POLLEN BEETLES AND REPRODUCTIVE SUCCESS OF THE ENDEMIC LUNDY CABBAGE: THE CONSEQUENCES OF AN APPARENT INVASION EVENT IN 2007

by

ROSY J.D. KEY², ROGER S. KEY², MOHINE ALAM¹ AND STEPHEN G. COMPTON^{1,3} ¹School of Biology, University of Leeds, Leeds, LS2 9JT ²Formerly Natural England, Peterborough ³Corresponding author, e-mail: s.g.a.compton@leeds.ac.uk

ABSTRACT

Lundy cabbage is a yellow-flowered crucifer endemic to Lundy. Pollen beetles (*Brassicogethes* spp.) are present routinely in its flowers, but exceptional numbers were present in 2007, probably as a result of mass migration from the mainland. We used the proportion of flowers failing to set fruit and the proportion of unhealthy flower buds to compare the plant's reproductive success in 2007 with nine subsequent years, when *Meligethes* numbers were much lower. It appears that in 2007, but not others, the nationwide expansion of oilseed rape production may have had negative consequences for this protected plant species.

Keywords: Brassicogethes, Coincya wrightii, Lundy, Meligethes, migration

INTRODUCTION

Lundy cabbage (Coincya wrightii) is one of the few endemic plants found only in the British Isles. Molecular evidence suggests that it is a post-glacial derivative of the more widespread C. monensis, the Isle of Man cabbage (Compton et al., 2007). Lundy cabbage is a short-lived perennial that grows on the cliffs and Sidelands of the eastern side of Lundy. It does not reproduce vegetatively and so relies entirely on sexual reproduction to maintain the size of its populations and to disperse to new ones. The conspicuous flowers are soft yellow and, and grouped into upright raceme inflorescences. Flowering occurs mainly from mid May to mid June, but ones in which buds, flowers or fruits are grazed off will continue to attempt to flower and some plants in flower can be present even in winter. Larger plants produce more flowers and more seeds, and large plants can generate several hundred fruits and thousands of seeds in a season (Compton & Key, 2000). Lundy cabbage fruits ('pods') are typical of less derived members of the cabbage family Brassicaceae. They are elongate and roughly cylindrical in cross section. Each fruit is divided into two parts, with a long basal siliqua that has a central septum running its length and two dehiscent valves, and a shorter terminal beak. Most of the seeds are in the siliqua, with just one or two seeds in the beak (Compton & Key, 2000). The seeds are dispersed mainly when the siliqua dehisces, but seeds in the beak can also be carried by the wind (Compton et al., 2010).

Lundy cabbage is unique among the British flora because it is the only host-plant for endemic insects, the Bronze Lundy cabbage flea beetle (Psylliodes luridipennis) and the Lundy cabbage weevil, Ceutorhynchus contractus 'var.' pallipes, which is considered currently to be an undescribed species (Compton *et al.*, 2002). In addition, the plant is eaten by several other insects, most of which are generalist herbivores that feed on a wide range of crucifer species (Compton & Key, 2000). Flies, butterflies, moths, ants, beetles, wasps, sawflies and solitary bees and bumble bees visit the flowers and are potential pollinators (honey bees are absent from Lundy). Wright (1936), after whom the plant is named, suggested that the adults of *Meligethes* spp., (Coleoptera: Nitidulidae) were the major pollinators of Lundy cabbage (Plate 1). These pollen beetles are now placed in a new genus, Brassicogethes (Audisio et al., 2009). However, although they are frequent floral visitors, and can become covered in pollen, these beetles are unlikely to be efficient pollinators of Lundy cabbage (Chifflet et al., 2011). Both their adults and larvae also feed on the petals and flower buds, as well as pollen, so their net effects are negative for the plants. Reflecting this, *Brassicogethes aeneus* and to a much lesser extent B. viridescens, are significant pests of cruciferous crops such as oilseed rape (Williams & Free, 1979; Kirk-Spriggs, 1996).



