LUNDY CABBAGE SEED DISPERSAL, SEED BANKS AND SEED GERMINATION AFTER RHODODENDRON CLEARANCE

by
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ABSTRACT
The seeds of Lundy Cabbage are routinely dispersed in two ways: when the lower sections of the fruits dehisce and when seeds retained in the 'beak' are carried by the wind. Soil collections showed that the plant has a large seed bank and fixed point photography suggests that that the seeds can probably remain viable in the soil for at least three years. Clearance of the alien *Rhododendron ponticum* is proceeding rapidly on Lundy. The germination of Lundy Cabbage seeds was not inhibited by soil from beneath rhododendron, but germination rates were higher in soil from the slates in the SE corner of the island than from granite soils.

Keywords: *Coincya, seeds, rhododendron, allelopathy, fixed point photography*

INTRODUCTION

Lundy Cabbage *(Coincya wrightii)* is a short-lived perennial known only from the cliffs and sidelands on the eastern side of Lundy. It does not reproduce vegetatively and so relies entirely on sexual reproduction to maintain its populations and establish new ones. Larger plants produce more flowers and more seeds, with large individuals producing several hundred fruits and thousands of seeds in a season (Compton and Key, 2000). The numbers of individuals in flower has varied by about a factor of ten during the 15 years that standardized counts have been made, apparently mainly in response to fluctuations in rabbit numbers, which in turn are driven by periodic outbreaks of myxomatosis (Compton *et al.*, 2004).

The distribution of Lundy Cabbage is relatively stable, extending from beneath the Marisco Castle northwards to Gull Rock, but within this range there are sub-populations where the plant is present every year and others where it appears in some years, but not others. The latter tend to be in relatively flat areas, where the plant cannot survive during periods when grazing pressure is high. How do these transient sub-populations appear? One explanation may be simply that seeds are being dispersed away from the core populations, where some plants produce seeds every year. Most of the transient populations of Lundy Cabbage are situated within a few metres of the edges of established sub-populations. Seed dispersal is to be expected over such relatively short distances, but what is perhaps surprising is that such dispersal takes place up steep slopes, where it cannot be aided by gravity.

LUNDY CABBAGE SEEDS AND SEED DISPERSAL

The structure of Lundy Cabbage fruits ('pods') is typical of more primitive (less derived) species in the Cabbage family (Brassicaceae, formerly Cruciferae). The pods are cylindrical in cross section and are divided into two parts with a long basal siliqua. This has a central septum running its length, two dehiscent valves and a shorter terminal beak (Plate 1). Around 95% of the seeds are in the siliqua, with the beak usually containing just one or two seeds (Compton & Key; 2000). Our observations suggest that this two-part fruit structure provides Lundy Cabbage with two forms of seed dispersal. The siliqua dehisces to release the seeds, whereas those in the beak are released only as the fruit wall decays (Plate 2). Seeds in the siliqua might be expected to disperse further than those in the beak, but this is not necessarily the case. Dehisced fruits, still retaining the seeds in the beak (and occasionally also seeds in the siliqua), eventually become detached from the plants and we have seen them blown for some distance. Updrafts, from easterly winds in particular, can carry pod valves (and even whole pods) up even steep slopes. This means that some of the seeds in the beak can end up further from parent plants than seeds released during dehiscence, but those in pods that are not moved by the wind end up beneath parent plants.

Longer distance dispersal events are likely to be rare, and not observed directly. Whether Lundy Cabbage seeds could survive passage through the guts of any of Lundy's mammals is unknown, but we have seen a domestic sheep walking in Millcombe with a Lundy Cabbage inflorescence hanging from its mouth. Similar behaviour (most likely involving a goat) may explain the appearance of a single plant next to the lighthouse steps on Lametry in 2007 after Lundy Cabbage was last seen there in 1993 (in a different area). Human activity is another possible explanation for the dispersal of those plants, of course.

Given that many Lundy Cabbage grow on sea cliffs, many seeds must end up in the sea. Its continuing absence from the mainland is therefore something of a mystery. This is not due to straightforward climatic limitations (experimental garden plants in northern England grow well and can resist temperatures down to at least minus 10^{o} C: SGC personal observations), and Lundy Cabbage seeds can remain viable after contact with seawater (Rich, 1999). Furthermore, the pods and seeds also float; four from 20 pods we placed in beakers that contained seawater were still afloat after seven days, and 23 from 30 individual seeds were also still floating after the same period of immersion.

