British & Irish Botany 8(2): 130-142, 2026

Is *Veronica verna* (Spring Speedwell; Veronicaceae) limited by its habitat requirements or its ability to disperse?

Johanna Jones[1]*, Norman Sills[2]

[1]Newmarket, UK/Plantlife International; [2]Mildenhall, UK

*Corresponding author: Johanna.jones@plantlife.org.uk

This pdf constitutes the Version of Record published on 28 August 2026.

Abstract
Effective conservation of rare plants requires an understanding of what limits their occurrence. The distribution of *Veronica verna* is limited to twelve sites in Britain and Ireland. When there is seemingly suitable habitat available which *V. verna* does not colonise, we need to understand whether it has ecological requirements that this habitat does not offer or lacks dispersal mechanisms for movement to occur. *Veronica verna* seeds were sown at nine sites in the Brecks and fruiting plants were counted over two years. In each of two years, at all but one site, plants grew sufficient seed to replace the experimental seed bank, with differences in soil chemistry having no association with numbers of plants grown. Lack of effective dispersal mechanisms therefore appear to be the limiting factor in the spread of Spring Speedwell. This suggests translocations to open sandy areas, with suitable management and monitoring have a good chance of success.

Keywords: dispersal mechanisms; Breckland; translocation; annual; soil chemistry

Introduction

Veronica verna L. (Spring Speedwell, Veronicaceae) is a small native winter annual plant (Fig. 1) limited in Britain and Ireland to 12 sites in nine localities in the area known as Breckland, on the Norfolk-Suffolk border (Breckland Flora Group recording data, held by author). Stroh (2017) describes *V. verna* as widely scattered throughout Europe to western and central Asia and Morocco, with northern range limits in Finland and naturalised in the USA, Canada (Crins *et al.*, 1987; Oldham & Zinck, 1997), New Zealand (Ferreira & McKinlay, 2000) and the Western Himalayas (Pennell, 1943). *V. verna* grows in arid, sandy soils, low in nutrients, with bare ground provided by summer droughts and disturbance by animals, especially European Rabbits (*Oryctolagus cuniculus*) which provide tightly grazed vegetation and bare areas for seed germination (Pankhurst *et al.,* 2021) with any one of these factors checking the growth of coarse vegetation (Watt, 1971; Fig. 2) Trist (1979) notes that in addition to heath, *V. verna* is found on the side of tracks where sand is blown up and in abandoned arable land, tolerating the range of 10-60% bare ground. *V. verna* seeds are tiny, 1 g contains approximately 8,300 seeds (compared with *V. triphyllos* for which 1 g contains approximately 2,330 seeds; Chapman *et al.*,

2018). Surveys by members of the Breckland Flora Group show that at six of the extant sites *V. verna* is located within a small area of the site, although there is seemingly abundant suitable additional habitat in the vicinity. To take effective conservation action we need to know whether failure to colonise reflects more fastidious ecological requirement than suspected, or a constraint on the ability of the species to disperse to new areas (Dolman & Sutherland, 1992; Ozinda *et al.*, 2004.)



Figure 1. *V. verna* is a small native annual plant limited to the Brecks in Britain and Ireland, with deep blue flowers and distinctively cut leaves



Figure 2. Typical habitat for *V. verna* is short, sparsely vegetated, sandy heathland, with rabbit disturbance, as exemplified by this site at Icklingham, Suffolk

Method

To investigate the ecological requirements of *V. verna*, we selected nine experimental sowing sites (Table 1). These comprised two extant native sites, two historical sites where the species was last recorded in 1946 and 1961, and five apparently suitable sites where *V. verna* has never been recorded. The five additional sites were selected based on the authors' knowledge of conditions at historical and extant *V. verna* populations. Three of these sites were located at Weeting Heath, distributed from north to south across Compartment 3. These were chosen because they offered variation in geology, subsequently confirmed by pH testing (Table 2), while experiencing very similar climatic conditions.

