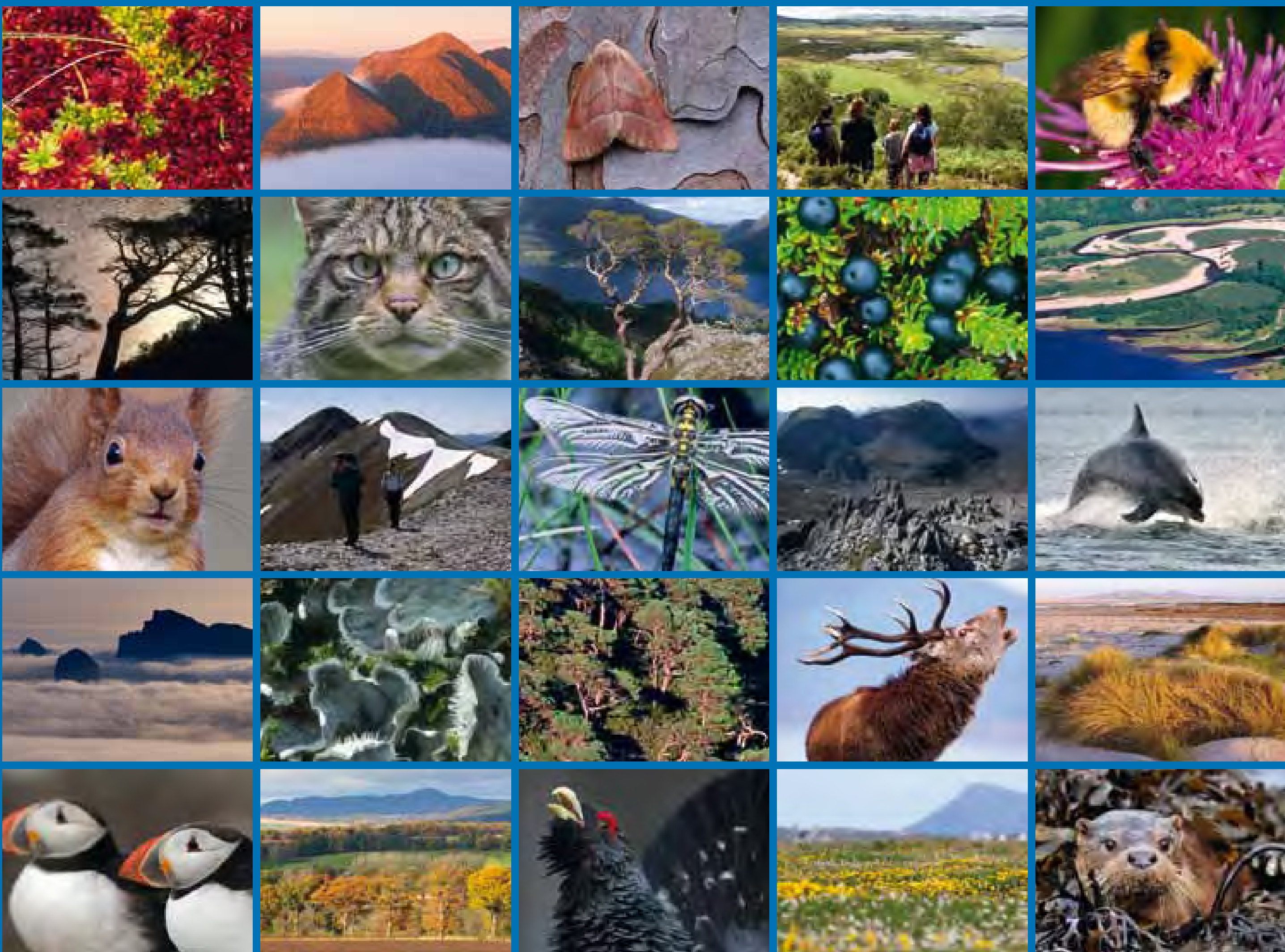
Scottish Natural Heritage
Commissioned Report No. 462

The Scottish Beaver Trial: Woodland monitoring 2010



COMMISSIONED REPORT

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COMMISSIONED REPORT

Summary

The Scottish Beaver Trial: Woodland monitoring 2010

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Background

In 2008, the Scottish Government approved a licence to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), to undertake a five-year trial reintroduction of the European beaver (*Castor fiber*) to Scotland after an absence of more than 400 years. In May 2009, three beaver family groups were introduced to Loch Coille-Bharr, Loch Linne/Loch Fidhle and Creagmhor Loch on land managed by Forest Enterprise Scotland (FES) at Knapdale, Argyll. Since 2009, additional releases have also taken place, and by November 2010, beaver groups were established in these three lochs and Lochan Buic. This is the second report describing the effects of beavers on riparian woodland at Knapdale, and summarises effects observed up until November 2010.

Main findings

- 31 transects comprising 111 (4×10 m) permanent vegetation plots have been established between zero and 30 m from the water's edge on five lochs at Knapdale.
- Downy birch was the dominant tree species on most plots, although alder, hazel, ash, rowan and willow also occurred as co-dominants or dominants with restricted distributions.
- Seventeen months after their release, beavers had directly affected trees in 35 out of the 111 vegetation plots. In those 35 plots an average of 21% of trees had been felled. A similar proportion of plots (18 out of 65) had been affected in 2009, when an average of 13% of trees had been felled in the affected plots.
- The most intensive tree felling was observed within 350 m of beaver lodges and no tree felling was observed in plots at distances greater than 730 m from lodges.
- As concluded in 2009, plots used by beavers included more birch and willow, but less alder, than an average plot.
- At November 2010, 74% of beaver effects (partial or complete felling of trees) detected were within ten metres of the water; at November 2009 the figure was 80%.
- The mean stem diameter of trees affected by beavers was 5.0cm, which was slightly smaller than the average stem size in plots which was 5.4cm. However, beavers often

felled substantially larger trees. One year previously, the average diameter of affected trees was 6.5cm, which was larger than the average tree diameter.

- A comparison of the use by beavers with the abundance of tree species indicates that willow and rowan are preferred species and alder and hazel are avoided species. Birch is both the most abundant species and the species most often used by beavers, but is used at a frequency commensurate with its abundance.

- By November 2010, resprouting stems were apparent from the stump or base of 44% of trees that had been directly affected by beavers, with these trees possessing a mean of 9 shoots of average length 12cm.

- The most vigorous resprouting was observed on ash, willow and rowan; poorer resprouting was observed on birch and very poor resprouting was observed on alder and hazel, although these latter species were rarely affected by beavers anyway.

- The degree of herbivory sustained by resprouting shoots could not be confidently estimated in either April or November, because most shoots were dormant and their desiccated ends were often snapped off, however it did not appear to be obviously unsustainable.

- All beaver-affected trees surrounding Creagmhor Loch were marked, measured and mapped, and their 5 nearest neighbours recorded. This exercise returned a similar picture of beaver foraging patterns to that derived from the permanent plots, in particular that beavers showed a strong preference for rowan and that their effects are largely limited to 10 m from the water.

- Trees most strongly affected by beaver activity were rowan growing within 4 m of the water (40% affected, mostly felled) and willows growing from 6 – 30 m from the water (30% affected). Both of these species regrow vigorously.

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This project is part of the independent monitoring programme for the Scottish Beaver Trial coordinated by SNH in collaboration with a number of independent monitoring partners. For further information go to:
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Acknowledgements

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1 BACKGROUND

The European beaver, *Castor fiber*, became extinct in Scotland by the end of the 16th century as a result of hunting combined with habitat loss (Kitchener and Conroy, 1997). Over recent years the potential for restoring this species to the natural fauna has been investigated. These investigations have resulted in a suite of information about the scientific feasibility and desirability of conducting such a reintroduction. Relevant documents published by Scottish Natural Heritage (SNH) can be viewed at the 'Other work on beavers' page at:
http://www.snh.gov.uk/protecting-scotlands-nature/safeguarding-biodiversity/reintroducing-native-species/scottish-beaver-trial/other-work-on-beavers/

Article 22 of the European Council Directive 92/43/EEC *on the Conservation of Natural Habitats and of Wild Flora and Fauna* (the 'Habitats Directive') requires the UK government to consider the desirability of reintroducing certain species (listed on Annex IV), including European beaver.

The Species Action Framework, launched in 2007 by Scottish Ministers, sets out a strategic approach to species management in Scotland. In addition, 32 species, including the European beaver, were identified as the focus of new management action for five years from 2007. SNH works with a range of partners in developing this work and further information can be found at
http://www.snh.gov.uk/protecting-scotlands-nature/species-action-framework/

In May 2008, the Minister for Environment approved a license to allow a trial reintroduction of up to four families of European beaver to Knapdale Forest, mid-Argyll. The licence was granted to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), who are working on behalf of the 'Scottish Beaver Trial' partnership. The trial site, Knapdale Forest in Argyll, is managed by Forest Enterprise Scotland (FES). Animals were caught in Norway in 2008, quarantined for six months and released in spring 2009. The initial release sites were Loch Coille-Bharr, Loch Linne/ Loch Fidhle and Creagmhor Loch. Further releases took place during 2010. The trial includes a five-year period of monitoring which will run until spring 2014.

2 AIMS AND OBJECTIVES

One condition of the licence is that SNH plays a lead role in coordinating an independent monitoring programme in collaboration with the project partners. The trial will therefore involve a number of independent monitoring sub-projects in order to address the primary aims, and at the end of the trial the outputs of the monitoring will be assessed and a decision made by Scottish Government on the next stage. This is a progress report on the woodland monitoring sub-project, which is being conducted by The James Hutton Institute (formerly Macaulay Land Use Research Institute) in partnership with Scottish Natural Heritage.

The objectives of this monitoring work are to:

1. Carry out a sample-based assessment of the composition and structure of the loch-side woodlands around the beaver release site;
2. Assess the nature and extent of beaver effects on the loch-side woodlands, again based on a representative sample of survey plots;
3. Assess seasonal variation in the effect of beavers on woody vegetation.

It is not intended to try to assess the effect of beavers on the woodland ground flora or on epiphytic species. It is likely that beaver will affect these species – either directly through grazing or indirectly through changing the woodland structure – but demonstrating such an effect with any degree of confidence is likely to be extremely difficult or impossible and would demand greater resources than are presently available.

Much of the loch-side vegetation in the trial area has been managed over the last few years to improve the habitat in preparation for the trial beaver release. As a result, the ground flora is already developing in response to this management. Distinguishing any change which may result from beaver activity from this background change is likely to be extremely challenging – especially over such a short period as five years.

Beavers are ecosystem engineers and can produce both direct and indirect effects upon woodlands. The most obvious direct effect is felling of trees. In other parts of their range, particularly during autumn and winter, beavers gnaw and fell trees for food and to obtain timber for the construction of lodges and dams. In the short term at least, tree felling can reduce the biomass of standing, living trees and change the age and size structure of woodlands. Longer-term changes may involve a shift in tree species composition. Many riparian tree species in Europe and North America evolved in the presence of beavers and other browsing herbivores and, given suitable conditions, respond to browsing of woody stems by producing abundant new growth. This can lead to the production of denser stands of woody vegetation producing abundant foliage, which can offer a valuable food resource not only to beavers but also to browsing ungulates and herbivorous insects (Jones *et al.*. 2009). However, the recovery of vegetation from beaver browsing and felling will be dependent upon the interaction of new shoots with subsequent browsing by both beavers and sympatric ungulate browsers (Hood and Bayley, 2009). Some woody species may also respond to browsing by altering the nutritional and anti-herbivore defensive chemistry of new growth, which can alter the food quality of this plant material for herbivores, sometimes in unpredictable ways (Veraart *et al.* 2006).

Because plant species differ in their tolerance of browsing and their competitive abilities, as well as their palatability to herbivores, sustained browsing of riparian woodlands by beavers may also alter their floristic composition. As well as herbivorous animals, human interests can also be influenced by changes in the structure and floristic composition of riparian woodlands. The appearance of loch and river shores can change, with significant aesthetic consequences. Access to the water from land may be hindered or facilitated and changed levels of shade on smaller watercourses may influence water temperatures, which in turn can affect the reproduction and survival of commercially and recreationally valuable fish species.

Many internationally important species of lichen rely on a continuity of old tree stems in open woodland. By maintaining a cycle of felling and re-growth, beaver activity may result in a loss of this habitat, or at least suppress future development of such habitat.

The most obvious indirect effect of beaver activity on lochside woodlands is flooding caused by beaver dams. Beavers build dams to raise the water level of lochs and watercourses but also to expand their potential foraging area into inundated woodlands and other habitats. Some tree species are intolerant of sustained flooding, and so flooding can increase the amount of standing dead timber but possibly also favour flood-tolerant species such as willows.

This report builds upon observations reported for the November 2009 monitoring period (Moore *et al.* 2010) and describes findings arising from monitoring periods in April 2010 and November 2010, up to a point in time 17 months after the release of beavers.

3 METHODS

3.1 Site Description and Beaver Releases

The loch-side and riparian woodland at Knapdale has been described by Armstrong *et al.* (2004) (Loch Linne and Loch Fidhle) and Brandon-Jones *et al.* (2005) (all loch-side and riparian woodland within the FES land at Knapdale). The release sites lie within the Taynish and Knapdale Woods Special Area of Conservation (SAC; EU code UK0012682), which comprises 44% broadleaf woodland as well as water bodies, extensive conifer plantations and smaller areas of bogs, marshes, water-fringed vegetation, fens, heath and scrub. One main reason for the designation of the area as an SAC is the presence of old sessile oak (*Quercus petraea*) woods with *Ilex* and *Blechnum*. In the years leading up to the Scottish Beaver Trial, extensive areas of conifer plantation have been cleared from Knapdale, particularly near the lochs, and in most places, dense downy birch (*Betula pubsecens*) regrowth has taken their place.

A decision was taken to restrict woodland monitoring with permanent plots to the strip of woodland within 30 m of loch shores, as it was anticipated, based on other studies of *C. fiber*, that most beaver effects would occur in this zone (Haarberg & Rosell 2006). Most woodlands in this zone at Knapdale are dominated by mature and regenerating birch and common alder (A*lnus glutinosa*). In many areas, willow species, particularly goat willow (*Salix caprea*) are abundant and rowan (*Sorbus aucuparia*) is widespread throughout the site, both as mature and sapling trees. Hazel (*Corylus avellana*) and ash (*Fraxinus excelsior*) are also common in some areas around the loch shores. Aspen (*Populus tremula*) is highly favoured by European beavers elsewhere, but is very rare at Knapdale and only occurs on rocky terrain, where it is inaccessible to beavers. *Q. petraea* is common and widespread at Knapdale, but within 30 m of the water it is limited to steep, often rocky terrain where the shore is precipitous and unsuitable for beavers.

Three family groups, comprising eleven beavers, were released at Knapdale in late May 2009. One group was released in each of Loch Coille-Bharr (four animals), Loch Linne / Loch Fidhle (four animals) (these lochs are continuous with one another) and Creagmhor Loch (three animals). Beavers were released into artificial straw bale lodges situated in areas that were expected to provide suitable browsing habitat nearby and minimise the likelihood of disturbance to the animals. These artificial lodges were located at the southern ends of Loch Coille-Bharr and Creagmhor Loch and on the island in Loch Linne/Fidhle. Subsequently, one Loch Linne beaver died, and all three beavers disappeared from Creagmhor Loch, although the adult male was subsequently recaptured and returned to the site. Prior to April 2010, the male at Creagmhor Loch was removed on welfare grounds because of ill health and subsequently died at Edinburgh Zoo. By this time, the family from Loch Coille-Bharr had established themselves in a lodge on the eastern shore of the small Dubh Loch to the east of Loch Coille-Bharr. These animals had also dammed the point where Dubh Loch naturally drains to Loch Collie-Bharr, flooding the surrounding broadleaf woodland and significantly expanding the area of Dubh Loch.

To reach the trial's aims of having established four pairs of beavers at Knapdale, two new pairs were released in 2010:

- one in June 2010 onto Creagmhor Loch,
- one in May 2010 onto un-named loch (south), called Lily Loch for the purposes of this report (British National Grid coordinates NR 78908 88570), just to the south of Lochan Buic. This loch is outwith the Taynish and Knapdale SAC but within the Forest Enterprise Scotland land-holding

The male from the Lily Loch pair died a few days later and the female moved herself to the nearby Lochan Buic. Another male beaver was released into that loch in September 2010.

At November 2010, there were beaver pairs/families established on four lochs at Knapdale: Loch Coille-Bharr/Dubh Loch, Loch Linne/Loch Fidhle, Creagmhor Loch and Lochan Buic/Lily Loch. The first two families each produced at least one kit in 2010. In anticipation of the 2010 releases, a number of additional monitoring transects were established around Lily Loch and Lochan Buic in April 2010. Figure 1 illustrates the locations of all lodges used by beavers during the survey period reported here.