LUNDY CABBAGE SEED BANKS

Seed banks offer an alternative explanation for the appearance of new sub-populations of Lundy Cabbage, especially those that re-appear in areas occupied in the past. Seed banks are reserves of viable seeds present in the soil (Roberts, 1981). They may be transient, with seeds remaining viable just a few months (*Rhododenron ponticum* has short-lived seeds of this type), or can be persistent, with seeds that may remain viable in the soil for many years. Depending on the longevity of the seeds and the time of year, a large proportion of the total individuals of a plant species may be present as seeds. A persistent seed bank could act as a source of new Lundy Cabbage plants whenever soil disturbance stimulates germination, and would be replenished by seed rain from successfully fruiting plants.

Lundy Cabbage seed germinates rapidly under warm, moist conditions. A germination rate of 83.3% by day 31 at 20^{o} C was recorded for seeds collected by hand from the soil in January 1996 (Compton and Key, 2000). Around 25% of these seeds germinated within seven days and over 80% within 21 days. In contrast, seeds collected directly from the plants in July did not germinate immediately, suggesting that they might need vernalization (exposure to cold temperatures) or that the seed coat may require scarification or other treatment before germination is initiated.

Experimental determination of the longevity of viable seeds in the seed bank is complex and necessarily long-term. One benefit of the photographic monitoring of Lundy Cabbage has been that it revealed the re-emergence of an isolated sub-population of Lundy Cabbage beneath the castle, which had not been seen for several years. Flowering was observed in 1993, but no plants were there again until 1997, at precisely the same location. It may not be coincidental that 1996 was a year when rabbit numbers were noted as being particularly high, causing widespread soil disturbance and areas that were bare of vegetation. This result provides circumstantial evidence that a persistent seed bank is present and that seed viability in the soil can be retained for at least three years. Locations where the plant has flowered in the past may become significant in the future if the population of Lundy Cabbage populations were to crash. They would be prime sites for artificial soil disturbance to release the seed bank.

The density and distribution of viable seeds in the soil was also assessed more directly. Soil samples were collected in January 1997. Use was made of the annual fixed-point photographic records to identify three areas where Lundy Cabbage had last flowered in the immediate vicinity one, two or three years previously (South of Millcombe, Landing Beach and Victoria Beach respectively). Ten soil samples, each with a surface area 15 cm x 15 cm and depth of 10 cm, were obtained from each of the three locations (Table 1). In addition, soil was sampled at Halfway Wall along two transects extending from one of the Buttresses to the cliff edge, 60 m away. No plants had flowered on this Sideland since at least 1993 (when annual recording commenced), but Lundy Cabbage flowers every year on the buttress, and also in some years on the cliffs immediately below. Along the 60 m transects the samples were concentrated at either end, close to potential seed sources on the buttress and the cliff-side, at approximately 1, 3, 5, 10, 25, 35, 50, 55, 57 and 59 m from the buttress (the last soil sample being one metre from the cliff edge). The volume of soil sampled at Halfway Wall was larger than at the other sites, with each sample 30 cm x 20 cm x 10 cm deep.

Germination of any seeds in the soil samples followed the method of Ter Heerdt *et al.*, 1996). The soil was first passed through a 6mm sieve to remove stones and vegetation and the sieved soil was then spread out in 30 cm x 20 cm seed trays to a depth of approximately 4 mm. The soil in the trays was kept moist for six weeks and maintained under lights at 20^{o}C. Any seedlings were removed as soon as they were sufficiently large to be recognised.

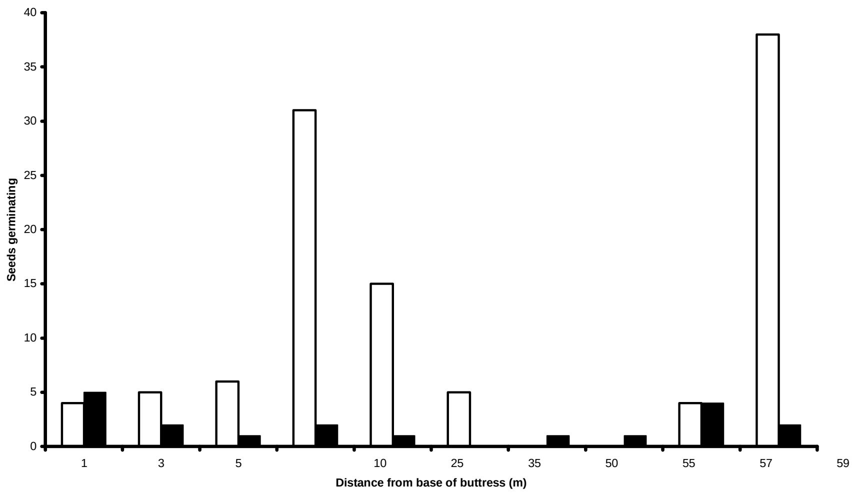
Seedlings emerged from soil collected at all of the locations, and from most of the individual samples (Table 1). Estimated densities of seeds in the soil ranged from 32-667 m^{-2}. The lower counts were from soil collected on the Sidelands at Halfway Wall, where Lundy Cabbage had not flowered for many years, if at all and the seeds will have originated either on the nearby buttress, or the sea cliffs. The numbers of seeds germinating from the soil at Halfway Wall varied greatly between samples, with generally fewer seeds detected north of the wall, and the samples with most seeds tending to be towards the two ends of the transect (Figure 1). This distribution is consistent with there being two seed sources: with seeds falling from plants flowering on the buttress, and from seeds blown up the