Plate 1: Brassicogethes viridescens (pollen beetle) adults are the most common and easily-seen beetles on the flowers of Lundy cabbage. They are often mistaken for the endemic Lundy cabbage flea beetle

Brassicogethes viridescens is usually the more common crucifer-feeding pollen beetle on Lundy, but *M. aeneus* is also present and was common on Lundy cabbage in 2007. Both species feed on a wide range of yellow-flowered crucifers (Kirk-Spriggs, 1996). The life history of *Brassicogethes* species can be summarised as follows: there is usually a single generation each year. Adults emerge from hibernation in the spring, seek out flowers to feed on pollen before visiting a narrower range of plant species to lay their eggs on developing buds, on which the larvae feed. Larval development (at least in *B. aeneus*) takes less than two weeks after which the larvae fall to the ground to pupate. Adults feed on pollen of a wide range of species again in the autumn, before entering the soil to hibernate (Lane, 1984; Kirk-Spriggs, 1996).

Most Lundy cabbage plants grow in areas inaccessible to grazing animals (goats, sheep and rabbits) and have to be viewed from a distance. Using binoculars, annual standardized counts of the numbers of Lundy cabbage in flower have been carried out each spring since 1994. These counts are supplemented by estimates of the proportion of plants that are not flowering that are based on the very limited areas where plants are accessible on foot. The estimated numbers of individuals in flower has varied by about a factor of ten between 1994 and 2017. During the first half of this period the variation in plant numbers was mainly driven by dramatic fluctuations in the numbers of rabbits on the island, which had boom periods ended by periodic outbreaks of myxomatosis (Compton et al., 2004). In more recent years the rabbit population on the island has been relatively stable, but the numbers of flowering Lundy cabbage have continued to fluctuate, though not as dramatically (S.G. Compton, R.S. Key and R.J.D. Key, unpublished data). Much of this variation may be climate-related, but a drop in the numbers of plants with flowers present in 2007 was apparently related to unusually high levels of insect damage to the inflorescences. Every inflorescence we could inspect closely had adult pollen beetles (Brassicogethes spp.) feeding on the buds and petals, and almost every flower had at least one adult pollen beetle feeding there. This stimulated us to monitor changes in flowering success, in order to determine whether 2007 was an exceptional year for pollen beetles and for the reproduction of the plants.

Lundy cabbage inflorescences mature from the bottom up, so that basal fruits, more central flowers and terminal flower buds can all be present at the same time. Any flowers that fail to set seed abscise and leave behind the short pedicel. The relative numbers of pedicels and fruits can provide an indication of the proportion of 'successful' flowers (Plate 2) and in the past the proportion of flowers that managed to produce fruits has been used as an index of pollen beetle damage to oilseed rape. However, this needs cautious interpretation, because in addition to insect feeding, climate, soil nutrition and pollination rates can all influence the ratio of successful/unsuccessful fruit set (Williams & Free, 1979; Kirk, 1992; Bartomeus *et al.*, 2015).



Plate 2: Inflorescence of Lundy cabbage showing developing fruits and bare stalks where there has been no fruit set

METHODS

During late May or early June in the years 2007 to 2017 we attempted to assess ratios of fruits to bare pedicels (where fruits had failed to form), and bud damage, on plants growing above and below the Sideland path on the north side of Millcombe and along the road from Millcombe to the Landing Beach, up to about 200m further south. Ten plants with at least three inflorescences displaying open flowers or pods were selected haphazardly in each area if a choice was available. Ten plants at the correct developmental stage were not always accessible in all three areas (17 and 28 rather than 30 plants were sampled in 2016 and 2017 respectively) and in 2012 a late flowering season meant that no suitable plants were available at the time of our survey. Within each inflorescence we counted the numbers of flowers (distinguished from buds if at least part of a petal had started to emerge), fruits, aborted pedicels, apparently healthy buds (green) and unhealthy/aborting buds (which start to turn yellow or brown before falling).