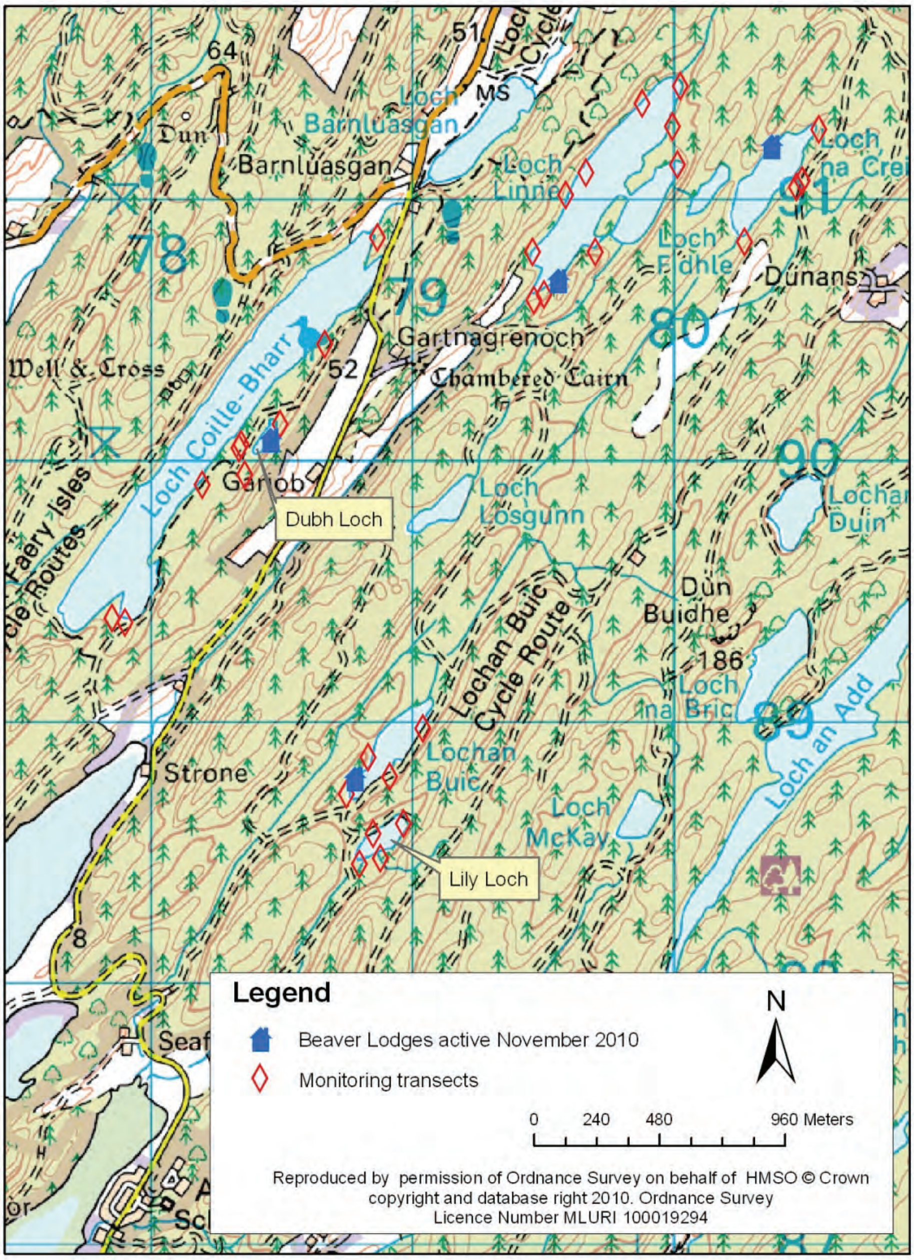

Figure 1. Locations of monitoring transects and active beaver lodges at Knapdale, November 2010.

3.1.1 Site access

All transect sites were accessed on foot from public car parks or from forestry roads.

3.2 Field Methods

3.2.1 Location of transects

Seventeen transects, each comprising from one to four plots, with 65 plots in total, were established at Knapdale in November 2009 (Moore *et al.* 2010). Those transects were positioned, radiating perpendicularly from the water's edge, around all lochs known to have been used by beavers at that time, so that all shores, other than those too steep to be used by beavers, were included. By November 2009, the lack of beaver field signs suggested that some of these areas were yet to be visited by beavers. To increase the likelihood that a reasonable number of transects would subsequently be visited by beavers, the choice of locations was further guided by the locations of active beaver lodges and the distribution of existing signs of beaver herbivory. A further 13 transects (43 plots) were established in April 2010, and one further transect (3 plots) established in November 2010, making a total of 111 plots across 31 transects. Most transects established in 2010 were positioned to monitor the impact of the newly released beavers at Lily Loch/Lochan Buic. Plot locations are indicated in figure 1.

Complete transects extend perpendicularly from the water's edge for 30 m (figure 2). In most cases, four rectangular plots are positioned along each transect, each 10 m wide (along the side parallel to the water's edge) and 4 m deep (along the side parallel to the transect). Plots are placed along the transect from 0 – 4 m, 6 – 10 m, 16 – 20 m and 26 – 30 m from the water. All four corners of each plot are marked with permanent wooden posts, and one post is marked with a numbered aluminium tag (at point A, figure 3). The geographic coordinates of each plot are also recorded at this point using a global positioning system (GPS). Where the loch shore is indented or projects into the loch beyond a straight line along the edge of the first plot, all land and trees up to the water's edge is considered to be part of the plot, and if necessary the position of the plot is adjusted such that its total area remains 40 m^2 (e.g. figure 3). In sites where the woodland is flooded, it is not always possible to access, nor to identify the edge, of the loch. In these instances, the transect is started at the closest point to the water body that allows safe working.

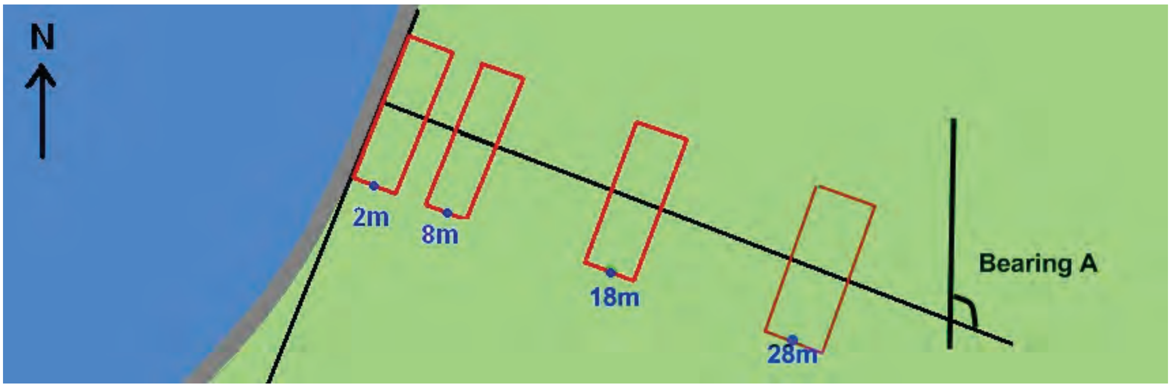

Figure 2. Schematic illustrating the arrangement of survey plots (red rectangles) along a transect, relative to a nearby loch (blue shading). Blue text indicates the distance of the midpoint of each plot from the water's edge. (Not to scale).

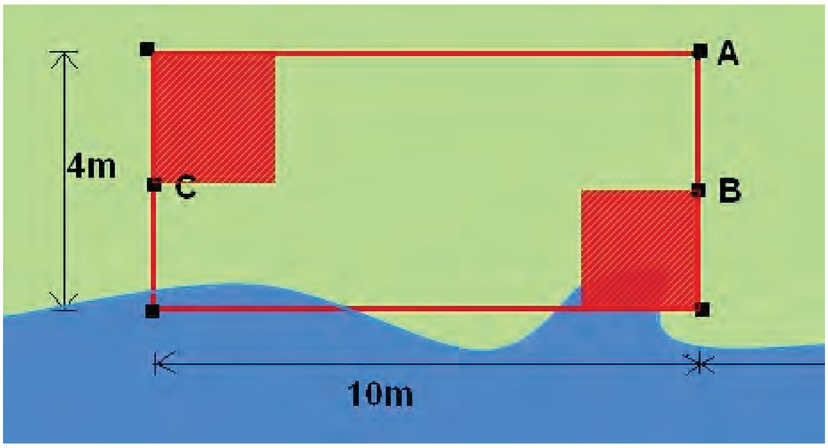

Figure 3. Dimensions of permanent vegetation plot, position of subplots for ground cover description within the plot (solid red squares) and several point locations referred to in the text.

On some sections of loch shore, deciduous broadleaf woodland extends for less than 30 m from the water before conifer plantations, paths, roads or inaccessible terrain are encountered. In these cases, transects included fewer than four plots. Where transects crossed small paths, it was occasionally necessary to shift a plot one or two metres towards or away from the water.

3.2.2 Plot measurements

Each plot was delineated with a line extended around its four corner posts while observers were on site. The slope of each plot, from its lowest to highest point, was measured using a clinometer, and where this was greater than zero, the aspect of the slope was also measured using a compass. Percentage vertical canopy cover and ground surface area covered by standing water were estimated to the nearest 5% and recorded for each plot. Several measurements were taken from a point midway along the right hand side of the plot when viewed from the waterside (point B, figure 3). Percentage horizontal vegetation density was measured across the plot from point B by estimating the percentage area obscured of a 50 × 50cm white board held by an assistant facing the observer from point C (figure 3). This was repeated with both the board and the observer's eyes at four different levels above the ground: 0 – 50cm, 50 – 100cm, 100 – 150cm and 150 – 200cm above the ground. At each visit, in each plot, one photograph was taken from point B, facing across the plot towards point C, with a camera supported 1.6 m above the ground by a monopod. The camera used was a Nikon Coolpix 5400, with its zoom set to the widest lens angle possible (28 mm). All photographs are archived at The James Hutton Institute and will form a sequence of photographs describing visual changes to the plots over the course of the Scottish Beaver Trial.

3.2.2.1 Subplot measurements of ground cover

Ground cover was described in two subplots within each plot. Subplots measured 2 × 2 m and were positioned in the front right-hand corner and back left-hand corner of the plot (when facing the plot from the water) as illustrated in figure 3. For each plot, percentage cover of the following types was estimated to the nearest 5%:

- standing water
- rock
- bare earth or mud
- grasses, sedges or rushes
- leaf litter
- woody litter (from small twigs to logs)
- ferns (including browned-off bracken)

- bryophytes
- dwarf shrubs (primarily *Calluna vulgaris, Myrica gale* and *Vaccinium* spp.)
- herbs

Because litter, for example, could overlie an area of grass which might overlap a layer of moss, the sum of all estimates in a plot was allowed to exceed 100%. Tree seedlings less than 1.3 m in height were also counted in each subplot.

3.2.3 Measurements of woodland and beaver effects

All trees greater than 1.3 m in height, regardless of stem diameter, were marked and recorded in each plot, along with stumps and fallen timber from trees which would originally have met this criterion. Working from one end of the plot to the other, each stem, or in the case of easily grouped clumps of smaller stems of a single species, each clump of stems was permanently marked with a uniquely numbered aluminium tag. Tags were affixed as close to the ground as possible, using either a small aluminium nail or, for some smaller stems, a length of wire encircling the stem. For each stem, stump or group of stems, an observer recorded the species; measured the diameter at height 20cm (or lower if a bifurcation occurred at 20cm or if beavers had severed the stem below 20cm) of each stem or stump using calipers; recorded whether the stem or stump was alive, dead or indeterminate; and assigned the stem(s) to one of 11 categories:

1. Site on a tree where a minor branch has been removed by beavers, typically overhanging the water (BCut).
2. Large log felled by beavers (BLog).
3. Tree partially felled by beavers i.e. the xylem has been incompletely severed, some phloem remains continuous between the stump and the upper part of the tree, but the upper part of the tree has fallen over and is resting on the ground or on other trees (BP)
4. Stump of a tree felled by beavers (BSt).
5. Upright tree gnawed by beavers; this included trees with a single bite-mark through to trees that are near toppling (BUp).
6. Upright stems growing from a log or horizontal tree trunk (LogUp).
7. Naturally fallen log (NLog).
8. Naturally partially fallen tree (NP).
9. 'Natural' tree stump – resulting from windfall or decay, but also including stumps sawn by humans (NSt).
10. Upright tree, unaffected by beaver gnawing, n.b. trees need not be vertical to qualify, some 'upright trees' are inclined at angles as low as 10 degrees from the ground (Up).
11. Trees that had previously been tagged but which could not be found on subsequent visits (Gone).

In a number of cases, trees branched at a point closer to the ground than the height at which stem diameters were measured (20cm); in these cases diameters were recorded for all stems at that height. Instances were also observed where trees branched at a point higher than 20cm, but beavers severed the branched stems above the branching point. In those cases, in addition to the 20cm diameter observers also measured the diameter where the stem was severed by beavers, and recorded this hierarchy of branching (see Appendix 1 for details). In some instances, secondary and even tertiary branching events were recorded below beaver gnawing.

Some tree stems and logs were leaning, either naturally, because they had been incompletely gnawed and partially felled by beavers or because they had been completely severed by beavers but were still supported above the ground by surrounding vegetation. The angle these stems made with the ground was recorded. From trees and stumps that had been gnawed by beavers, observers recorded the percentage of the circumference of the stem that had been gnawed. In the case of stumps of trees felled by beavers, this was almost always 100%. From stumps felled by beavers and partially felled and upright trees gnawed by beavers, observers also recorded the height above the ground at which gnawing had occurred. For stumps, this was taken from the highest part of the stump remaining. From upright trees, this was taken from the vertical midpoint of the gnawing. The lengths and diameters of any logs lying within the plot were also recorded, but only that part of the log lying within the plot boundary was included.

Observers also recorded any coppice resprouting from stumps or trees gnawed by beavers. All new shoots were counted and recorded separately as:

- "low shoots": shoots originating from stumps or below the gnawing damage on trees gnawed but not felled by beavers, or
- "high shoots": shoots originating from logs or above the gnawing damage on the stems of upright or partially felled trees gnawed by beavers.

The average and maximum shoot lengths were also recorded, and whether or not the longest shoot had been browsed. Where coppice resprouting had occurred and it had subsequently been browsed, observers recorded the extent of browsing effects on these shoots attributable to deer (Roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and Sika deer *Cervus nippon* are present at Knapdale) and/or to beavers on a three-point scale: 0 = none; 1 = detectable, less than half of shoots browsed; 2 = substantial, more than half of shoots browsed. Previous bark stripping by deer was evident on the trunks of many willows throughout Knapdale.

A series of illustrations of trees that have experienced a variety of beaver effects, and an example datasheet recording all required data about these trees, was produced for observers' reference in the field. Many permutations of tree growth form and beaver effect are more easily described by these illustrations than in text. This sheet is included as Appendix 1 at the end of this report.

3.2.4 Comprehensive mapping of beaver effects

In addition to the establishment and monitoring of permanent vegetation plots, a further approach was trialled in 2010 to assess the distribution of beaver impacts. At Creagmhor Loch, an attempt was made to locate all trees directly affected by beavers. In April 2010 all such trees or stumps were marked with aluminium tree tags, and surveyors recorded:

- tree species
- status of the tree (BSt, BP, BUp, Blog)
- diameter of the affected stem
- approximate distance to water
- location (with a GPS)
- species identities of the nearest five neighbouring trees/stumps
- whether neighbouring trees/stumps had been affected by beavers

The exercise was repeated and additional trees were marked and recorded in November 2010. Creagmhor Loch was chosen because it is relatively small and easy to walk around and to search for beaver signs. Although further releases were planned, it was unoccupied by beavers in April 2010, and so recording the extent of beaver impacts was not excessively onerous.

3.2.5 Timing of measurements

The fieldwork reported here was conducted in April and November 2010. Field visits have been planned for two time periods in each year of the monitoring programme so that, in future years, observers will be able to assess the full extent of coppice resprouting throughout the growing season from trees and stumps felled by beavers, as well as any beaver and deer herbivory that these shoots have suffered. During summer and autumn, beavers are expected to feed more on forbs and aquatic macrophytes in addition to the foliage of deciduous trees and to direct their diet more towards the bark and small twigs of woody vegetation as other foods become less available through winter (Krojerová-Prokešová *et al.* 2010). It is anticipated that spring fieldwork will reveal the full extent of tree felling and bark feeding that has occurred on dormant trees through the preceding winter and that autumn fieldwork will also allow the determination of the net biomass gain of new shoots resulting from the interaction of growth and browsing.

3.3 Analysis and presentation of results

The abundance of trees within plots was considered in two ways. First, the number of stems was counted, and second, the basal area of each stem was calculated (basal area = $\pi \times$ stem radius^2) and these were summed to give a total stem basal area (at height 20cm) for each plot. These totals included the stumps of trees recently felled by beavers, so as to provide the closest approximation of the plot structure 'pre-beaver', but excluded branches and logs felled by beavers and naturally felled logs and natural stumps.
Distances of transects from active lodge sites were calculated in a geographic information system by tracing the shortest path possible across the surface of the water body fronted by the two locations.

Where comparisons were made between trees directly affected by beavers and the total tree sample, the former category included all trees gnawed by beavers, whether they were still standing or whether only a stump remained.

4 RESULTS

4.1 Establishment of transects

The bearings and exact locations of the 31 transects and 111 plots established by November 2010 are listed in table 1. The locations of the plots are illustrated in figure 1. Seven different species were recorded as dominant or co-dominant species in at least one plot, however it should be noted that plot 244, which was dominated by *Q. petraea*, included only a single tree. Also two of the marked plots, plots 285 and 290 did not contain any trees. *B. pubescens* was dominant in the majority of vegetation plots. Note that species dominance in table 1 has been determined on the basis of number of stem diameters recorded, which may overestimate the abundance of *C. avellana* and to a lesser extent *Salix*, because many stems may have been recorded from a single stool or plant.

Table 1. Numbers and date of establishment of each transect/plot and the permanent tag numbers, British National Grid reference, distance from the water's edge, dominant woody species and presence or absence of beaver browsing in each plot within each transect. See Table 3 for 'Dominant species' code.