Table 1. Location and status of *V. verna* at the nine experimental sites

Site	Location	Site status
Icklingham Plain South	Icklingham, Suffolk	extant
Icklingham Triangle	Icklingham, Suffolk	extant
Lords Well Field	Eriswell, Suffolk	historical
Santon Heath	Santon Downham, Suffolk	historical
Hainsworth Heath	Cavenham, Suffolk	new
Lakenheath Fen	Lakenheath, Suffolk	new
Weeting Heath Central	Weeting, Norfolk	new
Weeting Heath North	Weeting, Norfolk	new
Weeting Heath South	Weeting, Norfolk	new

Experimental sowing was conducted in September 2022. At each site, five 0.25 m^2 quadrats were placed within an area assessed as suitable, having sparse vegetation and loose sandy soil. Within each quadrat, 500 seeds were sown, equivalent to 4 seeds per dm^2. No manual disturbance of the soil was undertaken during sowing, and the percentage of bare ground was recorded. For each experimental quadrat, an adjacent unsown control quadrat was also monitored.

In June 2023, the number of fruiting plants in each quadrat was counted. The length of the longest stem of each plant was measured, and estimates were made of the number of capsules per cm of stem and the number of seeds per capsule. Quadrats were revisited in the second year, when fruiting plants were again counted and vegetation cover was assessed.



Figure 3. At Weeting Heath sites, quadrats were placed in a line, at set distances from marker posts. Quadrat frames were then used to enable seeds to be sown evenly across each experimental area

The relationship between the count of *V. verna* at sites and soil chemistry was examined. Soil was tested for pH, and presence of nitrogen, calcium, magnesium, phosphorus, potassium and sodium. Soil samples were collected in July 2023 from the central point between each of the quadrats at six of the sites. For the remaining three sites, all located within Weeting Heath, two soil samples were taken; one was collected from the scrape and one from the bank. Initially, soil samples were collected using an auger but the soil was found to be too friable to do so accurately, so a hand trowel was used to collect a cube of 10 cm diameter of soil from each location, weight approximately 500 g, and the soil placed in a sealed clean plastic bag and sent to Norse Eastern Norfolk Partnership Laboratory for analysis.

Association of soil characteristics with count of *V. verna* was calculated using Spearman's rank (n=12) and significant associations would be considered to be found where $p<0.05$.

Results

Fruiting plants were found at all sites except Santon Heath, with capsules estimated to produce 2,300 – 10,330 seeds in the first year and 530 – 26,460 seeds in the second year (Table 3).

In the first summer, June 2023, *V. verna* was found in four of the 45 control quadrats at three of the nine sites (Table 2).

Table 2. Count of *V. verna* found in control quadrats in June 2023 at each of the experimental sites

Site	Count of *V. verna*
Hainsworth Heath	0
Icklingham Plain South	2
Icklingham Triangle	0
Lakenheath Fen	0
Lords Well Field	0
Santon Heath	0
Weeting Heath South	0
Weeting Heath Central	8
Weeting Heath North	2

Results from the analyses of soil samples (Table 4) showed a range in pH (4.65 - 8.31) across sites and the presence of minerals at the sites. However, there was no significant association between count of plants at the sites in year 1 or 2 and pH or presence of minerals with the exception of Phosphorus which in Year 1 had a significant positive association with count of *V. verna* though not in Year 2 (Table 5).

Vegetation cover increased at the majority of sites during the two years of the experiment. At sites with growth of thick grass, such as at Hainsworth Heath or the banks of Weeting Heath sites, *V. verna* growth was much reduced, with tiny (1 mm) plants found under a mass of grass, or plants had grown long and spindly. However, no significant association was found between the count of plants and the percentage of bare ground present (r_s = -0.2023, p (2-tailed) = 0.5508); grasses cover (r_s = 0.44647, p (2-tailed) = 0.16864) (n=12) or of moss cover (r_s = -0.04, p (2-tailed) = 0.902 in the second year of the experiment, June 2024 (Table 6)

Table 3. Counts in June 2023 and June 2024 of *V. verna* plants, average number of stems per plant and average height of the tallest stem of plants with fruit at each site (for June 2024 includes plants outside experimental quadrats), with minimum number of seeds produced at each site (rounded to nearest 10) from an estimate of two capsules per cm of stem height and 10 mature seeds per capsule. Additional capsules on multi-stemmed plants are excluded. Site status shows which sites have extant native populations, had historical populations or where *V. verna* had not previously been recorded (new)