Table 1: Lundy Cabbage germination from soil samples collected in January 1997

Ten replicate samples were collected from each location. The total surface area sampled was 225 cm^2, except at Halfway Wall (600 cm^2). Samples from the Sidelands below the Halfway Wall Buttresses were taken both north and south of the wall.

Location	Description	Germinating			
		Mean (sample $^{-1}$)	S.D.	Range	Estimated mean density (m^{-2})
Landing Beach	Grassy slope below castle	15.00	10.10	1-32	667
Victoria Beach	Close to sea level	8.80	4.94	3-16	391
S. of Millcombe	Grassy slope among rocks	13.10	10.46	2-30	582
Halfway Wall (S.)	Slope between buttress and cliff	10.80	13.26	0-38	180
Halfway Wall (N.)	Slope between buttress and cliff	1.91	1.52	0-5	32

Figure 1: The numbers of Lundy Cabbage seeds that germinated from soil samples collected parallel to Halfway Wall between the buttresses and the sea cliffs 60 metres below. Open bars south of the wall, closed bars north of the wall



slope from the plants growing at or below the cliff edge. Normally these seeds never result in mature plants, because of grazing, but flowering occurred within a year of a rabbit and stock exclosure being erected in the same area, just south of Halfway Wall.

The germination technique we used provides a good indication of the densities of seeds that are available for immediate germination in the soil, but does not necessarily record all the seeds that are present (Brown, 1992). Our results will therefore have underestimated the Lundy Cabbage seed densities. Even so, quite impressive seed numbers were detected, even at locations where flowering had not taken place the previous year or years. This, together with the fixed-point photography, suggests that there is a persistent seed bank for Lundy Cabbage. The results from Halfway Wall also suggest that seed can be dispersed for distances of at least 30 m. Whatever the relative contributions of seed persistence and dispersal, it is clear that Lundy Cabbage seeds are abundant in the soil, and are not restricted to areas where the plant flowered recently.

LUNDY CABBAGE REGENERATION AFTER RHODODENDRON CLEARANCE

Rhododendron ponticum is an evergreen alien shrub reaching around 5 m in height. It produces huge numbers of tiny seeds, with a single plant capable of producing a million or more each year (Cross, 1975). These seeds can be dispersed several hundred metres by the wind, but it believed that there is no persistent seed bank (Cross, 1975). Rhododendron produces dense shading and litter, acidifies the soil and may also release toxins into the soil (Richardson *et al.*, 1998, Nilsen *et al.,* 1999, Nilsen, 2002). This combination results in the exclusion of virtually all other plant species (other than mosses) from beneath rhododendron stands on Lundy, including Lundy Cabbage.

Rhododendron was introduced to Lundy as an ornamental in the early 19th Century (Marren, 1973). A major fire on the eastern side of the island in 1926 apparently led to the establishment of several large patches that are still present. Rhododendron has been seen as the main threat to the continuing survival of Lundy Cabbage (Compton *et al.,* 1999, 2002), but its removal from the cliffs and sidelands of Lundy is now well underway, with the hope that the rhododendron can eventually be replaced by native vegetation that includes Lundy Cabbage. Given that rhododendron is known to modify the soil beneath it, it is important to know whether this is unsuitable for the germination of Lundy Cabbage.

We compared the germination success of Lundy Cabbage seeds that were placed in soils from a variety of sources. Soil samples were collected in December 1997 from sites where rhododendron had been cleared a few years previously, or had just been cleared by Angus Tillotson and colleagues (from *Ropeworks*, a specialist consultancy working under contract to English Nature/Natural England). The samples included soils collected from beneath large blocks of rhododendron, as well as from relatively small isolated bushes. Paired control soil samples were also collected from adjacent areas where it was believed rhododendron had never been present (Table 2).