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species[%]	Beaver sign[#]
1. Dubh N	11/09	211	NR 78494 90138	0 m	BETPUB	Y
		212	NR 78500 90140	6 m	BETPUB	Y
		213	NR 78509 90139	16 m	BETPUB	N
		214	NR 78512 90162	26 m	BETPUB/SORAUC	N
2. Linne SW	11/09	3015	NR 79461 90798	0 m	BETPUB	N
		3016	NR 79457 90799	6 m	ALNGLU/BETPUB	Y
		217	NR 79450 90808	18 m	ALNGLU/BETPUB	Y
		218	NR 79445 90814	26 m	BETPUB	N
3. Coille-Bharr SE	11/09	219	NR 77900 89380	0 m	BETPUB/ALNGLU	N
		220	NR 77899 89375	6 m	BETPUB	N
		221	NR 77892 89369	16 m	BETPUB	N
		222	NR 77885 89361	26 m	BETPUB	N
4. Creagmhor S	11/09	223	NR 80271 90836	0 m	BETPUB	N
		224	NR 80272 90834	6 m	BETPUB	Y
		225	NR 80265 90823	16 m	BETPUB	N
		226	NR 80258 90815	26 m	BETPUB	N
5. Fidhle N	11/09	227	NR 80014 91133	0 m	BETPUB	N
		228	NR 80018 91141	6 m	BETPUB	N
		229	NR 80021 91149	16 m	BETPUB	N
		230	NR 80027 91157	26 m	BETPUB	N
6. Dubh S	11/09	231	NR 78360 89946	0 m	BETPUB	N
		232	NR 78359 89946	6 m	Salix/BETPUB	Y
		233	NR 78353 89929	16 m	Salix/BETPUB	Y
		234	NR 78355 89924	26 m	Salix/BETPUB	Y
7. Linne SW	11/09	235	NR 79588 91016	0 m	BETPUB/ALNGLU	Y
		236	NR 79576 91020	6 m	Salix/BETPUB	Y
		237	NR 79575 91022	16 m	Salix/BETPUB	Y
		238	NR 79592 91033	26 m	BETPUB	N
8. Linne W	11/09	239	NR 79665 91103	0 m	CORAVE	Y
		240	NR 79665 91097	6 m	CORAVE	N
		241	NR 79645 91126	16 m	CORAVE	N
		242	NR 79640 91118	26 m	CORAVE	N
9. Coille-Bharr	11/09	243	NR 77851 89397	0 m	ALNGLU/BETPUB	N

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species[%]	Beaver sign[#]
SSE		244	NR 77846 89391	6 m	QUEPET	N
		245	NR 77843 89387	16 m	BETPUB	N
		246	NR 77823 89384	26 m	BETPUB	N
10. Creagmhor E	11/09	247	NR 80471 91047	0 m	BETPUB/FRAEXC	Y
		248	NR 80472 91039	6 m	BETPUB	Y
		249	NR 80475 91031	16 m	BETPUB	Y
		250	NR 80484 91026	26 m	BETPUB	N
11. Coille-Bharr E	11/09	251	NR 78195 89908	0 m	ALNGLU/SORAUC	N
		252	NR 78202 89905	10 m	BETPUB/SORAUC	N
		253	NR 78209 89899	20 m	BETPUB/SORAUC	N
12. Creagmhor N	11/09	254	NR 80555 91267	0 m	BETPUB	N
		255	NR 80561 91273	6 m	BETPUB	Y
		256	NR 80567 91281	16 m	ALNGLU/BETPUB	Y
		257	NR 80574 91285	26 m	BETPUB	N
13. Creagmhor NE	11/09	258	NR 80492 91072	0 m	BETPUB/SORAUC	Y
		259	NR 80493 91073	6 m	BETPUB	N
		260	NR 80501 91064	16 m	BETPUB	N
		261	NR 80510 91058	26 m	BETPUB	N
14. Linne N	11/09	262	NR 80026 91434	0 m	ALNGLU	N
		263	NR 80029 91439	6 m	BETPUB	N
		264	NR 80037 91451	16 m	ALNGLU/BETPUB	N
		265	NR 80043 91459	26 m	BETPUB	N
15. Linne SE	11/09	269	NR 79466 90614	0 m	ALNGLU/BETPUB	Y
		270	NR 79463 90611	6 m	BETPUB	Y
16. Linne SE	11/09	271	NR 79503 90635	0 m	BETPUB	Y
		272	NR 79506 90626	6 m	BETPUB	Y
		273	NR 79512 90619	16 m	BETPUB	Y
		266	NR 79518 90614	26 m	BETPUB	Y
17. Coille-Bharr N	11/09	276	NR 78867 90853	0 m	ALNGLU	N
		277	NR 78873 90863	6 m	ALNGLU	N
		278	NR 78877 90863	16 m	ALNGLU/Salix	N
		279	NR 78882 90873	26 m	BETPUB	N
18. Lily NW	4/10	201	NR 78851 88572	0 m	ALNGLU/Salix	N
		202	NR 78849 88578	6 m	ALNGLU	N
		203	NR 78844 88583	16 m	BETPUB	N
19. Linne NE	4/10	204	NR 79994 91278	0 m	BETPUB	Y
		205	NR 79998 91276	6 m	BETPUB	Y
		206	NR 80007 91276	16 m	BETPUB	N
		207	NR 80017 91276	26 m	BETPUB	N
20. Lily N End	4/10	280	NR 78965 88611	0 m	ALNGLU	N
		281	NR 78968 88615	6 m	ALNGLU/BETPUB	N
		282	NR 78975 88619	16 m	ALNGLU	N
		283	NR 78986 88623	26 m	BETPUB	N
21. Linne NW	4/10	284	NR 79879 91366	0 m	ALNGLU/CORAVE	Y
		285	NR 79877 91369	6 m	-	-
		286	NR 79870 91374	16 m	CORAVE	N
		287	NR 79864 91381	26 m	CORAVE	N
22. Lily SE	4/10	288	NR 78879 88477	0 m	Salix	N
		289	NR 78884 88473	6 m	ALNGLU	N
		290	NR 78881 88462	16 m	-	-
		291	NR 78885 88451	26 m	BETPUB	N

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species[%]	Beaver sign[#]
23. Lily SSE	4/10	292	NR 78798 88455	0 m	ALNGLU/Salix	N
		293	NR 78798 88450	6 m	BETPUB	N
		294	NR 78803 88441	16 m	BETPUB	N
		295	NR 78809 88430	26 m	BETPUB	N
24. Lochan Buic SW	4/10	296	NR 78747 88723	0 m	BETPUB/Salix	N
		297	NR 78738 88715	6 m	BETPUB	N
		298	NR 78730 88719	16 m	BETPUB	N
		299	NR 78726 88719	26 m	BETPUB	N
25. Lochan Buic NE	4/10	2101	NR 79040 88975	0 m	BETPUB/ALNGLU/CORAVE	Y
		2102	NR 79054 88964	6 m	ALNGLU/BETPUB	N
		2103	NR 79067 88965	16 m	CORAVE	N
		2104	NR 79063 88977	26 m	BETPUB/CORAVE	N
26. Linne E	4/10	274	NR 79699 90798	0 m	BETPUB	Y
		275	NR 79705 90794	6 m	BETPUB	Y
		300	NR 79710 90785	16 m	BETPUB	Y
		2105	NR 79718 90780	26 m	BETPUB	N
27. Dubh W	4/10	2705	NR 78346 90062	0 m	BETPUB/SORAUC	Y
28. Dubh SW	4/10	2706	NR 78338 90049	0 m	BETPUB/SORAUC	Y
29. Coille Bharr NE	4/10	2894	NR 78665 90445	0 m	ALNGLU/CORAVE	N
		2895	NR 78670 90441	6 m	ALNGLU	N
		2896	NR 78675 90437	16 m	ALNGLU/SORAUC	N
		2897	NR 78703 90399	26 m	BETPUB/SORAUC	N
30. Lochan Buic E	4/10	2921	NR 78914 88790	0 m	BETPUB/Salix	N
		2922	NR 78915 88785	6 m	BETPUB/CORAVE	N
31. Lochan Buic W.	11/10	3221	NR 78832 88864	0 m	ANLGLU/BETPUB	N
		3223	NR 78828 88863	6 m	BETPUB	N
		3223	NR 78817 88862	16 m	BETPUB	N

* From nearest edge to water.
[%] Species codes are listed in table 3.
[#] Beaver sign includes any gnawing or felling of woody vegetation up until Nov 2010

4.2 Ground cover in subplots

Estimates of ground cover and counts of seedlings in the two subplots of each vegetation plot, at the time plots were established, are presented in table 2. Exposed rock was fairly uncommon in plots at Knapdale because it was usually overgrown by moss and/or grass. Seedlings were uncommon in plots. It should be borne in mind that the results of these ground cover surveys are very season-specific, and quite different results might be returned at times of the year other than April or November.

Table 2. Mean percent ground cover of ten categories estimated in November 2010 in 2×2m subplots and mean number of woody seedlings per subplot at plot establishment.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
1; 0m	65	0	20	0	25	0	7.5	15	0	0	0
1; 6m	12.5	0	5	32.5	40	1.25	10	60	10	0	0
1; 16m	0	0	0	0	60	1.25	40	60	1.25	0	0
1; 26m	0	0	2.5	0	65	0	32.5	90	0	1.25	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
2; 0m	0	0	2.5	50	35	26.25	1.25	30	25	0	0
2; 6m	10	0	10	3.75	45	15	2.5	42.5	1.25	3.75	0
2; 18m	0	0	5	5	65	8.75	12.5	85	0	0	0
2; 26m	1.25	0	7.5	7.5	65	3.75	10	90	0	0	0
3; 0m	0	0	0	70	32.5	2.5	3.75	11.25	10	2.5	0
3; 6m	0	0	0	65	17.5	6.25	6.25	27.5	1.25	2.5	0,5
3; 16m	0	0	0	55	65	2.5	3.75	5	2.5	2.5	1
3; 26m	1.25	0	0	30	70	12.5	6.25	27.5	2.5	2.5	0
4; 0m	5	0	0	75	7.5	1.25	0	26.25	6.25	0	0
4; 6m	2.5	0	5	87.5	10	2.5	0	10	0	1.25	0
4; 16m	1.25	0	1.25	5	27.5	12.5	1.25	85	2.5	0	0
4; 26m	1.25	0	0	30	42.5	12.5	1.25	55	0	0	0
5; 0m	0	0	0	97.5	15	2.5	2.5	2.5	30	1.25	0
5; 6m	1.25	0	5	72.5	30	0	1.25	17.5	0	1.25	0
5; 16m	0	0	0	45	45	1.25	7.5	45	7.5	1.25	0
5; 26m	0	0	0	50	30	1.25	1.25	13.75	36.25	2.5	0
6; 0m	100	0	0	25	2.5	2.5	0	2.5	0	0	0
6; 6m	100	0	5	32.5	2.5	2.5	0	3.75	0	0	0
6; 16m	2.5	0	5	47.5	7.5	1.25	1.25	50	0	0	2,5
6; 26m	10	0	37.5	25	35	8.75	3.75	45	1.25	2.5	0
7; 0m	1.25	2.5	2.5	2.5	40	3.75	57.5	20	17.5	2.5	0
7; 7m	0	2.5	1.25	1.25	50	17.5	37.5	27.5	13.75	2.5	0
7; 16m	0	10	1.25	1.25	47.5	2.5	3.75	17.5	42.5	2.5	0
7; 26m	0	10	0	0	45	1.25	26.25	37.5	50	1.25	0
8; 0m	0	0	1.25	55	65	2.5	0	3.75	1.25	2.5	0
8; 6m	0	0	1.25	20	75	3.75	3.75	6.25	0	2.5	0
8; 16m	0	0	1.25	17.5	80	2.5	3.75	8.75	0	2.5	0
8; 26m	0	1.25	1.25	17.5	67.5	2.5	2.5	15	0	2.5	0
9; 0m	27.5	0	0	60	35	0	0	6.25	0	37.5	0
9; 6m	0	0	2.5	77.5	52.5	2.5	0	2.5	1.25	3.75	0
9; 16m	2.5	0	1.25	20	70	3.75	5	42.5	2.5	2.5	0
9; 26m	0	0	1.25	6.25	80	12.5	6.25	35	2.5	3.75	0
10; 0m	2.5	0	2.5	55	25	3.75	7.5	42.5	1.25	0	0
10; 6m	0	0	2.5	25	40	5	22.5	65	2.5	7.5	0,5
10; 16m	0	0	5	60	35	3.75	1.25	32.5	2.5	1.25	0
10; 26m	2.5	0	2.5	30	37.5	1.25	11.25	47.5	0	30	0
11; 0m	25	0	0	45	27.5	0	17.5	32.5	10	0	0
11; 10m	0	0	0	26.25	12.5	3.75	21.25	55	6.25	0	0
11; 20m	0	0	0	15	17.5	7.5	1.25	80	22.5	0	0
12; 0m	12.5	0	3.75	60	3.75	2.5	0	20	0	3.75	0
12; 6m	2.5	0	2.5	50	2.5	2.5	26.25	27.5	0	2.5	0
12; 16m	25	0	1.25	10	37.5	2.5	12.5	45	2.5	6.25	0
12; 26m	0	0	1.25	40	2.5	1.25	11.25	10	33.75	2.5	1
13; 0m	0	0	2.5	40	47.5	3.75	5	32.5	17.5	2.5	0
13; 6m	0	0	0	42.5	42.5	3.75	1.25	15	47.5	1.25	1,5
13; 16m	0	0	0	2.5	75	7.5	17.5	30	1.25	1.25	0,5

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
13; 26m	0	0	1.25	20	75	2.5	20	37.5	2.5	2.5	0
14; 0m	0	7.5	2.5	85	17.5	15	6.25	30	0	2.5	0
14; 6m	0	5	0	87.5	7.5	3.75	20	12.5	0	2.5	0
14; 16m	0	0	2.5	67.5	32.5	1.25	25	2.5	0	5	0
14; 26m	1.25	0	2.5	97.5	35	3.75	5	5	0	6.25	0
15; 0m	18.75	0	1.25	45	20	1.25	0	47.5	1.25	0	0
15; 6m	5	0	0	60	20	8.75	2.5	20	1.25	1.25	0
16; 0m	0	0	1.25	37.5	40	11.25	6.25	18.75	17.5	1.25	0
16; 6m	0	0	0	27.5	22.5	2.5	40	37.5	17.5	1.25	0
16; 16m	0	0	0	60	15	6.25	12.5	5	0	1.25	0
16; 26m	0	0	0	32.5	35	3.75	12.5	55	0	1.25	0
17; 0m	11.25	0	2.5	67.5	42.5	1.25	1.25	2.5	2.5	2.5	8,5
17; 6m	15	0	1.25	65	27.5	0	3.75	6.25	1.25	2.5	5,5
17; 16m	25	0	15	50	47.5	3.75	2.5	3.75	1.25	3.75	1,5
17; 26m	0	0	0	17.5	72.5	2.5	8.75	20	1.25	2.5	1
18; 0m	85	0	10	35	20	3.75	0	12.5	15	1.25	0
18; 6m	0	0	0	77.5	40	1.25	1.25	32.5	0	2.5	0
18; 16m	5	0	35	17.5	50	0	7.5	35	1.25	22.5	0
19; 0m	0	0	2.5	42.5	12.5	3.75	47.5	12.5	0	0	0
19; 6m	0	0	0	80	15	17.5	2.5	16.25	2.5	0	0
19; 16m	0	0	0	60	45	1.25	10	40	12.5	0	2,5
19; 26m	0	7.5	0	7.5	70	0	10	92.5	45	0	0
20; 0m	100	0	0	65	2.5	0	0	0	0	0	0
20; 6m	75	0	5	47.5	20	0	0	0	0	5	0
20; 16m	5	0	2.5	87.5	40	0	0	15	0	6.25	0
20; 26m	0	0	0	40	50	27.5	1.25	55	0	0	0
21; 0m	2.5	2.5	5	60	40	1.25	7.5	22.5	5	2.5	0
21; 6m	0	0	10	17.5	7.5	0	70	0	0	0	0
21; 16m	0	0	0	37.5	17.5	3.75	50	40	0	2.5	0
21; 26m	0	0	35	15	65	0	35	12.5	0	1.25	0
22; 0m	100	0	0	40	70	2.5	0	0	0	0	0
22; 6m	7.5	0	1.25	72.5	62.5	5	0	5	0	1.25	0
22; 16m	0	0	0	92.5	17.5	0	1.25	7.5	0	3.75	0
22; 26m	12.5	0	5	37.5	45	2.5	1.25	21.25	0	21.25	0
23; 0m	100	0	0	67.5	25	0	0	1.25	0	0	0
23; 7m	37.5	0	0	75	37.5	1.25	0	7.5	0	0	0
23; 16m	0	0	1.25	2.5	75	3.75	2.5	75	0	0	0
23; 26m	0	0	0	20	62.5	6.25	2.5	67.5	0	0	0
24; 0m	2.5	0	2.5	15	10	0	0	92.5	2.5	0	0
24; 6m	0	0	0	65	22.5	1.25	0	32.5	0	0	0
24; 16m	0	0	0	16.25	55	1.25	0	80	0	0	0
24; 26m	0	0	45	7.5	65	5	2.5	45	0	1.25	0
25; 0m	0	10	15	22.5	55	6.25	1.25	35	1.25	1.25	0
25; 6m	0	0	0	0	0	0	0	0	0	0	0
25; 16m	0	0	0	55	50	0	10	45	1.25	1.25	0
25; 26m	0	0	0	65	35	3.75	12.5	22.5	2.5	2.5	0

Transect; plot	Percent Cover										
	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
26; 0m	17.5	0	2.5	25	10	7.5	55	20	1.25	0	0
26; 6m	0	0	0	10	25	7.5	17.5	82.5	2.5	0	0
26; 16m	0	0	2.5	2.5	45	10	7.5	70	16.25	0	0
26; 26m	0	0	0	0	55	22.5	2.5	92.5	0	0	0
27; 0m	100	0	0	0	0	0	0	0	0	0	0
28; 0m	45	0	35	1.25	20	1.25	15	12.5	5	1.25	0
29; 0m	0	2.5	0	25	60	2.5	5	55	2.5	2.5	2
29; 6m	0	0	0	60	40	2.5	17.5	20	0	5	1,5
29; 16m	0	0	0	7.5	20	2.5	35	35	2.5	25	0
29; 26m	17.5	0	7.5	7.5	45	0	25	60	2.5	15	0
30; 0m	2.5	0	25	26.25	30	3.75	15	37.5	1.25	1.25	0
30; 6m	0	0	0	32.5	25	25	1.25	55	1.25	5	0
31; 0m	0	0	0	65	22.5	2.5	17.5	5	1.25	2.5	0
31; 6m	0	0	0	27.5	37.5	2.5	2.5	37.5	0	0	0,5
31; 0m	0	0	2.5	1.25	47.5	3.75	13.75	62.5	2.5	0	0

4.3 Vegetation composition and structure in plots

Fourteen tree species were identified in the vegetation plots. However, as trees were not in leaf during fieldwork, willows could only be identified to genus, meaning that tree species diversity has been underestimated. However, most *Salix* at Knapdale is believed to be *S. capraea*. Table 3 lists the total number and summed basal area of all tree species measured. Numerically, *B. pubscens* is clearly dominant, and only *A. glutinosa, C. avellana, Salix* spp. and *S. aucuparia* can also be considered abundant. When total basal area was considered, the dominance of *B. pubescens* over *A. glutinosa* was less marked. This can be largely explained by the widespread occurrence of dense thickets of young, small birch trees which have grown in place of recently cleared conifer plantations throughout Knapdale. *A. glutinosa* made a substantial contribution to the total basal area despite its more modest stem count, because it most commonly occurs as large trees right at the water's edge.