					June 2023			June 2024	
Site	**Site Status**	**Count of plants**	**Mean number of stems per plant**	**Mean height of tallest stem (cm)**	**Min. count of seeds**	**Count of plants**	**Mean number of stems per plant**	**Mean height (cm) of tallest stem**	**Min. count of seeds**
Hainsworth Heath	new	72	1.0	3.4	4,900	22	1	4.3	1,890
Icklingham Plain South	native	62	1.0	3.1	3,840	21	1.2	2.8	1,180
Lords Well Field	historical	32	1.8	4.0	2,560	17	1.1	3.8	1,290
Lakenheath Fen	new	27	1.7	4.8	2,590	38	1	4.3	3,270
Weeting Heath North	new	18	1.8	6.4	2,300	11	1	2.4	530
Santon Heath	historical	0	-		0	0	-	0	0
Icklingham Triangle	native	41	1.6	3.1	2,540	150	1.6	4	12,000
Weeting Heath South	new	63	2.3	8.2	10,330	189	1.1	7	26,460
Weeting Heath Central	new	33	4.1	5.8	3,830	61	3.8	7.9	9,640
Total/(Mean) across sites		**348**	**(1.7)**	**(4.3)**	**32,890**	**509**	**(1.3)**	**(4.1)**	**46,620**

Table 4. Soil analyses from each site with counts of *V. verna* in Year 2 (June 2023). (N Nitrogen; Ca Calcium; Mg Magnesium; P Phosphorus; K Potassium; Na Sodium; WH Weeting Heath.)

	Count of plants	pH	N, Total Oxidised TOxN (water sol 2:1) mg/kg	Ca mg/kg	Mg mg/kg	P mg/kg	K mg/kg	Na mg/kg
Hainsworth Heath	72	7.19	<1	2300	345	672	364	<50
Icklingham Plain South	62	5.32	<1	73	210	361	243	<50
Icklingham Triangle	41	5.65	<1	218	231	316	226	<50
Lakenheath Fen	27	5.79	7	822	125	131	148	<50
Lords Well Field	32	5.02	<1	327	233	440	317	<50
Santon Heath	0	4.65	<1	125	99	273	153	<50
WH South base	27	7.87	4	69200	705	4100	501	222
WH South bank	36	7.76	12	5620	393	516	348	<50
WH Central base	15	5.8	2	84	165	273	175	<50
WH Central bank	18	4.67	17	109	216	299	251	<50
WH North base	8	8.31	4	115000	793	323	345	57
WH North bank	10	8.02	21	21100	524	364	403	<50

Table 5. The association between soil characteristics and count of *V. verna* at each site in years 1 and 2 of the experiment. Association is calculated using Spearman's rank (n=12) and the p value is provided in brackets. Significant associations are in bold

	Year 1	Year 2
pH	0.01404 (0.96547)	-0.11268 (0.72734)
Calcium	-0.04211 (0.89662)	-0.02817 (0.93075)
Magnesium	0.20702 (0.51855)	0.03521 (0.91349)
Phosphorus	**0.5993 (0.03945)**	0.05644 (0.8617)
Potassium	0.39298 (0.20633)	-0.04226 (0.89626)

Table 6. Percentage vegetation present across all quadrats at each site at start of Year 1 and end of Year 2, with total count of *V. verna* plants. (WHS: Weeting Heath South; WHC: Weeting Heath Central; WHN: Weeting Heath North)