Soils collected from areas where seeds might naturally be present were searched by eye, then spread out in seed trays and kept warm and moist to stimulate germination of seeds (of any species) that were present naturally, which were then removed. In January 1998 the soil samples were then sown with 40 Lundy Cabbage seeds per tray and maintained under lights at 20^{o}C. The seed had been collected in summer 1997 and was checked before sowing for apparent viability and any misshapen or shrivelled seeds were removed. Germination was recorded at regular intervals and the experiment was terminated 31 days later.

Around one third of the seeds germinated during the course of the experiment (Table 3). Germination rates had a mean of 30.9% from the soils that were associated with rhododendron, compared with 37.0% in the control soils, but this difference was not significant (paired $t_{[10]} = 0.95$, P (two tailed) = 0.36). Among the samples from beneath rhododendron there was little difference between germination rates from soils beneath small rhododendron bushes (six samples, mean germination = 27.9%), the large rhododendron block (three samples, mean = 35.8%) and the area where rhododendron had been cleared several years previously (two samples, mean = 32.5%).

The most notable contrast in germination rates was not associated with rhododendron, but with substrate. Among the soil samples, germination rates had a mean of 49.5% in the slate soils (the more southerly five samples), compared with 26.7%

on the granite (six samples). This difference was significant ($t_{[9]} = 2.28$, P (two tailed) = 0.05). This difference was not because the slate control samples were collected away from sea cliffs, as there was no significant overall difference between cliff-side and Sideland germination rates (cliff (4 samples), mean germination = 31.9%, Sideland (7 samples), mean = 40.0%; $t_{[9]} = 0.64$, P (two tailed) = 0.54). The importance of substrate was also present with the soil samples taken beneath rhododendron, where mean germination rates from slate soils were 40.5%, compared with 22.9% from granite soils.

Table 2: Locations of soil samples from beneath rhododendron and from adjacent rhododendron-free areas

The locations of Rhododendron patch N° 5 and Broad Coombe are given in Compton *et al.,* 1998. The small plants above Brazen Ward ranged from seedlings up to small bushes.

Location	n paired samples	Rhododendron	Incline	Geology
Landing Beach	2	Small patch	Sideland	Slate
Rhododendron Patch N° 5	3	Large block	Sideland	Slate
Broad Coombe	1	Small patch	Cliff	Granite
Quarter Wall Coombe	2	Small patch	Cliff	Granite
Brazen Ward	2	Large bushes removed by 1989	Sideland	Granite
Brazen Ward	1	Small plants	Cliff	Granite

Table 3: The numbers of Lundy Cabbage seeds germinating in soils from the locations described in Table 2

Forty seeds were sown in each replicate, using soils from beneath rhododendron and from adjacent soil clear of rhododendron.

Location	Soil sources	
	Rhododendron	Nearby
Landing Beach	22	12
Landing Beach	16	17
Rhododendron Patch N° 5	13	31
Rhododendron Patch N° 5	17	27
Rhododendron Patch N° 5	13	12
Broad Coombe	8	10
Quarter Wall Coombe	9	14
Quarter Wall Coombe	7	10
Brazen Ward (Sideland)	14	7
Brazen Ward (Sideland)	12	6
Brazen Ward (Cliff)	5	17

CONCLUSIONS

Lundy Cabbage seeds can be dispersed over distances of at least several tens of metres. There is also evidence for a considerable seed bank which, from a conservation perspective, is reassuring, because these seeds can act as a reserve if the population suffers from one or more years when reproduction is low or absent. The results of the germination studies were also encouraging from the point of view of the restoration of Lundy Cabbage into areas that are cleared of rhododendron because there was no evidence that soil from beneath rhododendron inhibits the germination of fresh Lundy Cabbage seed. This conclusion that has been confirmed by events after recent rhododendron clearance, where large numbers of Lundy Cabbage have appeared almost immediately and successfully flowered (Plate 3).

The difference we recorded in germination success on slate and granite soils may prove to be important for Lundy Cabbage population dynamics, but a much larger survey, explicitly taking into account factors such as salinity and pH, will be needed before too much can be made of this result.

ACKNOWLEDGEMENTS

Our thanks to Angus Tillotson (Ropeworks) for making cliff-side sampling possible and to the island's wardens, assistant wardens and rangers, past and present, for their help and advice.

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Plate 1: Entire fruit ('pod') of Lundy Cabbage. Note the long dehisced lower segment, which can contain numerous seeds and the short indehiscent terminal segment which normally contains just one or two seeds *(Photo: Roger Key)*

Plate 2: Dehisced and dehiscing fruits of Lundy Cabbage (*Photo: Roger Key)*

Plate 3: Lundy Cabbage on the Eastern Sidelands, flowering in an area cleared of rhododendron the previous year *(Photo: Roger Key)*