Table 3. Total number of upright stems and total basal area of all tree and shrub species recorded in plots at November 2010. Asterisked rows indicate species categories that were summed and treated as a single category in most data summaries and analyses.

	Common name	Code	Species	Stem Count	Total basal area (cm^2)	Median diameter (cm)
*	Sycamore	ACEPSE	*Acer pseudoplatanus*	2	4	1.5
	Black alder	ALNGLU	*Alnus glutinosa*	534	112,100	5.0
	Downy birch	BETPUB	*Betula pubescens*	2986	121,403	3.0
	Hazel	CORAVE	*Corylus avellana*	375	12,065	3.0
*	Hawthorn	CRAMON	*Crataegus monogyna*	5	162	2.0
*	Douglas fir	PSEMEN	*Pseudotsuga menziesii*	1	3	2.0
	Ash	FRAEXC	*Fraxinus excelsior*	58	10,595	7.0
*	Holly	ILEAQU	*Ilex aquifolium*	1	79	10.0
*	Bog myrtle	MYRGAL	*Myrica gale*	11	37	2.0
*	Sitka spruce	PICSIT	*Picea sitchensis*	26	7,216	5.5
*	Sessile oak	QUEPET	*Quercus petraea*	6	1,444	2.0
*	Wild rose	ROSACI	*Rosa acicularis*	1	1	1.0
	Willow	Salix	*Salix* spp.	509	15,260	4.0
	Rowan	SORAUC	*Sorbus aucuparia*	395	7,736	2.0

Common name	Code	Species	Stem Count	Total basal area (cm^2)	Median diameter (cm)
TOTAL			**4,910**	**288,105**	

* Collapsed into “Other” category for most data analyses

The majority of stems marked and measured in the plots were standing trees unaffected by beavers. However, stems, stumps and branches were recorded in all 11 status categories (table 4). By November 2010, 10% of trees in the vegetation plots had been directly affected by beavers, however these accounted for only 4.8% of the total basal area.

Table 4. Eleven status classes used to classify trees and tree parts in the plots, codes used to record them, and the numbers of each class recorded in vegetation plots in November 2010.

Status	Code	Count	Total basal area (cm^2)
Site where a minor branch removed from standing tree	BCut	7	6
Log felled by beavers	BLog	26	2 273
Tree partially felled by beavers	BP	33	3 774
Stump of tree felled by beavers	BStump	379	8 229
Upright tree gnawed by beavers	BUp	62	2 441
Upright stems growing from a log	LogUp	28	251
Naturally fallen log	NLog	39	13 212
Naturally partially fallen tree	NP	1	1 809
Natural tree stump	NStump	9	264
Upright tree, unaffected by beavers	Up	4 422	271 707
Tagged 2009, missing 2010	Gone	20	20
TOTAL (excl. ‘Gone’)		**5 006**	**303 966**

Because beavers are expected to have the greatest effect on woodland near to the water’s edge, different tree species may vary in their susceptibility to beaver herbivory if their distributions differ in relation to distance from water. Figure 4 shows how the abundance of each tree species differs with distance from the water. The density of *A. glutinosa, C. avellana* and *F. excelsior* decrease and the density of *B. pubescens* increases with distance from water. It is clear that the greatest number of large *A. glutinosa* were found near the water’s edge. *S. aucuparia* was most abundant within 4 m of the water.

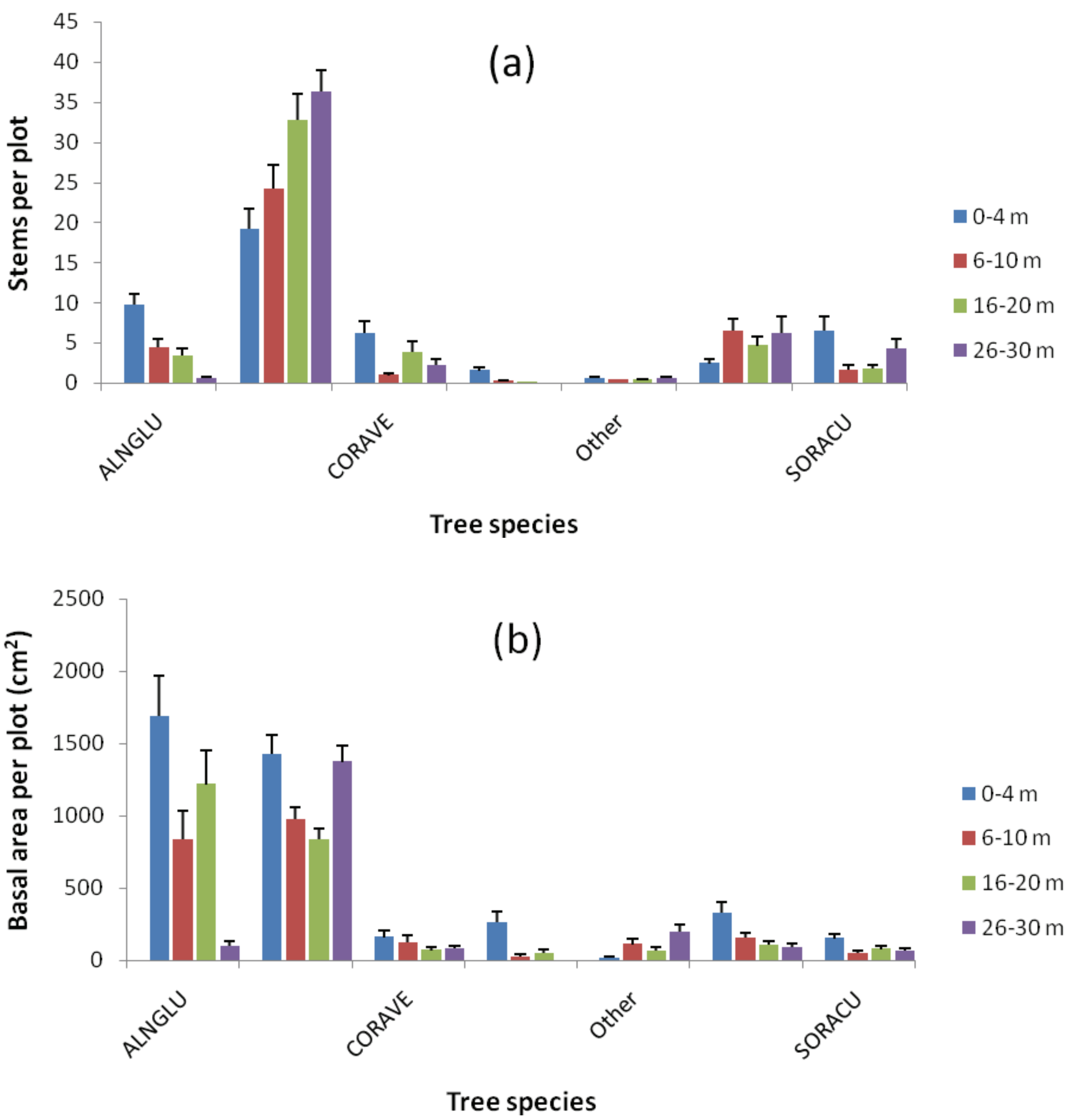

Figure 4. (a) Mean number of stems per plot and (b) mean total basal area per plot for seven common tree species in plots positioned at increasing distances from the water's edge. Error bars indicate 1 standard error.

4.4 Beaver effects

Beaver effects were obvious on most loch shores around Knapdale by November 2010, with the exceptions of Lily Loch (because the animals released there moved and established a lodge in nearby Lochan Buic) and Loch Coille-Bharr proper (the beavers originally released there spend most of their time in the flooded Dubh Loch, where they have built a substantial lodge). The most widespread effects were direct, on trees which had been partially or completely felled by beavers. Beaver gnawing or felling of trees was observed on 17 of 31 transects and in 35 of 111 vegetation plots, and the percentage of trees and of total basal areas of trees used by beavers in those 35 plots is shown in figure 5. On average, in plots where direct beaver effects had occurred, 17% of stems had been gnawed or felled and 25% of the basal area had been felled completely by November 2010. In comparison, data from November 2009 showed that 13% of stems in beaver-affected plots had been gnawed or felled by that time and 18% of the total basal area had been felled completely. In an extreme case of localised beaver impacts, in plot 270, 63 stumps of trees felled by beavers were observed, accounting for 64% of stems and 76% of the total basal area. This plot is in transect 15; very close to a large active beaver lodge on Loch Linne.

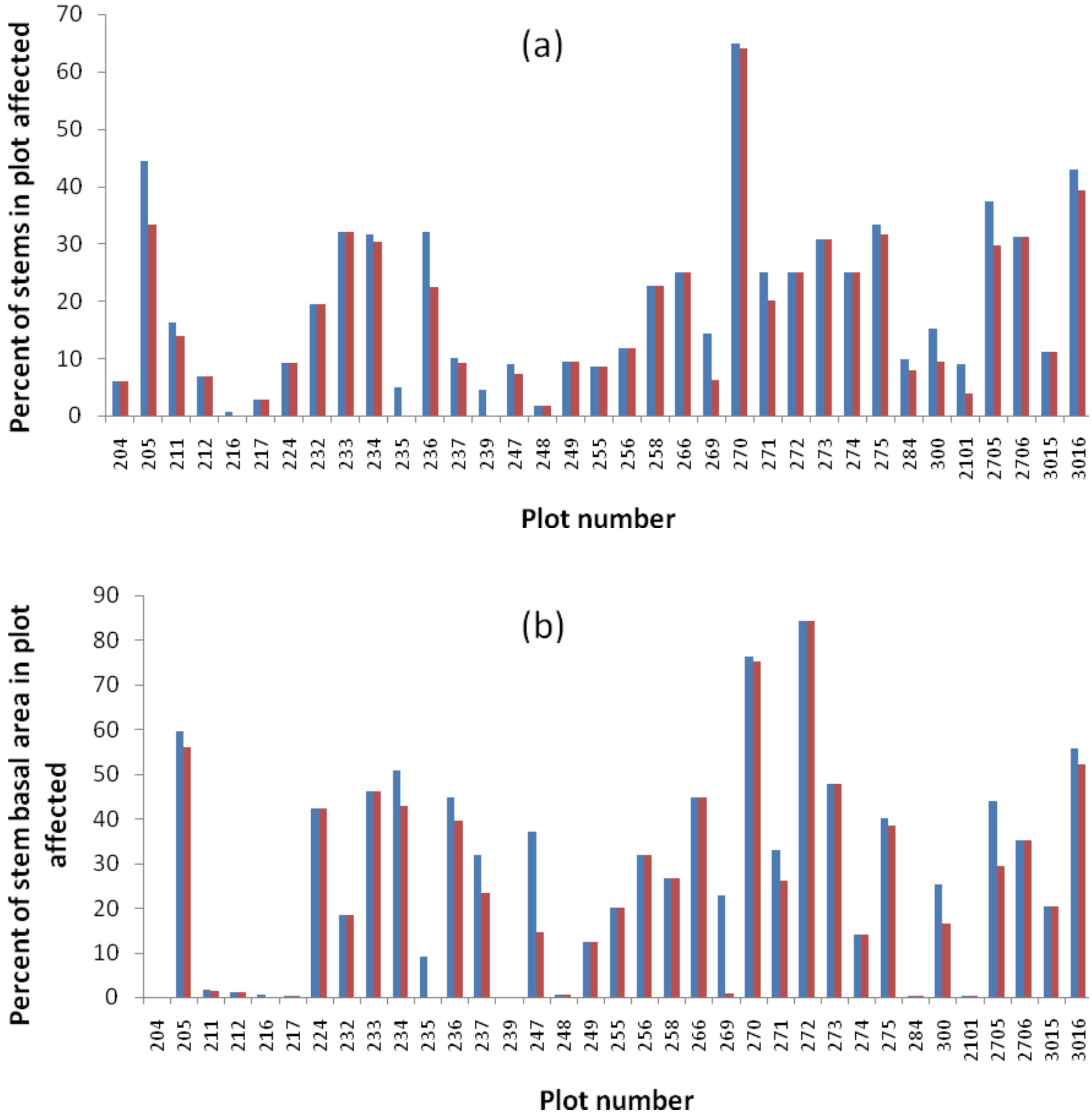

Figure 5. Percentage (a) of stems gnawed and felled by beavers and (b) of total basal area gnawed and felled by beavers in all vegetation plots where beaver effects were observed. Blue bars indicate all trees gnawed by beavers and red bars indicate only those trees felled by beavers.

Most woody plant material that had been felled had been removed from the plots by beavers and relatively little felled timber remained even where numerous stumps with signs of beaver gnawing were present. Exceptions were large stems and tree canopies that had not fallen all the way to the ground and remained out of reach of beavers. By November 2010, it was obvious that much timber had been removed from where it had been felled. Lodges were established on all lochs; the longest-established lodges on Loch Linne and Dubh Loch were very large with substantial amounts of timber, mostly long poles of diameters 5 – 10cm (figure 6). Similarly, the beavers on the Dubh Loch had continued to develop their dam and this contained a very large volume of similarly sized lengths of timber too (figure 6). On heavily affected lengths of shore, trails were evident where beavers had dragged timber to the water. At sites on the water's edge, piles of smaller branches and twigs lay stripped of their bark at beaver feeding sites (figure 7). Along some lengths of loch shore, substantial amounts of timber could be observed cached just below the water's surface.

Figure 6. Lodge (left) and beaver dam (right) showing timber used for building.

Figure 7. Beaver feeding site.

In areas where trees, particularly willows, grew densely, it was common to observe that beavers had felled a tree which had subsequently failed to fall because it was supported by neighbouring trees. In these instances, beavers sometimes severed the trunk two or even three times, but still did not always cause the tree to fall to the ground. Sometimes these entire trees were effectively 'replanted' directly into the mud or soft earth, and it will be interesting to see how many of these take root in future. Several instances of root development on such cuttings could be observed in plots in the area flooded by Dubh Loch by November 2010. Beaver cuttings can be an important mechanism of plant establishment for willow in North America (Cottrell 1995).

Beaver gnawing and tree felling were easily identified and could not be easily confused with natural or human-made damage (figure 8). Almost all beaver gnawing observed on woody stems was apparently directed at felling the tree in question, although in some instances, only minimal gnawing had occurred; this may indicate sampling behaviour and that the trees in question were rejected by beavers (figure 8). Beaver gnawing occurred at a variety of heights on the tree stem, mostly between 0 and 70cm (figure 9). The mean height of gnawing was 30cm. In contrast to November 2009, when little gnawing was observed below 20cm, a substantial proportion of stumps were found gnawed right to the ground.

Figure 8. Trees directly affected by beavers. Top: felled birch trees, bottom left: beaver tooth marks on a sampled birch tree and bottom right: only woodchips and small lumps of xylem remain from the trunk of this felled tree.

One major established beaver dam was present at Knapdale throughout 2010. This dammed the point at which Dubh Loch naturally drains into Loch Coille-Bharr, at a low point in a long rocky ridge which runs along much of the eastern shore of Loch Coille-Bharr. A superficial examination of the dam at Dubh Loch indicated that its structure incorporated several pre-existing obstacles such as large tree trunks and rocks, but no very large pieces of beaver-felled timber. Rather, the timber included in the dam mostly comprised lengths of stems of diameter < 10cm (figure 6).