Site	Survey date	Count of plants	Bare	Grass	Moss	Other vegn	lichen
Hainsworth Heath	**09/08/2022**		71.4	8.5	0.0	19.8	
	03/06/2024	22	3.7	94.7	0.6	1.2	
Icklingham Plains South	**24/08/2022**		78.4	10.6	1.6		8.8
	04/06/2024	21	46.2	3.8	18.0	7.2	20.4
Icklingham Triangle	**24/08/2022**		81.4	5.0	11.4	2.2	
	04/06/2024	150	48.2	6.0	19.8	21.2	0.0
Lakenheath Fen	**06/08/2022**		50.6	8.0	40.4		
	01/06/2024	38	4.0	82.0	12.0	2.0	
Lords Well Field	**24/08/2022**		53.6	8.6	37.8		
	04/06/2024	17	8.0	12.0	56.0	24.0	
Santon Heath	**23/08/2022**		91.8	8.2			
	22/02/2024	0	2.0	25.6	55.0	0.0	2.2
WHS base	**08/09/2022**		82.0	5.0		13.0	
	05/06/2024	4	45.3	0.0	28.0	24.0	
WHS bank	**08/09/2022**		98.5			1.5	
	05/06/2024	185	4.0	68.0		28.0	
WHC base	**07/09/2022**		87.0			12.0	
	05/06/2024	0	91.3	7.0	0.0	0.3	0.0
WHC bank	**07/09/2022**		100.0				
	05/06/2024	61	18.0	65.0	0.0	17.0	
WHN base	**07/09/2022**		94.0			4.3	
	05/06/2024	11	70.7	2.3	13.3	13.7	0.0
WHN bank	**07/09/2022**		98.0			2.0	
	05/06/2024	0	2.5	22.0		76.0	

Discussion

Currently *V. verna* grows at a few locations in the Brecks, and within these locations it is limited to very small areas, despite the presence of adjacent habitat similar in vegetation type, presence of bare ground, level of disturbance and aspect. In this experiment at all sites but one (Santon Heath), sufficient seed was produced by plants to replace those sown. That no significant association was found between pH and chemical composition of the soil at the sites investigated, with the exception of Phosphorus in Year 1, and counts of plants, suggests that presence of *V. verna* is not limited by pH or chemical composition of the soil. The successful germination of seeds in the experimental area also suggests that successful establishment is not limited by specific mycorrhizal associations. This experiment therefore provides evidence that the paucity of transport mechanisms, rather than soil chemical properties, explains the limit to the locations of current populations. Quinn *et al*. (1994) found that plants with poor dispersal ability tended to have more aggregated

distributions than plants with good dispersal ability which fits with these results for *V. verna*. Pocock *et al*. (2006) expanded this work, finding ecological traits, including dispersal mode, to be a significant influence on the spatial pattern of rare and scarce plant species distributions.

Veronica verna was found in four of the control quadrats. As these plants were within 10 cm of the experimental quadrats this is not considered to be evidence that seeds of this species were present in these areas prior to the experiment. The control quadrats were located adjacent to the experimental quadrats to enable them to be re-located speedily. This was an error: almost certainly seeds were either blown into the control quadrats as they were sown: it was windy when they were sown at Weeting Heath, or they were moved the few centimetres into the control quadrats by animals or rain.

There was no association between the count of plants and the cover of either bare ground or grasses. The result is probably confounded by results from the sites at Weeting Heath, where the scrapes had very low counts of plants and high levels of bare ground; here there was much trampling and disturbance of the bare soil by ponies and this probably resulted in many germinating seedlings being destroyed. However, this result also lacks nuance. Observation of sown plants showed that *V. verna* can grow in areas with low-growing mosses, with plants emerging through mosses up to 5cm in height, and at the edges of vegetation, but is not able to grow among, or compete with, dense grass cover. For example, one of the sites, Hainsworth Heath has only recently been reverted from arable and here the cover of coarse vegetation increased from 8% at the start of Year 1 to 94% by June of Year 2. While some *V. verna* managed to struggle through this vegetation, they were spindly and weak and, unless gardened, this population would almost certainly die out. However, at other sites, just small patches of bare ground allowed seed to germinate. *V. verna* germinates from October onwards, with germination continuing in February to March. Plants have to survive both the frosts and the dry climate of Breckland. Some less coarse vegetation, such as mosses, appeared to provide suitable conditions possibly providing shelter from frost and sun and conserving moisture in its shade, benefiting small *V. verna* seedlings Figure 4. This fits the findings of Nabe-Nielsen (2021), who observed that in dry grassland in Denmark, *V verna* was found at the transition between bare sand and dense vegetation, created by areas having an 'intermediate' disturbance regime. However, a dense cover of mosses may also assist in stabilising soils, so reducing opportunities for the creation of bare ground via wind, rain or animals and potentially retain water around *V. verna* plants which could have a rotting effect on young seedlings. It would be useful to investigate further the role of moss in *V. verna* growth, recognising that different moss species may have different effects.