RESULTS

In most years we were able to sample 30 inflorescences. The numbers of buds present on the plants varied greatly, depending in part on the age of the inflorescence (older inflorescences have no buds remaining). 2007 was noteworthy in that it was the only year when the number of aborting buds outnumbered those that appeared to be healthy (Table 1). The relative numbers of flowers to fruits and the pedicels of aborted flowers was also highly variable, reflecting variation in the ages of the inflorescences (later developing inflorescences had a higher proportion of flowers). The year 2007 was again exceptional, with the lowest numbers of flowers and pods per inflorescence and the highest numbers of aborted pedicels (Table 1). Comparisons of between-year differences in the proportion of stalks that had fruits present (Figure 1 upper) and the proportion of buds that appeared to be healthy (Figure 1 lower) illustrate the considerable variation present, but also emphasise that 2007 was an exceptional year for the plant.

Table 1 : Annual variation in the numbers of apparently healthy (green) and aborting
(yellow or brown) flower buds, open/opening flowers, successful fruits ('pods') and
bare pedicels in Lundy cabbage inflorescences. SD=standard deviation

Year	Healthy buds		Unhealthy buds		Flowers		Successful fruits		Bare pedicels	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
2007	3.97 (4.77)	0-23	5.01 (2.98)	0-17	1.68 (1.95)	0-7	1.74 (2.74)	0-14	13.48 (8.63)	0-49
2008	2.67 (4.00)	0-15	0.32 (0.92)	0-5	4.11 (3.72)	0-15	11.16 (9.46)	0-48	6.17 (6.77)	0-36
2009	4.17 (4.01)	0-12	3.53 (2.27)	0-11	4.10 (3.00)	0-12	15.73 (11.88)	1-47	7.53 (6.26)	0-25
2010	3.19 (3.29)	0-12	1.70 (1.70)	0-5	3.93 (2.42)	0-11	14.50 (8.93)	2-53	3.14 (3.48)	0-18
2011	1.97 (3.45)	0-17	0.83 (1.85)	0-10	2.31 (2.36)	0-10	12.52 (6.93)	0-34	9.99 (6.88)	0-46
2012	-	-	-	-	-	-	-	-	-	-
2013	5.98 (5.17)	0-20	1.94 (1.79)	0-6	7.96 (3.49)	0-21	13.48 (7.51)	2-31	2.81 (5.06)	0-28
2014	4.56 (6.35)	0-31	1.53 (1.85)	0-9	1.81 (2.03)	0-10	5.61 (5.42)	0-25	12.58 (7.24)	0-41
2015	3.87 (4.23)	0-18	1.88 (1.27)	0-5	4.84 (2.91)	0-13	8.63 (7.07)	0-36	4.26 (4.52)	0-22
2016	3.25 (2.96)	0-11	1.90 (1.82)	0-7	4.00 (2.84)	0-11	5.80 (5.08)	0-14	7.02 (7.30)	0-44
2017	6.55 (5.26)	0-23	2.49 (2.03)	0-9	3.30 (2.49)	0-13	10.00 (7.60)	0-29	7.70 (6.72)	0-36



Figure 1: Upper: Annual variation in the proportion of stalks on Lundy cabbage inflorescences that had fruits ('pods') present. Lower: Annual variation in the proportion of buds that appeared healthy

DISCUSSION

The numbers of seeds produced by crucifers such as oilseed rape and Lundy cabbage depends more on the proportion of buds that are successful than the number of buds initiated (Diepenbrock, 2000). Flowers that produce only bare stalks can be common, even in commercial oilseed rape crops, where as few as 40% of the stalks may produce fruits on some plants (Williams & Free, 1979). Our annual estimates of Lundy cabbage reproductive success, based on the proportion of healthy buds and successful fruit-to-empty pedicel ratios, confirm that 2007 was an exceptionally poor year for the plant. In none of the subsequent ten years was there such a high proportion of buds considered to be unhealthy and in all the subsequent years a higher proportion of flowers managed to