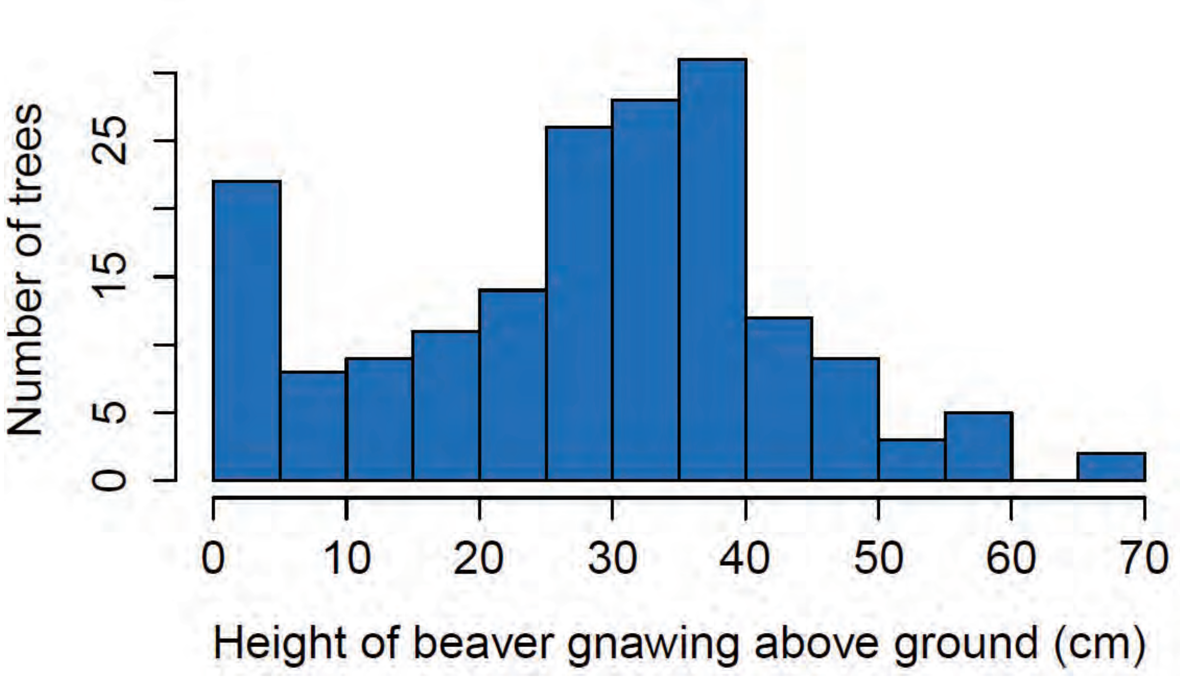

Figure 9. Histogram illustrating the distribution of heights of beaver gnawing above the ground. Size classes are labelled with their upper limits.(mean = 29.4cm)

The dam at Dubh Loch has substantially expanded the area of that water body into the surrounding woodland and across a nearby Forestry Commission road and walking track. Since November 2009, the beavers had continued to improve the dam, consequently expanding the flooded area reported in the previous report (Moore *et al.* 2010). It was noted that the water level behind the dam and hence the extent of the flooded area varied significantly between monitoring sessions. The water level was relatively low in April 2010, compared with both November 2009 and November 2010 (Figure 10). One reason that beavers flood areas of woodland is to improve their access to that woodland. As a further measure, they excavate canals through woodland and several of these were observed in the shallow flooding to the south of Dubh Loch, including one that intersected transect 6. In the process of constructing these canals, existing vegetation and soil or mud had been pushed to the side of the canals which are up to 50cm wide and deep. Aquatic macrophytes were also observed in these canals.

Figure 10. Water levels at the Dubh Loch beaver dam during monitoring in November 2009 (left) and April 2010 (right).

4.4.1 Use of transects by beavers

The establishment of transects was partly guided by existing beaver effects, making these data unsuitable for a formal analysis of the factors influencing beaver preferences for vegetation communities present in different transects. However, 17 of the 31 transects included trees that had been gnawed by beavers and the extent of beaver effects along each transect was also variable. Figure 11 shows that the most heavily affected plots were on transects close to (within 200 m) beaver lodges but that direct beaver effects were detected up to 500 m and in the case of one plot, 730 m from active lodges.

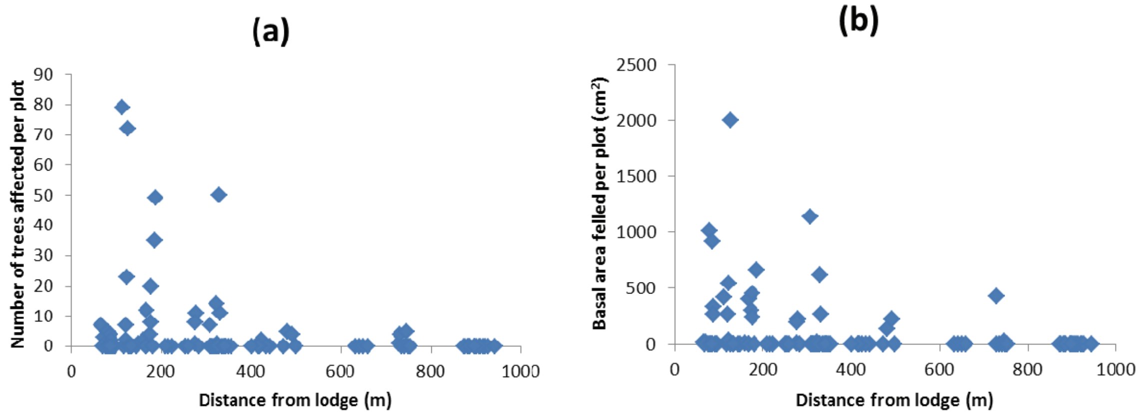

Figure 11. Beaver effects as a function of distance of plots from lodges. (a) Number of stems affected by beavers per plot and (b) basal area of trees felled per plot plotted against distance of each plot from the nearest beaver lodge.

4.4.2 Use of plots by beavers

A comparison of plots used by beavers with plots not used by beavers may inform how the vegetation community and proximity to water influence the likelihood that a plot will be used by beavers. Figure 12 compares the abundance of each of the major tree species in plots not used by beavers to their abundance in plots that were used by beavers. These data suggest that beavers may have preferentially used plots dominated by dense birch and that they may strongly avoid plots dominated by large alder trees. Plots used by beavers also tended to possess substantially more stems of *Salix* and rowan than plots that were not used.

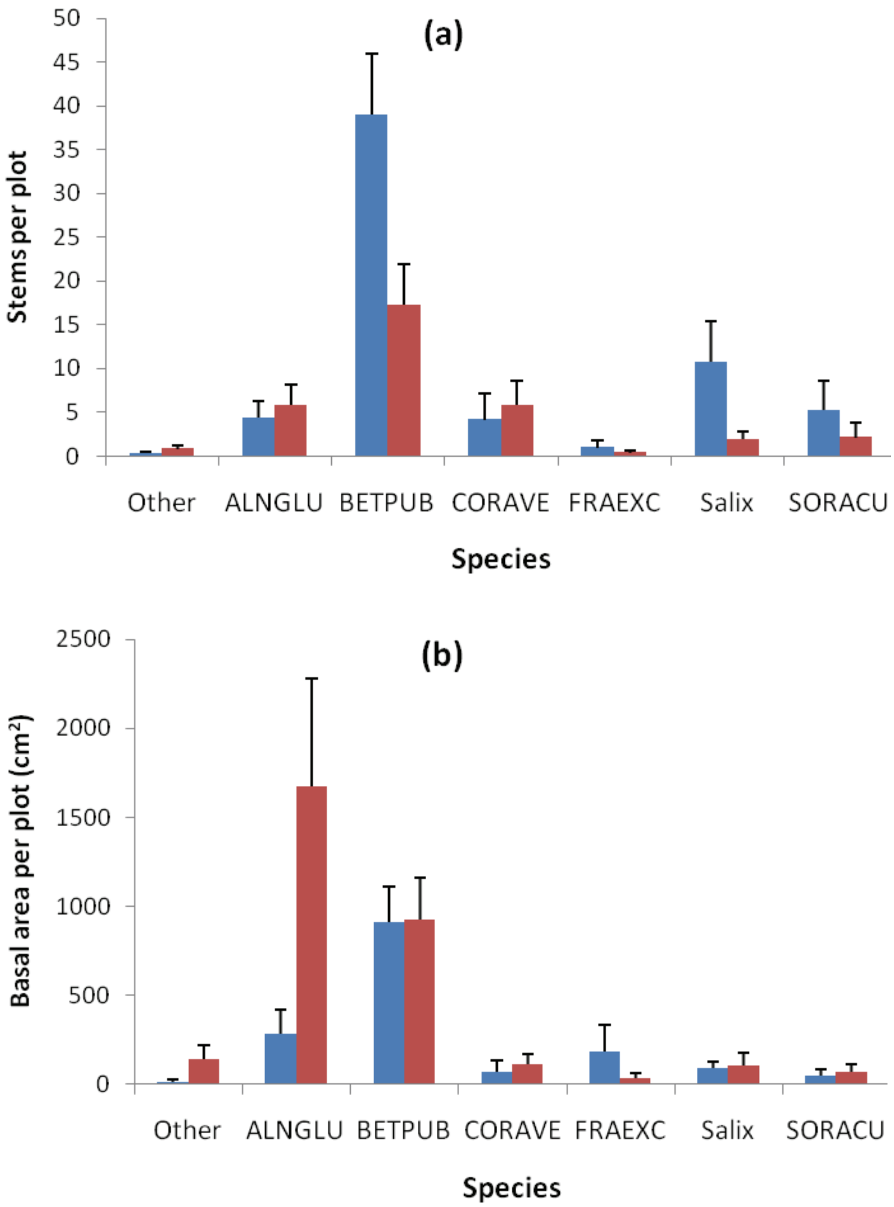

Figure 12. (a) Mean number of stems per plot and (b) mean total basal area of each tree species in plots without (red bars; n = 47) and with (blue bars; n = 18) evidence of beaver browsing. Error bars indicate 1 standard error; species codes from table 3.

Figure 13 illustrates how beaver effects varied with plot proximity to water. After correcting for the different numbers of plots at different distances from the water, approximately 72% of trees affected by beavers were found within 10 m of the water's edge. The equivalent value calculated in November 2009 was 80%, and this difference may suggest that beavers now have to move further from the water to find preferred trees. The greatest effect was observed between 6 – 10 m from the water, rather than in the plots right at the water's edge. Beaver effects observed in the plots 26 – 30 m from the water accounted for 12% of effects seen; in November 2009 these accounted for less than 5% of beaver effects. It should be noted, however, that trees affected at this distance were almost exclusively *Salix*, and some of these were growing in flooded areas.

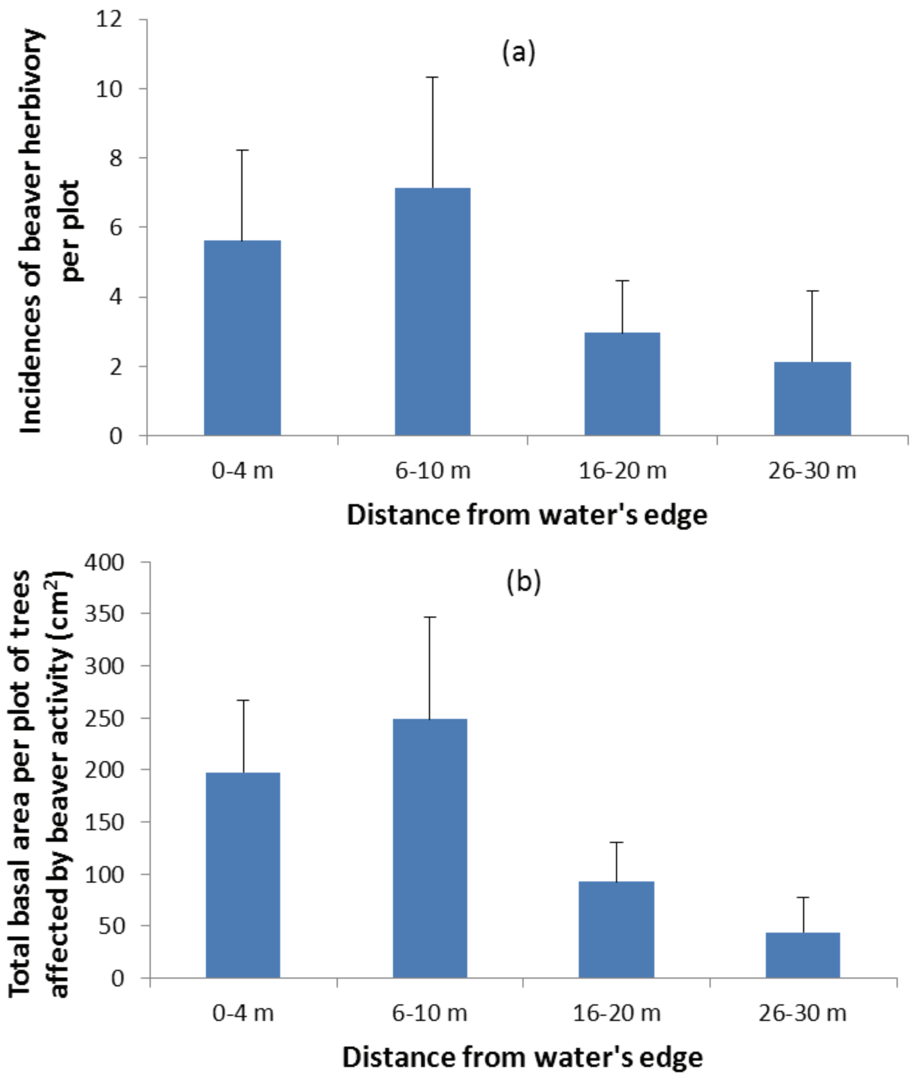

Figure 13. Distribution of beaver effects, shown as mean number of incidences per plot and mean total basal area of affected trees, against distance from water's edge. Error bars indicate 1 standard error.

4.4.3 Use of tree species by beavers

Different tree species differ in their abundance and spatial distribution at Knapdale but also in their suitability as food sources for beavers. Consequently, it is expected that the proportional use of preferred species should be greater than their proportional availability and conversely that that of avoided species should be less than their availability. It is clear that the majority of direct beaver effects observed at Knapdale were on *B. pubescens*.

Figure 14 shows that although fewer individual stems of *B. pubescens* were browsed than suggested by its availability, the total basal area browsed was greater than expected. This suggests that beavers tended to favour large birch trees over the small birch trees typical of thickets of birch regrowth. Figure 14 also strongly suggests that *A. glutinosa,* and large trees in particular, were avoided by beavers, while *Salix* and *S. aucuparia* were fairly strongly preferred. *F. excelsior* was used at a rate similar to its abundance, while *C. avellana* was used much less than its abundance would suggest, and when it was used, only very small branches were gnawed. It should be noted however that the availability of hazel is somewhat misleading, because it is less widespread than other tree species. Where it occurs, very large numbers of small stems were often recorded growing from a small number of stools.

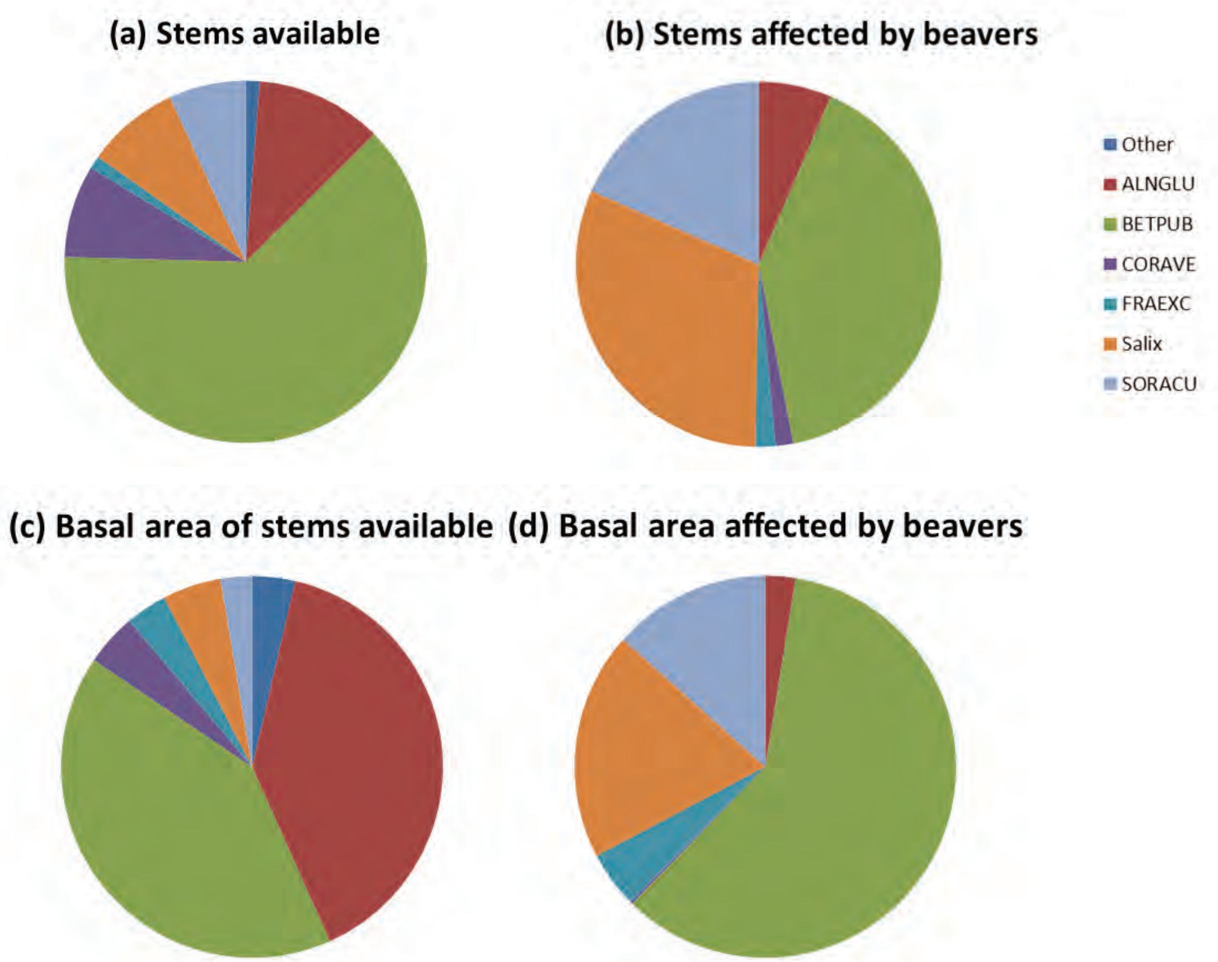

Figure 14. Proportional composition by species of (a) total number of stems in plots at Knapdale and (b) total number of these stems gnawed by beavers attributable to major tree species, and proportions of (c) total summed basal area of stems in plots at Knapdale and (d) total summed basal area of these trees chewed by beavers. Species codes can be found in table 3.