Figure 4. A *V. verna* plant emerges through moss, which may provide shelter from frost and maintain a moist environment for young seedlings

Plants failed to grow at just one site, Santon Heath. This may be because this site is reverted from forestry and here the surface of the ground has developed a crust of hardened compacted soil, which may have both prevented seeds gaining access to adequate moisture and nutrients to germinate and survive, if they remained on the crust, or prevented any seedlings below the crust breaking through to the light.

It is possible that *V. verna* has lost its historical means of dispersal. seeds are tiny and easily blown by the wind as the authors found when sowing seed in the experimental areas. Wind-blow was once a common feature in Breckland, W.G. Clarke (1925) describes 'fine sand blown to a depth of an inch or more over large areas of heath and plantation', but over the last centuries the landscape has become increasingly enclosed and vegetated. While soil is still wind-blown over bare or sparsely vegetated agricultural land, air-movement over the heaths in which *V. verna* is found may be inadequate to carry enough seeds to germinate successfully to form new, noticeable populations in the limited areas of suitable substrate.

Pakeman et al. (1998, 1999, 2002), and Dellafiore et al. (2010), amongst others, found that dispersal of seed by animal dung (endozoochory), including rabbit pellets, plays a role in seed movement. There has been a crash in the Rabbit population in the Brecks since the spread of Rabbit haemorrhagic disease across the UK (Duff et al., 2020). The loss of Rabbits has reduced suitable available habitat for

V verna. If Rabbits were also involved in seed dispersal this could also partly explain the failure of *V. verna* populations to expand into new areas. In a limited experiment, one of the authors, NS, gathered 700 rabbit pellets from an area with a strong population of *V. verna* (count in the thousands) in fruit and laid them on a seed tray in his garden for a year. However, no *V. verna* germinated from these pellets. Repeating this experiment may be worthwhile.

Historically, *V. verna* was found at 'plough cleaning' sites, areas where after finishing work ploughs were run through sandy soil to clean their metal blades. Possibly, plough cleaning provided a means of transport that the plant lacked, moving seeds from areas where *V. verna* was growing to new sites, with the nature of the activity at the same time providing suitable areas of bare ground for germination of seeds. However, as the number of sites with *V. verna* has dwindled, with sites lost to, for example, development and agriculture, the higher nutrient levels and the loss of rabbits have reduced the occurrence of suitable habitat in remaining arable areas so the chances of such movement happening has reduced. In Ontario, Canada, where *V. verna* is a non-native species, it was found within provincial parks, usually in dry, sandy, heavily disturbed campsites (Crins *et al.* 1987). Crins *et al. s*uggest that seeds may be mixed with sand and camping equipment and so moved from one site to the next, an interesting alternative mechanism for dispersal to plough cleaning.

This experiment has demonstrated that *V. verna* seeds are capable of germinating in a variety of sites and therefore that translocations to areas within the native range where plants will not be swamped by vegetation and have a regular programme of suitable management and monitoring have a good chance of success. For example, at the south end of a heath on the Elveden Estate *V. verna* occurs within an area of 540 m^2 which is vulnerable to stochastic events. Adjacent to this population are ample suitable sandy open areas into which the population could be expanded by seed sowing. Such translocations could be seen as mimicking historical plough cleaning. Similarly, if historical sites for *V. verna* are returned to suitable condition, with open friable soil and the control of coarse vegetation, it would be possible to sow seeds and be optimistic of success. Conversely, this also demonstrates that without natural transport mechanisms providing extensions to current sites, or the creation of new ones, this species' future in the Brecks will be limited to the twelve small areas where it is currently found and will be dependent on these areas staying suitable for *V. verna* to remain part of the British flora.