develop into fruits. The small proportion of stalks that supported the development of fruits in 2007 was even more striking and suggests that damage to the flowers was unusually high. The low flowering success among the plants that year was also reflected in a smaller proportion of plants that had any flowers visible at the time of our visit. This estimate of the proportion of plants with or without any flowers has to be treated with caution because it is based on only a small fraction of the total population area, but in 2007 the proportion of plants with visible flowers was nonetheless the lowest we have recorded in the 24 years when equivalent estimates are available, and almost half the frequency recorded in any other year (S.G. Compton, R.S. Key and R.J.D. Key, unpublished data). It is highly likely that the reduced reproductive success in 2007 was a consequence of damage caused by the exceptional numbers of Brassicogethes present on the inflorescences that year. Their feeding damage to the petals was clearly evident; almost every flower had the beetles present and, although their densities were not quantified, we estimated that there was an average of more than one Brassicogethes adult per flower. This can be compared with spray threshold guidelines ranging from 15 beetles per plant down to three beetles per plant for control of *B. aeneus* on winter oilseed rape (Lane, 1984; Hansen, 2004). Many of the Lundy cabbage plants had more than 15 beetles on individual inflorescences in 2007.

In most years, our limited collections have found that of *B. viridescens* is by far the more abundant of the two species on Lundy cabbage, and in some years we have failed to record any *B. aeneus*. This was not the case in 2007, when there were very large numbers of B. aeneus. Adults of this species utilise a far wider range of host plants than their larvae (Ouvrard et al., 2016). Lundy cabbage is the only large perennial crucifer on the island, and there are only minimal numbers of other yellow-flowered crucifers. It is therefore unlikely that the exceptional numbers of Brassicogethes in spring 2007 was the result of exceptional recruitment from within the island. A more plausible hypothesis is that the island received an 'invasion' of *B. aeneus* from the mainland in the spring of that year. Significant increases in the UK acreage of oilseed rape from the 1980s led to increased pest problems for this crop, and an increased need for chemical control (Lane & Cooper, 1989). This major increase in the availability of a suitable host plant is likely to have increased the numbers of *B. aeneus* across the country as a whole (Hokkanen, 2000). Adult B. aeneus are highly mobile and can disperse over large distances (Tamir et al., 1967; Junk et al. 2016; Juhel et al., 2017; Mauchline et al. 2017), so the less than 20 kilometres that separate Lundy from mainland England is unlikely to be a significant barrier for this species. Significant invasions are nonetheless clearly rare and B. aeneus does not represent a threat to the abundance of the cabbage and its associated endemic insects. The exceptional situation in 2007 presumably resulted from an unusual combination of factors, though the meteorological Office summary of the weather for May that year suggests it was not exceptional (https://www.metoffice.gov.uk/ climate/uk/summaries/2007/may).

ACKNOWLEDGEMENTS

We would like to thank Derek Green, the island wardens, and their assistants for all the help they have provided to the 'cabbage counters' over the years.