Figure 15 shows for each species the proportion of beaver-affected trees with either all, most, or a small amount of bark removed. These data provide an indication of whether some trees were more likely to be abandoned after beavers had started gnawing them, but before the tree was felled. For *B. pubescens, A. glutinosa, C. avellana* and *F. excelsior*, about 20% of affected trees were abandoned by beavers before they were completely felled. *Salix* and *S. aucuparia*, however, were nearly always completely felled once the beavers had commenced. This supports other evidence suggesting that *Salix* and *S. aucuparia* are preferred species. It may also suggest that they are easier to fell.

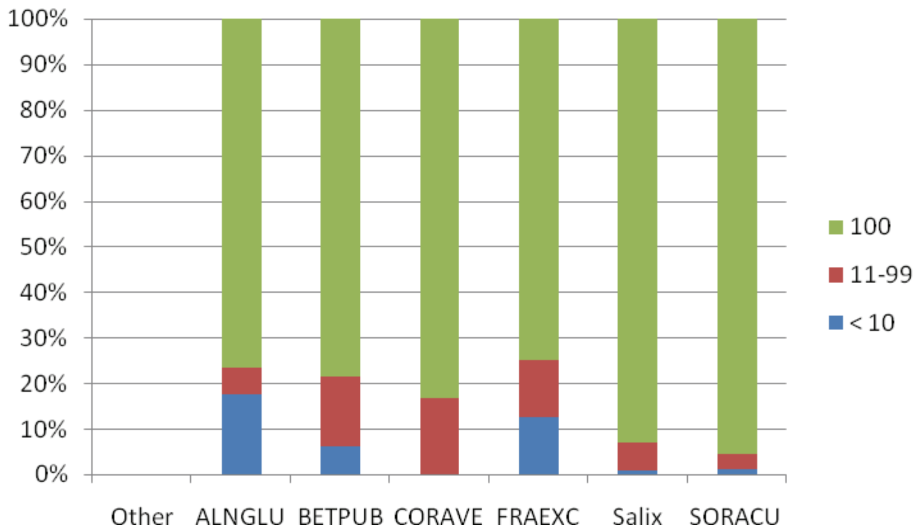

Figure 15. Percentage of trees directly affected by beavers in each of three classes of percentage bark removed, by species. Trees for which 100% of bark has been removed were nearly always recorded as beaver stumps (BSt), trees with 11 – 99% of bark removed were partially felled (BP) or beaver-affected, upright trees (BUp), and trees with < 10% of bark removed were beaver-affected upright trees (BUp).

Because beavers show a preference for trees closer to the water, the distribution of tree species relative to the water's edge will influence their exposure to beavers. Figure 16 shows the proportion of trees of each species affected to varying extents by beavers at the four different distances from the water's edge.

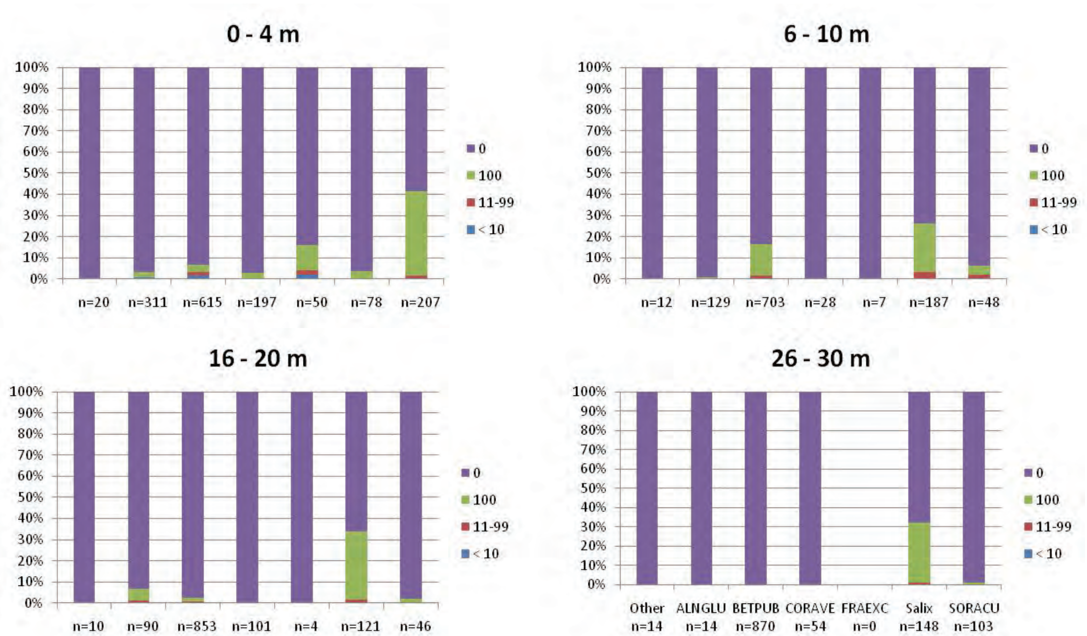

Figure 16. Percentage of trees affected by beavers, as indicated by % bark removed, at four distances from water. Trees with 100% bark removed are stumps of completely felled trees. Species order is the same for all graphs.

Half of all rowan trees observed were in the plots closest to the water, and less than two years after the release of beavers, more than 40% of these trees had been felled. The figure is almost identical if considered in terms of basal area. Large rowan stumps are often gnawed right to the ground by beavers, removing all bark and probably reducing the possibility of resprouting, and given the rate of removal to date, it seems that large rowan trees at the water's edge may be eliminated from this very narrow strip. However, as rowan trees further away from the water were rarely affected by beavers, this is likely to have only a very small effect on the abundance of rowan more widely. A very high proportion of stems of *Salix* species have also been affected. In their case, the opposite pattern was observed: trees growing at the water's edge (often in the water) were less used than trees further inland, of which 25 – 30% of stems were affected. This likely reflects the fact that willows are more common in wetter or even flooded areas, where beavers are more comfortable foraging away from the main water bodies.

4.4.4 Use of individual trees by beavers

The ultimate effect of beavers on woodland structure at Knapdale will be strongly influenced by which individual trees beavers fell. Figure 17 compares the distribution of stem diameters amongst all trees measured in the vegetation plots and among trees gnawed or felled by beavers. Numerically, the vegetation surrounding the lochs at Knapdale is dominated by small trees, reflecting the extensive areas of recent regrowth of birch, in particular, described by Brandon-Jones *et al.* (2005). The median and mean tree diameters in plots were 3cm and 5.3cm respectively. The median and mean diameters of trees directly affected by beavers were 4cm and 4.9cm. It seems that beavers use very small trees (diameter ≤ 2cm) less than their availability would suggest, and mostly use trees of diameter 2 – 6cm. Trees larger than 6cm diameter were used approximately in proportion to their abundance. In plots, only nine trees of diameter ≥ 20cm were observed to have been directly affected by beavers, however trees of this size and considerably larger were commonly observed both as stumps and partially felled trees throughout the trial area more widely, particularly close to the water.

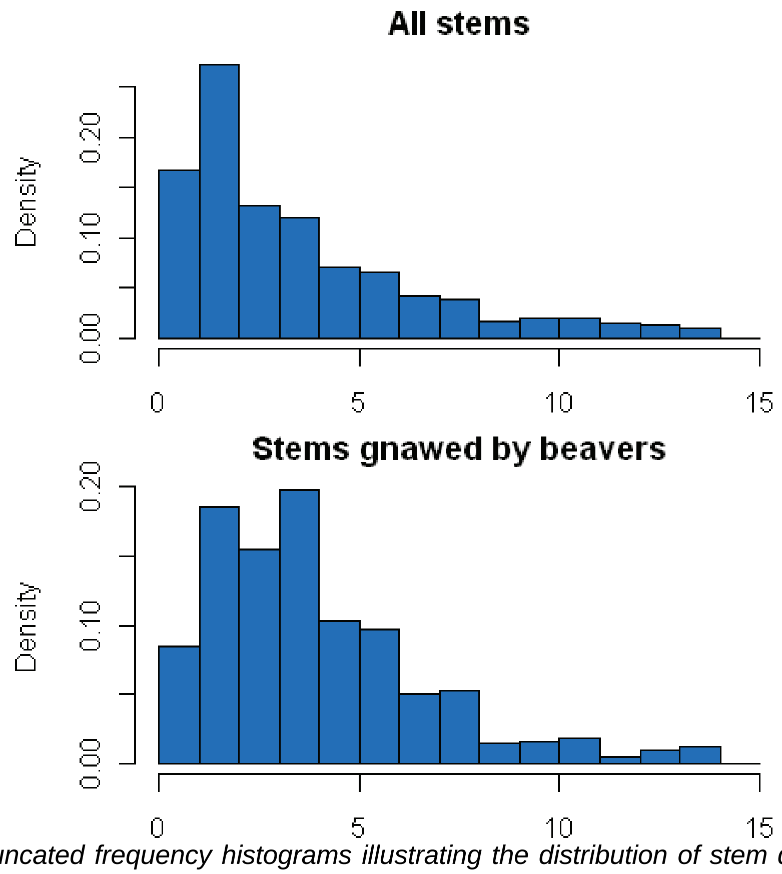

Figure 17. Truncated frequency histograms illustrating the distribution of stem diameters of all trees recorded in plots at Knapdale (above) and the distribution of stem diameters of trees gnawed or felled by beavers in the plots (below). These histograms are truncated; beavers also use some trees larger than 15cm diameter.

4.5 Resprouting and subsequent deer and beaver browsing

An important factor that will influence beaver impacts on riparian woodland in the medium to long-term is resprouting of felled trees. The key reason for monitoring the woodland twice per year is to consider browsing by deer and beavers on new shoots during the non-growing season as well as browsing and net growth during the growing season. In November 2009, no new sprouts were observed on beaver stumps in the permanent plots, and few were observed elsewhere in the trial site (Moore *et al.* 2010). There was, unsurprisingly, little change by April 2010, as the intervening period was unfavourable for plant growth. Hence, results presented here summarise patterns of resprouting on trees directly affected by beavers, in particular stumps and partially felled trees, observed in November 2010.

Figure 18 shows numbers of new shoots growing from the stumps or bases of trees felled by beavers, and figure 19 shows the average lengths of shoots from stumps and trees which had resprouted. The mean number of shoots was 4, but the median and modal values were zero. Overall, resprouting was observed on 44% of affected stumps/trees. The mean average shoot length across all resprouting stumps was 13.1cm.

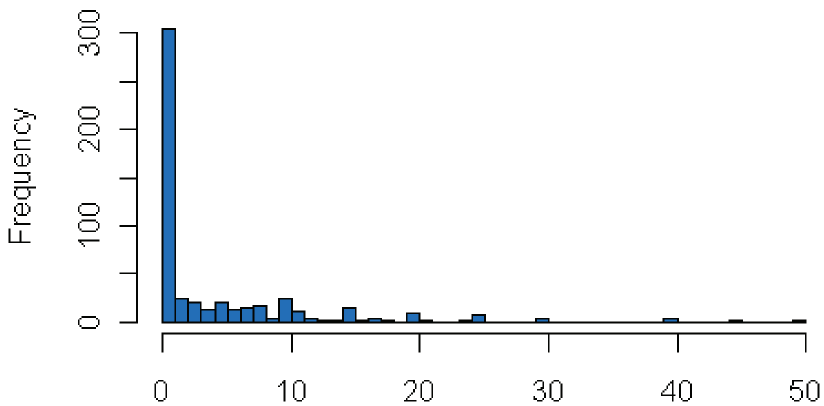

Figure 18. Histogram illustrating the distribution of numbers of new shoots observed growing from the stumps of trees previously felled by beavers in November 2010.

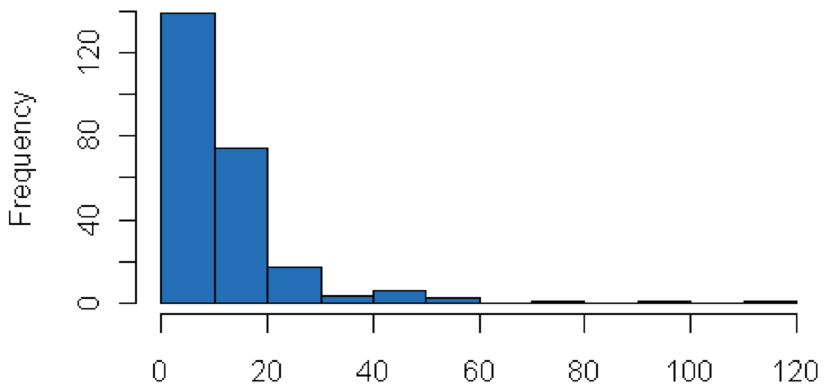

Figure 19. Histogram showing distribution of average shoot lengths (in mm) resprouting from the stumps and bases of all trees gnawed by beavers, November 2010. Instances where no resprouting was observed are not included.

Figure 20 shows resprouting by species and shows some clear differences. Ash, willow and rowan are reliable resprouters and usually produce several long, thick shoots. About half the affected birch had resprouted by November 2010, producing moderate numbers of fairly short, thin shoots. These sprout densely from the stump and many of them seem to senesce rapidly. Hazel is thus far a fairly poor resprouter, and alder is very poor.

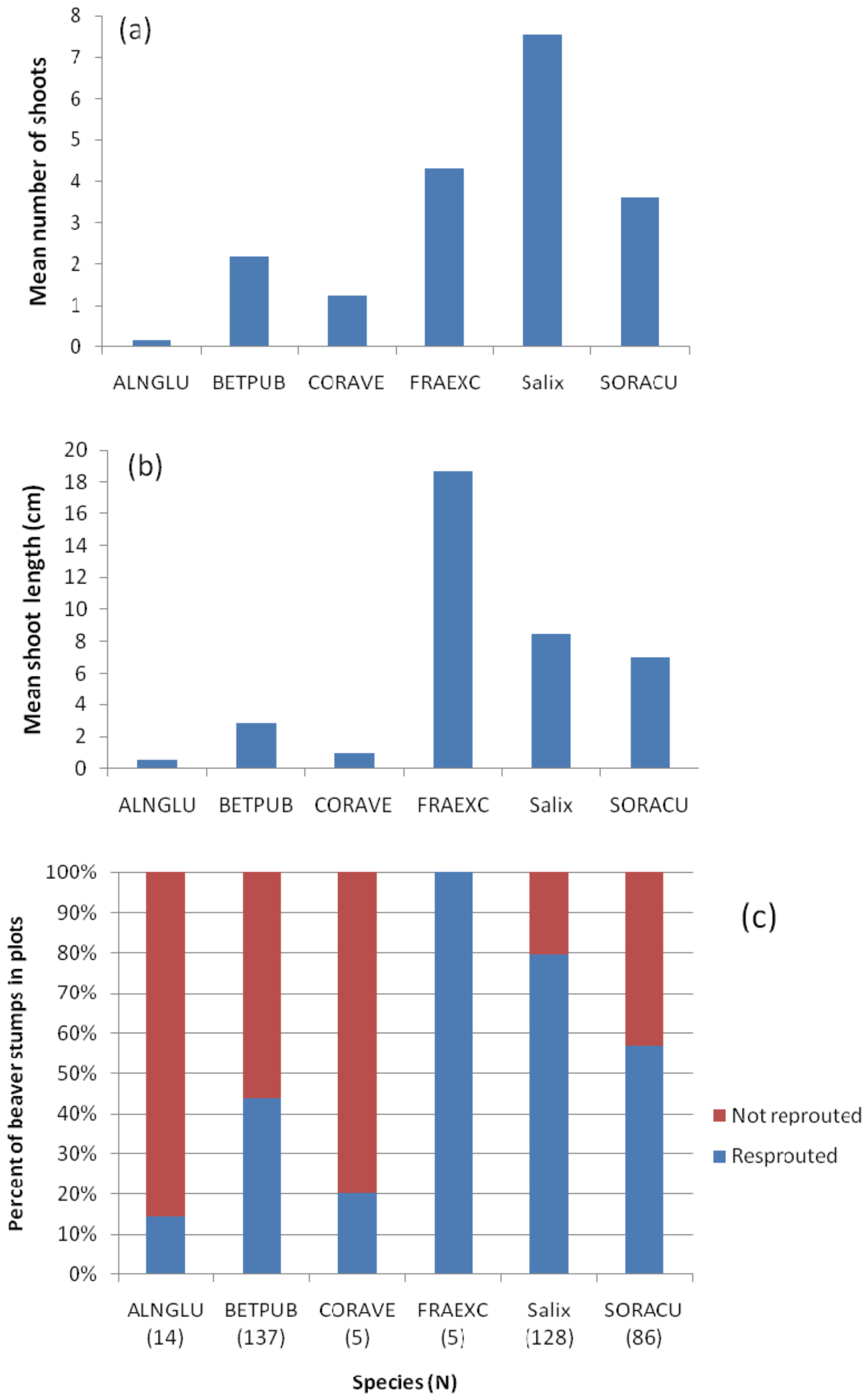

Figure 20. (a) Mean number and (b) mean length of shoots in cm observed growing from stumps and base of trees gnawed by beavers in November 2010 and (c) percentage of beaver stumps with and without new resprouting shoots. Number of stumps observed is indicated under each species label.

