspect of the site (Figure 3.1), in the early hours of the day the site is in shade. This is an important factor in the night cooling observed in the OTCs (Figure 3.10).

The night time cooling of the OTCs is possibly a way of investigating the predicted changes in diurnal temperature variation (Section 1.4.2. and Figure 1.10), as it could be used as a proxy for the effects of increased diurnal temperature variation. If the diurnal temperature range increases as predicted, this coupled with the lapse rate, could lead to an increased risk of frost damage to plants, and could be a mechanism which limits the upward migration of plants from lower vegetation zones (Körner 1999, 2000). Currently the day time lapse-rate in Scotland generally reduces temperature by about 1℃ per 100m and by about 0.4℃ per 100m during the hours of darkness (Harrison 1997). Observations from the chamber experiment show that despite an increase in soil temperature and day time air temperature, the lower night time air temperature was enough to prevent an expected increase in growth by the target plants in the OTCs.

The increase in soil temperature in the OTCs was far more in line with expectation, as such increases have also been reported by other studies

(Kennedy 1995a, Welker *et al.* 1997, Totland & Nyléhn 1998, Walker *et al.* 1999, Richardson *et al*. 2002, Kudo & Suzuki 2003).

Soil Moisture

Soil moisture recorded within the OTCs was lower than in the Controls, as shown in Figure 3.14. While the ANOVA (Table 3.8) shows a statistically significant difference between the treatments, the variance is far larger between the blocks than between the treatments, so this result should be regarded with caution.

In many studies measurements of soil moisture have not be reported, but it is likely that this is a common effect. Reductions in soil moisture within the OTCs, as occurred in the current study, have been reported in other studies (Kennedy 1995a, Henry & Molau 1997, Marion *et al*. 1997), but these reductions are not considered to be significant (Henry & Molau 1997, Marion *et al*. 1997).

Other observations

When dismantling the site, other plants within the OTCs were observed to have increased in size compared with those outwith the OTCs and inwith the caged treatments, similar to those reported be Gugerli & Bauert (2001) and Kudo & Suzuki (2003). Due to time restraints and adverse conditions no measurements were taken.

3.5. Conclusions

The environmental treatments did not cause large enough changes in environmental variables to change the balance from facilitation to competition. This may have been due to counteracting between environmental variables within the treatments, e.g. soil temperature increased and wind speed decreased, while air temperature decreased at the same time.

The only significant change in above ground biomass was seen in the with and without neighbours treatment for *A. alpina*. It had been expected that a change would be seen in both target species. However this change is most likely due to differences in planting, i.e. the meristems of all *A. alpina* plants were accidentally exposed. This is thought to have resulted in reduced biomass due to exposure to lower air temperatures in the without neighbours treatment, while the exposure of the meristems had less of an effect due to the shelter provided in the with neighbours treatment.

This study may have been too short-term, given the slow growth rate of the plants, a longer term study would be more appropriate for investigating potential change from facilitation to competition. The effects of wind and temperature need to be isolated and tested, which is best done in the field, as the combined interactions maybe more important than either wind or temperature alone. There is also a need to investigate any changes in nutrient availability due to the effects of the environmental treatments in the field.

The study was only done at one site in the eastern Highlands of Scotland. As the effects of continental vs. oceanic influences have not been investigated sufficiently yet, there would be value in repeating this style of experiment at several sites on an east west gradient.

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