REFERENCES

- Audisio, P., Cline, A.R., De Biase, A., Antonini, G., Mancini, E., Trizzino, M., Costantini, L., Strika, S., Lamanna, F. & Cerretti, F. 2009. Preliminary reexamination of genus-level taxonomy of the pollen beetle subfamily Meligethinae (Coleoptera: Nitidulidae) *Acta Entomologica Musei Nationalis Pragae* 49, 341-504
- Bartomeus, I., Gagic, V. & Bommarco, R. 2015. Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic and Applied Ecology* 16, 737-745
- Chifflet, R., Klein, E.K., Lavigne, C., Le Féon, V., Ricroch, A.E., Lecomte, J. & Vaissière, B.E. 2011. Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. *Journal of Applied Ecology* 48, 689-696
- Compton, S.G. & Key, R.S. 2000. Coincya wrightii (O.E. Schulz) Stace. Journal of Ecology 88, 535-547
- Compton, S.G., Key, R.S & Key, R.J.D. 2002. Conserving our little Galapagos Lundy, Lundy cabbage and its beetles. *British Wildlife* 13, 184-190
- Compton, S.G., Key, R.S. & Key, R.J.D. 2004. Lundy cabbage population peaks are they driven by rabbits and myxomatosis? *Annual Report of the Lundy Field Society* 2003 53: 50-56
- Compton, S.G., Craven, J.C., Key, R.S. & Key, R.J.D. 2007. Lundy Cabbage: past, present and future. *Proceedings of the 60th Anniversary Symposium of the Lundy Field Society*, 161-178
- Compton, S.G., Norton, R., Straker, R., Walker, C. & Key, R.S. 2010. Lundy cabbage seed dispersal, seed banks and seed germination after rhododendron clearance. *Journal of the Lundy Field Society* 2: 45-52
- Diepenbrock, W. 2000. Yield analysis of winter oilseed rape (*Brassica napus* L.): a review. *Field Crops Research* 67: 35-49
- Hansen, L.M. 2004. Economic damage threshold model for pollen beetles (*Meligethes aeneus* F.) in spring oilseed rape (*Brassica napus* L.) crops. *Crop Protection* 23, 43-46
- Hokkanen H.M.T. 2000. The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. *Entomologia Experimentalis et Applicata* 95, 141-149
- Juhel, A.S., Barbu, C.M., Franck, P., Roger-Estrade, J., Butier, A., Bazot, M. & Valantin-Morison, M. 2017. Characterization of the pollen beetle, *Brassicogethes aeneus*, dispersal from woodlands to winter oilseed rape fields. *PLOS ONE* 12, e0183878
- Junk, J., Jonas, M. & Eickermann, M. 2016. Assessing meteorological key factors influencing crop invasion by pollen beetle (*Meligethes aeneus* F.) past observations and future perspectives. Meteorologische Zeitschrift 25, 357-364
- Kirk, W.D.J. 1992. Insects on cabbages and oilseed rape. Naturalists' Handbooks 18, 1-66. Pelagic Publishing
- Kirk-Spriggs, A.H. 1996. *Pollen Beetles*. Handbooks for the Identification of British Insects 5 (6a). Royal Entomological Society
- Lane, A., 1984. Oilseed rape handbook. The Open University Press, Milton Keynes
- Lane, A. & Cooper, D.A. 1989. Importance and control of insect pests of oilseed rape. *Aspects of Applied Biology* 23, 269-275

- Ouvrard, P., Hicks, D.M., Mouland, M., Nicholls, J.A., Baldock, K.C.R., Goddard, M.A., Kunin, W.E., Potts, S.G., Thomas, T., Veromann, E. & Stone, G.N. 2016. Molecular taxonomic analysis of the plant associations of adult pollen beetles (Nitidulidae: Meligethinae), and the population structure of *Brassicogethes aeneus*. *Genome* 59, 1101-1116
- Mauchline, A.L., Cook, S.M., Powell, W., Chapman, J.W. & Osborne, J.L. 2017. Migratory flight behaviour of the pollen beetle *Meligethes aeneus*. *Pest Management Science* 73, 1076-1082
- Tamir, L., Šedivy, J., Bergmannova, E. & Hanker, I. 1967. Further experience obtained in studies on dispersal flight of *Meligethes aeneus* F., marked with P 32. *Acta Entomologica Bohemoslovaca*, 64, 325-332
- Williams, I.H. & Free, J.B. 1978. The feeding and mating behaviour of pollen beetles (*Meligethes aeneus*) Fab. and seed weevils (*Ceutorhynchus assimilis* Payk.) on oilseed rape (*Brassica napus* L.). Journal of Agricultural Science 91, 453-459
- Williams, I.H. & Free J.B. 1979. Compensation of oilseed rape (*Brassica napus* L.) plants after damage to their buds and pods. *Journal of Agricultural Science* 92, 53-59
- Wright, F.R.E. 1936. The Lundy Brassica, with some additions. *Journal of Botany* 74, (Suppl.) 1-8