Figure 21 illustrates resprouting from a variety of species at Knapdale. During November survey, it was difficult to be sure which shoots had been browsed, as many shoots, particularly birch, had withered below the point of browsing. It was also difficult to be sure of the herbivore responsible or to distinguish browsed shoots from shoots that had died for other reasons. Many shoots which had died back were snapped, sometimes with the tip still attached, in a manner suggesting physical disturbance other than browsing.

Figure 21. Resprouting stumps of trees previously felled by beavers. Clockwise from top left: Bird cherry, *Prunus padus*, on Loch Linne; resprouting rowan stumps near Dubh Loch; Dormant ash sprout

with a withered tip, April 2011; dormant willow shoot with uncertain browsed status; resprouted rowan shoots browsed by a beaver, April 2011; resprouting rowan.

Although not discussed in this report, monitoring in April 2011 has found resprouting on beaver-affected stumps to have become more widespread at Knapdale in parallel with the increase in availability of resprouted shoots. Furthermore, these signs of recent herbivory by both deer and beavers are more readily distinguishable both from each other and from non-browsing shoot damage, probably because browsing had occurred outside the growing season, when shoots were already dormant and consequently the shoots have not withered in response to browsing.

4.6 Seasonal differences in beaver effects

Because trees in the plots are individually permanently marked and monitored for the duration of this study, all beaver effects that occur after initial marking of these trees can be detected. Because a large proportion of plots were not established until April 2010 (and even November 2010), the comparison here considers only sites that were established in November 2009. Table 5 shows the number of incidences of six different types of browsing events (e.g. the transition from a standing tree (Up) to a beaver stump (BSt) during two periods: that from November 2009 to April 2010 (non-growing) and that from April 2010 to November 2010 (growing). The most common transition observed was from standing tree → beaver stump. More standing tree → gnawed standing tree transitions were observed in the non-growing period, but more standing tree → beaver stump transitions were observed in the growing period. More beaver effects were detected in the growing period (n = 91) than the non-growing period (n = 73), but this is in line with the fact that the growing monitoring period was longer than the non-growing one. The greatest proportion of observed transitions involved *Salix* trees.

Table 5. Numbers of stems that changed status between monitoring session, by species. Period 1 was between November 2009 and April 2010, Period 2 was between April 2010 and November 2010. Species codes are summarised in Table 3. Stem status codes are summarised in Table 4.

	Species	ALNGLU		BETPUB		CORAVE		FRAEXC		Salix		SORAUC	
	Period	1	2	1	2	1	2	1	2	1	2	1	2
Change of stem status	Up→BUp	1	0	4	2	2	0	1	0	6	2	0	0
	Up→BP	0	0	2	1	0	0	0	0	1	3	1	0
	Up→BSt	1	3	6	10	0	0	0	1	29	47	8	2
	Up→gone	0	1	5	6	0	0	0	1	1	1	0	0
	BP→BSt	0	0	2	0	0	0	0	1	0	0	0	0
	BUp→BP	0	0	3	0	0	0	0	0	0	0	1	0
	BUp→BSt	0	0	1	0	0	0	0	0	0	5	0	0

4.7 Comprehensive mapping of beaver effects: Creagmhor Loch

By November 2010, beavers were well-established in Creagmhor Loch, and their effects could be readily detected around the loch (figure 22). By that monitoring session, 549 beaver-affected trees had been detected and marked around Creagmhor Loch (figure 23), and the species identities of each tree's five nearest neighbours was also recorded. These are mapped in figure 24. Table 6 shows how many partially felled trees, beaver-affected upright trees and beaver stumps of each species were found. Beaver stump (BSt) was the most common category of affected trees, and birch the most commonly affected species. Table 7 shows the mean diameter and total basal area of affected trees of each species. Birch trees accounted for about half of the total affected basal area, and rowan trees accounted for a quarter, although they made up a smaller proportion of the number of affected stems. Rowan stems affected by beavers tended to be larger than affected trees of other species.

Figure 22. The western shore of Creagmohr Loch.

A comparison of the species of trees used by beavers and of neighbouring trees is shown in figure 25. Rowan and willow were used more often than expected from their abundance, and birch rather less, reflecting the results of the permanent vegetation plots. Figure 26 shows distances from the water of affected trees; 77% were within 10m of the water's edge, although ten were about 50m from the water. NB around much of the loch, beaver foraging is constrained by the presence of conifer plantations beginning 10 – 20m from the water.

Table 6: Numbers of beaver-affected trees of each species in each of three status classes observed around Creagmhor Loch, November 2010.

	BP	BUp	BSt	all
ALNGLU	0	2	18	**20**
BETPUB	27	16	179	**223**
CORAVE	1	5	57	**63**
FRAEXC	0	0	7	**7**
Salix	3	7	155	**165**
SORAUC	3	2	66	**71**
TOTAL	**34**	**32**	**482**	**549**

Table 7: Mean diameter & total basal area of 6 species of tree used by beavers around Loch Creagmhor

	mean diameter (cm)	total basal area (cm^2)
ALNGLU	4.0	491
BETPUB	6.9	11 429
CORAVE	4.1	1 355
FRAEXC	4.1	121

Salix	4.9	3 976
SORAUC	8.4	6 489
TOTAL		**23 864**

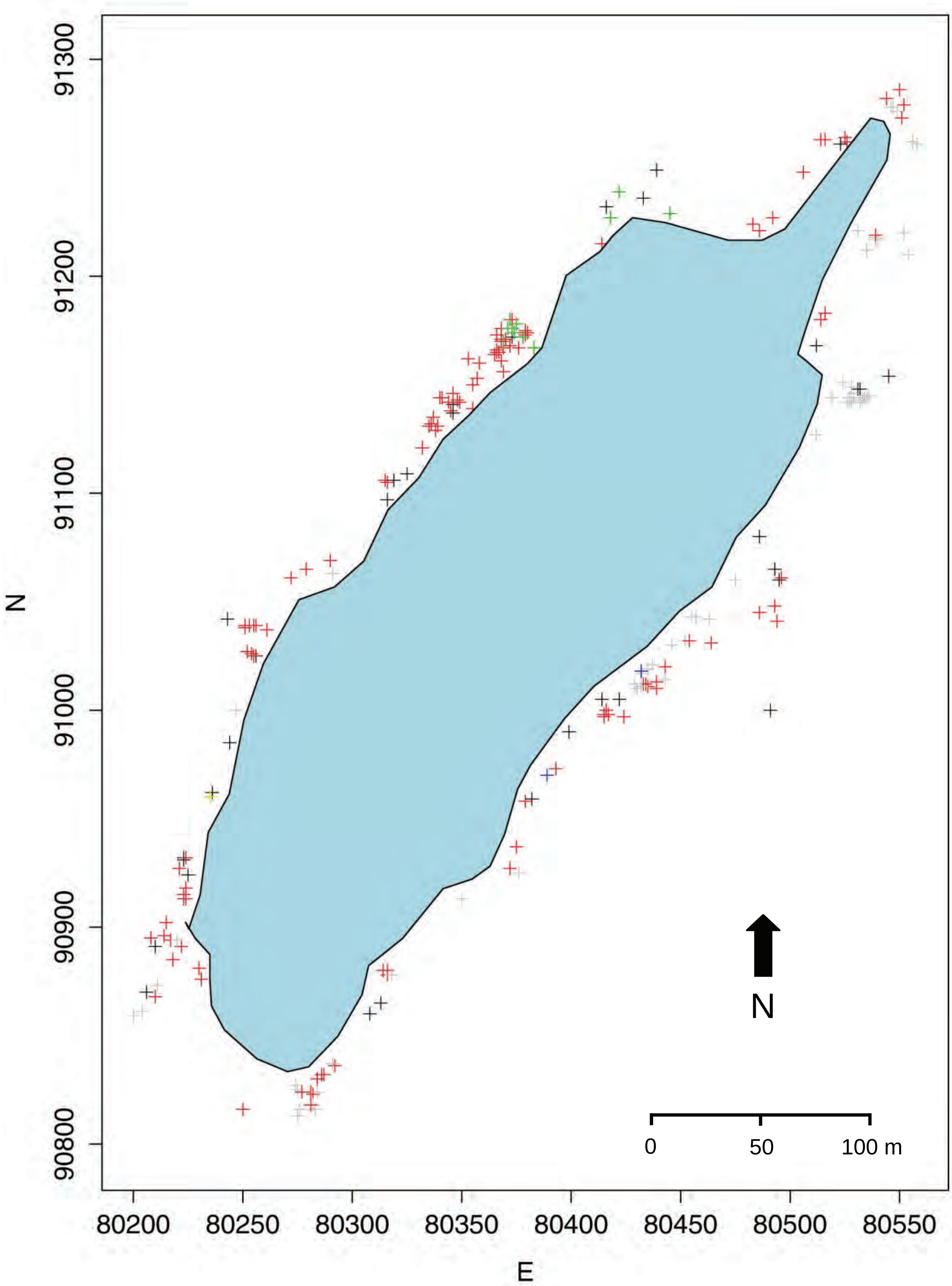

Figure 23. Beaver-affected trees marked on Creagmhor Loch, November 2011.

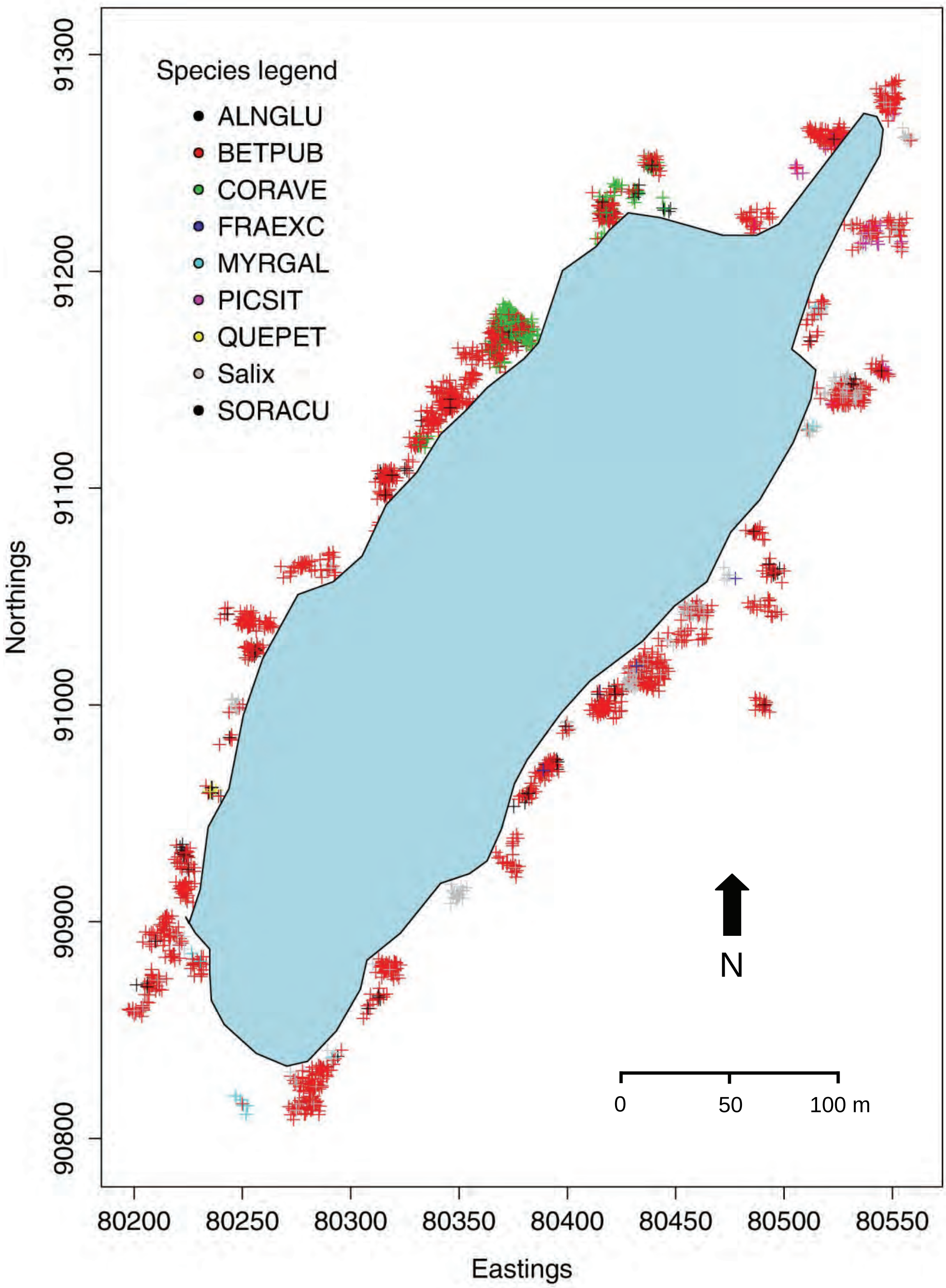

Figure 24. Trees neighbouring each beaver-affected tree surrounding Creagmhor Loch, November 2010. These trees were mapped by jittering the recorded locations of the beaver-affected trees which they neighbour

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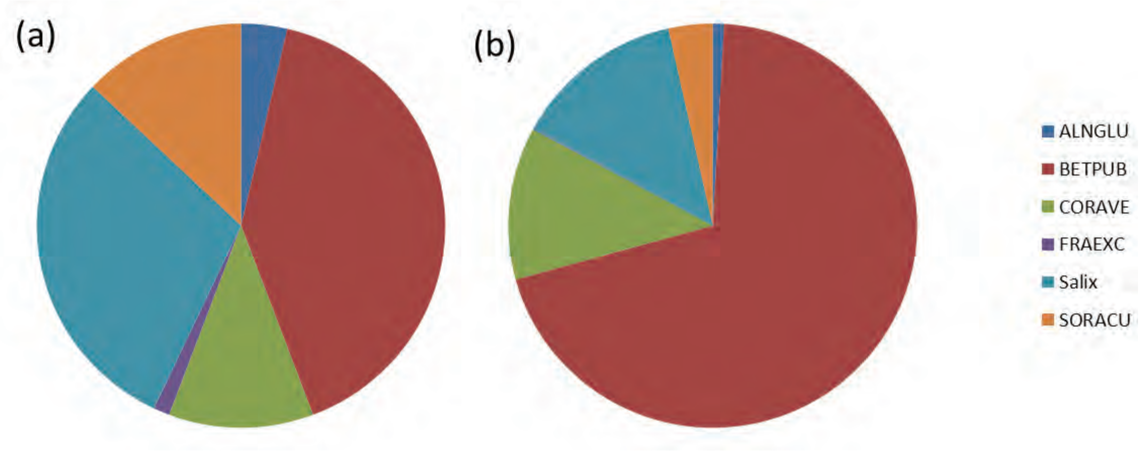

Figure 25. Tree species composition (by number of stems) of trees (a) affected by beavers and (b) of trees neighbouring affected trees, around Creagmhor Loch, November 2010.

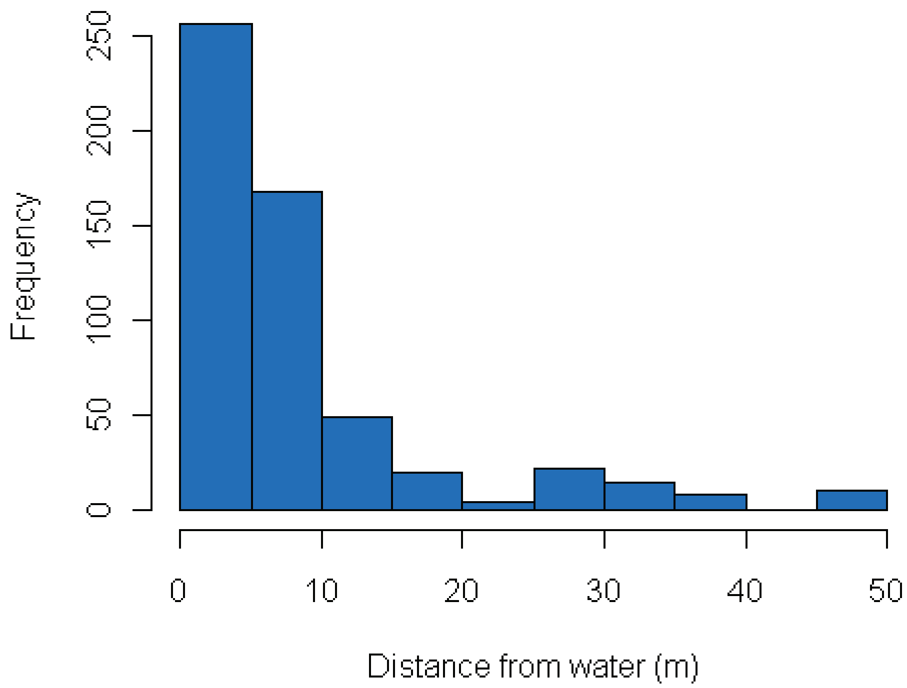

Figure 26. Histogram showing distribution of distances from water of all observed beaver impacts on trees around Creagmhor Loch.

5 DISCUSSION

The fieldwork reported here was conducted 12 and 18 months after the initial reintroduction of beavers to Knapdale in early summer 2009. Over that period there has been some variation in the numbers and locations of beavers, so any interpretation of trends in beaver foraging patterns should still be treated with some caution. Beavers had gnawed and felled a substantial number of trees in marked plots by November 2010, presumably partly for immediate consumption of their inner bark, twigs, shoots and leaves and partly for construction of lodges and dams and for caching under water. Food caching is a behavioural characteristic that is advantageous to beavers that regularly experience harsh winters and for which access to food resources is restricted by ice for long periods, as was the case for the reintroduced beavers in their former home, Norway. In one study in Massachusetts, the median date at which American beavers (*Castor canadensis*) commenced food caching behaviour was week 41, i.e. early October (Busher, 2003). The limited information available to date suggests that beavers at Knapdale used trees at very similar rates throughout the year observed. This may reflect the fact that these animals are still very actively building lodges and in at least one case, a dam.