Acknowledgements
The landowners and managers for access and encouragement, without which we would not have been able to run this experiment, in particular to Paul Dickinson, Elveden Estate; Andy Palles-Clark, Forestry England; Chris Hainsworth, Natural England; James Symonds, Norfolk Wildlife Trust; David Rogers, RSPB.

Breckland Flora Group volunteers whose knowledge contributes much to the background to this project and whose surveying enables us to understand the current status of *V. verna*.

To all those who have recorded *V. verna* in the Brecks, on whose legacy our work is based.

To those who provided valuable advice, in particular Tim Pankhurst, Dr Jenny Richards, Prof. Bill Sutherland and James Symonds. Thanks to Dr Ian Denholm, Julia Masson and Dr Rachel Warmington for their helpful suggestions on the manuscript. Particular thanks to the reviewers for their comments and suggestions which greatly improved the manuscript. All omissions and errors remain the authors' responsibility.

References

Chapman, T, Pocock, S, Davies, R. 2019. *Propagation Protocols for 10 Threatened Cornfield Annuals.* London: Royal Botanic Gardens Kew.

Clarke, W.G. 2025. In: *Breckland Wilds*. London: Robert Scott, Roxburghe House, Paternoster Row E.C.

Crins, W.J., Oldham M.J. & Sutherland, D.A. 1987. *Veronica verna* (Scrophulariaceae), an overlooked element of the naturalized flora of Ontario. *The Michigan Botanist* 26:161-165.

Dellafiore, C.M., Gallego Fernández, J.B. & Muñoz Vallés, S. 2010. The rabbit (*Oryctolagus cuniculus*) as a seed disperser in a coastal dune system. *Plant Ecology* 206:251–261.

Dolman, P.M. & Sutherland, W.J. 1992. The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology* 29:402-413.

Duff, P., Fenemore, C., Holmes, P., Hopkins, B., Jones, J., He, M., Everest, D. & Rocchi, M. 2020. Rabbit haemorrhagic disease: a re-emerging threat to lagomorhps. *Veterinary Record* 187**:**106-107.

Nabe-Nielsen, L.I., Reddersen, J. & Nabe-Nielsen, J. 2021. Impacts of soil disturbance on plant diversity in a dry grassland. *Plant Ecology* 222:1051–1063.

Pakeman, R.J., Attwood, J.P. & Engelen, J. 1998. Sources of plants colonizing experimentally disturbed patches in an acidic grassland, in eastern England. *Journal of Ecology* 86:1032-1041.

Pakeman, R.J., Engelen, J. & Attwood, J.P. 1999. Rabbit endozoochroy and seedbank build-up in an acidic grassland. *Plant Ecology* 145:83-90*.*

Pakeman, R.J., Digneffe, G. & Small, J.L. 2002. Ecological correlates of endozoochory by herbivores. *Functional Ecology* 16:296-304.

Pankhurst, T., Shellswell, C.H., Cooke, E., Moyse, R. & Waller, M. 2021. *Looking after Spring Speedwell Veronica verna: Ecology and Conservation Portfolio*. Salisbury: Plantlife.

Pocock, M.J.O., Harley, S., Telfer, M., Preston, C.D. & Kunin, W.E. 2006. Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology* 94:581-596.

Quinn, R.M., Lawton, J.H., Eversham, B.C & Wood, S.N. 1994. The biogeography of scarce vascular plants in Britain with respect to habitat preference, dispersal ability and reproductive biology. *Biological Conservation* 70:149-157.

Stroh, P. 2017. Species account: *Veronica verna*. Botanical Society of Britain and Ireland. [online]. [Accessed 22 April 2026]. Available at: https://bsbi.org/learn/resources/species-accounts/veronica-verna.

Trist, P.J.O. 1979. *An Ecological Flora of Breckland.* EP Publishing Ltd.

Watt, A.S. 1971. Rare species in Breckland: Their management for Survival. *Journal of Applied Ecology* 8:593-609.

Copyright retained by author(s). Published by BSBI under the terms of the Creative Commons Attribution 4.0 International Public License.

ISSN: 2632-4970

https://doi.org/10.33928/bib.2026.08.130