The effect of beavers at Knapdale already extends beyond the direct effects of gnawing and felling of trees. A substantial area has been flooded by a beaver dam at Dubh Loch and vegetation changes can be expected in the flooded woodland. Beavers browse throughout the flooded area, further from Dubh Loch than would otherwise be expected. Flood-tolerant species such as willows and alder may survive there while less flood tolerant species may die but persist for some time as standing dead timber. Ultimately, the vegetation may shift from broadleaf deciduous woodland to swamp or bog.

5.1 Woody vegetation at Knapdale

Ideally, this woodland monitoring program would have commenced with a survey of baseline vegetation conditions in the plots before beavers were reintroduced. Uncertainty surrounding several aspects of the releases made this impractical, however. For example, the precise locations of the artificial lodges used for the releases was not known long in advance and the use of space by beavers post release could not be confidently predicted, making siting of transects too speculative to be justified. Despite the absence of such baseline data, the persistence of stumps of trees felled by beavers prior to the first survey has allowed the reconstruction of an almost complete picture of woodland structure and species composition prior to the release. All stumps of trees felled by beavers in vegetation plots were identified, tagged and measured. Estimates of stem density and total basal area in each plot will only differ from the true baseline figures if trees branched above the site of beaver gnawing but below 20cm. Other measures that may have changed from their baseline values since the beavers' introduction include estimates of canopy cover, estimates of horizontal vegetation density and estimates of ground cover, particularly where beavers had caused flooding or canalisation. Any direct effects of beavers on trees that have occurred since monitoring plots were established will have been detected.

Since the previous report (Moore *et al.* 2010), the number of monitoring plots at Knapdale has been almost doubled, however the mixture of woodland types included has not changed substantially. The most numerous tree species in vegetation plots, by a considerable margin, was *B. pubsecens*. Dense stands of young regrowth of this species, as well as larger, old trees, occur throughout the area. In many places birch has rapidly colonised areas from which conifer plantations were removed to meet Natura Special Area of Conservation obligations in earlier years. These early successional woodlands are dynamic communities and it will be of great interest to monitor their development in the presence of beavers. *A. glutinosa* is also widespread and common at Knapdale, but in contrast to *B. pubescens*, it occurs primarily as large trees at the water's edge, and for this reason accounts for a similarly large proportion of total tree basal area. *Salix* spp., *C. avellana, F. excelsior* and *S. aucuparia* were also common in plots and have previously been identified as important components of European beaver habitat elsewhere in Europe (Haarberg & Rosell, 2006, Macdonald *et al.* 1997).

5.2 Beaver browsing preferences and effects

Because the positioning of transects was partially guided by pre-existing beaver herbivory, the plots selected are not an entirely unbiased sample of loch shore, however the number of transects established at Knapdale is now such that all vegetation types are represented and a clear picture of beaver preferences is emerging.

Based upon a comparison of used to available tree sizes, the preferred tree size for beavers was from 3 – 6cm diameter, and smaller trees were less preferred, although still commonly used. Beavers also used larger trees. Affected trees up to 30cm diameter were detected in plots, but outwith the plots many still larger trees were also observed to have been affected. A study of foraging by beavers in Telemark, Norway (the source of the reintroduced beavers) found that beavers there tended to use smaller trees than is the case at Knapdale to date (Haarberg & Rosell, 2006). In Telemark, 95% of cut stems were ≤ 5cm diameter and these accounted for 47% of the basal area affected, whereas only 70% of cut stems were ≤ 5cm at Knapdale, accounting for only 15% of affected basal area. This difference may reflect the fact that the habitat at Knapdale has no recent beaver browsing history, whereas past beaver effects in Telemark may have resulted in fewer large trees being available to foraging animals. This has some implications for the woodland structure. First, beavers may not, at least so far, be playing a strong direct role in thinning the dense birch regrowth stands around the lochs which often comprise very small (diameter 1 - 2cm) trees, and second, their focus on larger trees may significantly reduce the standing biomass of these communities and increase the amount of light reaching smaller trees and the ground. It is clear that beavers will fell or attempt to fell even very large trees.

Results suggest that beavers are showing a strong preference for willow and rowan, and that they avoid alder. However, other trees are used largely in proportion to their availability. Haarberg & Rosell (2006) found in Telemark that beavers' species preferences could be ordered willow > rowan > birch > *Prunus* > others > alder > conifers, which is almost perfectly consistent with the patterns observed at Knapdale. Note that the alder present in Telemark is *Alnus incana,* not *A. glutinosa*.

Results to date confirm observations from other populations that beaver effects are confined to areas close to water, primarily within 10 m of the shore, although beaver effects were distributed slightly further inland in this monitoring period compared with the previous (2009) period, and effects have been recorded up to 50 m away from the lochs. Where conditions allow, beavers will feed from the water on overhanging branches and trees growing right at the water's edge. Opportunities for this type of feeding seem to be limited at Knapdale, as loch shores are sometimes steep or rocky and often are vegetated with large mature trees such as birch and alder rather than by dense thickets of preferred tree species such as willow or aspen. Many parts of Knapdale are not suitable for assessing how far beavers forage from the water, because the narrow strip of broadleaf woodland is hemmed in by dense conifer plantation. Nonetheless, continued monitoring will reveal whether beavers venture further inland as foraging opportunities close to the water become fewer or as the populations expand and/or young animals disperse. One striking observation supported by casual observations as well as by plot data is that foraging beyond 20 m from the water was primarily (and exclusively, in the case of the plots), targeted at *Salix* trees.

At some places in Knapdale, although rarely in monitoring plots, substantial numbers of trees partially or completely cut by beavers remain partially upright, supported by neighbouring vegetation. This is most common in areas of dense vegetation, such as along the south-western shore of Loch Linne. In most areas, however, the majority of felled biomass has been removed for construction, caching or eating elsewhere, or consumed on the spot by beavers. Even some very large trees have been almost entirely removed, as illustrated in figure 8. As a consequence, the riparian woodland is not generally becoming cluttered with dead wood, and indeed in parts it is beginning to feel more open, particularly when larger, spreading, waterside trees are removed. Waterside rowans seem to have been particularly affected by beaver activity, with 40% of trees and basal area of this species having been felled in plots within 4 m of the water.

At this stage it is too early to draw any firm conclusions about the longer-term response of woody vegetation to beaver browsing, however 44% of beaver–affected trees showed evidence of resprouting by November 2010. By contrast, no resprouting was observed in November 2009. This indicates a substantial lag between tree felling and resprouting for most trees, and it should be borne in mind that many stumps recorded in 2010 will have been felled only a short time prior to recording, so many of the 56% of trees with no new shoots may yet resprout. Timing and likelihood of resprouting may also be sensitive to the time of year at which beaver impacts occur. It was observed that the stumps of many large, older trees, particularly of rowan and birch, have failed to resprout even if they were felled prior to November 2009. Because in many cases beavers have de-barked these stumps right to ground level, the prospect of these trees resprouting may be reduced. Rowan, willow and ash are proving to be vigorous resprouters, and provided that subsequent herbivory on these shoots is sustainable, they may survive well. Summer and autumn of 2011 should provide telling information on the impact of herbivores, particularly deer, on these shoots.

In 2010 another approach to determining beaver browsing preferences was included in addition to the use of permanent vegetation plots. The mapping of every beaver-affected tree around Creagmhor Loch largely confirmed the picture that had emerged from the plots concerning the sizes of trees used by beavers, their species preferences and the distance at which they forage from water. The data collected may provide further insight if subjected to spatial analysis of beaver effects and a formal analysis of species preferences based upon comparisons of focal trees with neighbouring trees. However such an analysis has not been possible to date due to time and financial constraints.

5.3 Assessment of monitoring methodology and future monitoring plans

The permanent woodland monitoring plot methodology is serving its purpose well. Tree tags and plot markers have proved robust and durable. Some transects established on Lily Loch and Loch Coille-Bharr are arguably of marginal interest now that beavers have established patterns of movement focussed on other lochs, however low-level beaver activity continues to be detected on these lochs (as of April 2011) and they will continue to be monitored for the duration of the Scottish Beaver Trial.

Flooding has continued to make some areas difficult to access on occasion. One plot established in flooded woodland at the Dubh Loch in April 2010 has not been safely accessible since. Both in this plot and in others around the Dubh Loch, high water levels have also made it difficult to read tree tags when they are submerged. During fieldwork in November 2010, water levels in the Lily Loch were observed to fluctuate very dramatically over a timescale of hours during a week of frequently heavy rain.

The monitoring visit to Knapdale following the monitoring reported here is taking place from 28 March – 15 April 2011.

6 CONCLUSIONS

By November 2010, 31 transects had been established around the shores of Loch Coille-Bharr, Dubh Loch, Loch Linne, Loch Fidhle, Creagmhor Loch, Lily Loch and Lochan Buic at Knapdale. Transects extended 30 m inland from the shore and most comprised four 4 × 10 m permanently marked plots. In each plot, all trees, stumps and branches, dead or alive and standing or felled (3026 in total) were permanently marked with uniquely numbered metal tags, identified to species (or for *Salix*, genus), and their diameter measured. All beaver effects on these trees were recorded. More than half of these plots were established in November 2009 and have now been monitored in three periods. These plots will continue to be monitored biannually throughout the Scottish Beaver Trial to describe the effects of beavers on woodland structure and composition.

At least 16 tree species were recorded from plots, but only six occurred in substantial numbers. These were *B. pubescens, A. glutinosa, C. avellana, F. excelsior, S. aucuparia* and *Salix* spp. Most plots were dominated by *B. pubsecens*, often in conjunction with one or more other species.

By November 2010, beavers had been present at Knapdale for 17 months and had produced noticeable effects on woody vegetation. Trees had been gnawed or felled by beavers in 35/111 plots, and in those plots, a mean of 21% and a maximum of 64% of the stems present had been affected. Most effects were observed on transects less than 500 m from active beaver lodges. Plots used by beavers included more *B. pubescens* and *Salix*, but less *A. glutinosa* than an average plot. Although beaver effects were detected to greater distances from the shore, 72% of effects occurred within 10 m of the water. Although *B. pubescens* accounted for the greatest proportion of trees browsed by beavers, *Salix* and *S. aucuparia* also made very substantial contributions. Between them, these three species accounted for most of the trees felled by beavers at Knapdale. Beavers show particularly strong preferences for *Salix* and will travel further inland to browse it than they will for other species and for *S. aucuparia*. Large *S. aucuparia* trees growing at the water's edge are particularly favoured and 40% of these have been removed from plots. Although it is browsed occasionally, beavers also appear to avoid *A. glutinosa*. Beavers in plots affected a substantial number of large trees, although they mostly favoured trees of diameter 3 - 6cm.

44% of trees felled by beavers were resprouting with new shoots by November 2010. *Salix*, *F. excelsior* and *S. aucuparia* were particularly vigorous resprouters. The structure of riparian woodland at Knapdale in future will be strongly influenced by the interaction between the growth of new shoots from beaver stumps and subsequent browsing of these shoots by deer and beavers.

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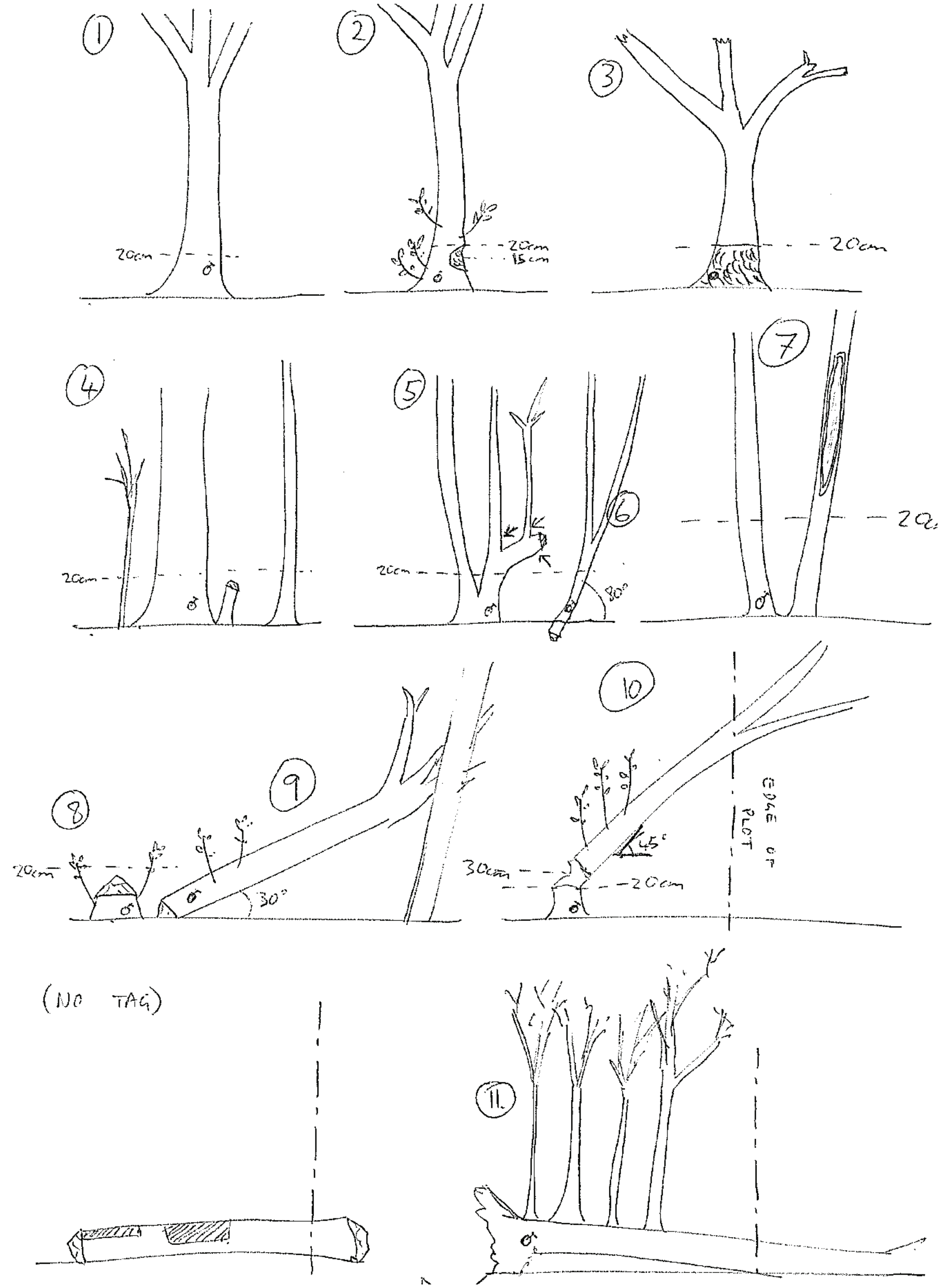
8 APPENDICES

APPENDIX 1. Reference illustrations used in the field encompassing most tree, stump and log forms encountered with various types of beaver effect. Accompanying example datasheet with entries corresponding to numbered illustrations.



Scottish Beaver Trial: Woodland Monitoring. 302-460. Autumn 2009. Version 2.

Loch: COILLE BHAR Transect: 7 Distance: 0 to 4 m. Page 1 of 1
Plot Tag: 235

Tag No.	Species or count	Diam.(20cm)	Status	Angle	Alive Y/?/N	bark rmvd	low shoot	high shoot	avge. shoot	Deer	Beav	Height chopped	log length
#[a]	CODE	cm	[b]	deg	Y/?/N	%[c]	count[d]	count[e]	cm	0/1/2[f]	0/1/2[f]	cm	m[g]
1	SORACU	15	Up		Y	0	0	0	--	--	--	--	--
2	BETPUB	10	B, Up		Y	50	2	2	20	0	0	15	--
3	QUEPET	20	B, Up		N	100	0	0	0	0	0	20	--
4	BETPUB	15,3,1	Up		Y	0	0	0	0	0	0	--	--
	"	2	B, St		Y	100	0	0	0	0	0	15	--
5	Salix	5	Up		Y	0	0	0	0	0	0	--	--
	"	8											
	"	5, 3	Up		Y	0	0	0	0	0	0	--	--
	"	6	B, St		Y	100	0	0	0	0	0	30	--
6	"	4	B, Br	80	Y	0	0	0	0	0	0	--	3
7	SORACU	4	Up		?	0	0	0	0	0	0	--	--
		4	Up		?	deer	0	0	0	0	0	--	--
8	ALNGLU	15	B, St		Y	100	2	--	20	1	0	15	--
9	"	15	B, Log	30	Y	0	--	2	20	1	0	--	3
10	SORACU	20	B, P	45	Y	100	0	3	50	0	0	30	2
—	BETPUB	25	B, Log	0	?	20	--	0	0	0	0	--	2
11	SALCAP	30	N, Log	0	Y	0	0	0	0	0	0	--	4
		3,3,4,5	Up		Y	0	0	0	0	0	0	--	--

a: bracket paired stumps & logs; **b:** For stumps, logs & partially felled, indicate B (beaver) or N (natural) then Up=upright; St=stump; P=partially felled; Log; Branch **c:** % of circumference or % of log w/in plot, "deer" for old deer bark stripping; **d:** <30cm; **e:** >30cm; **f:** 0=none, 1=detectable, 2=significant; **g:** within plot boundaries.

APPENDIX TWO: sample plot photographs.

Plot 258:Nov 2009:

Plot 258, Nov 2010:

Plot 270: Nov 2009:

Plot 270, April 2010:

Plot 270, November 2010:

Plot 211,November 2009:

Plot 211, April 2010:

Plot 211. November 2010:

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