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Phytosociological notes on hedges in South Ayrshire, Scotland

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Abstract On the basis of four relevées of hedges around Straiton en Dailly in South Ayrshire, Scotland, some features of hedges are discussed. On the basis of the brambles, the vegetation of these hedges can be assigned to the *Pruno-Rubion sprengelii*, which comprises the bramble scrubs of circumneutral and nutrient rich soils in West Europe (Haveman et al. 2017, Haveman & de Ronde 2019). Until now, this alliance was thought to be restricted to the northwestern edge of the European continent, but based on these relevées and the known distribution area of *Rubus nemoralis* and *Rubus polyanthemus*, both characteristic for the *Pruno-Rubion sprengelii*, large parts of North England and Scotland have to be included in the distribution area of the alliance.

The *Pruno-Rubion sprengelii* is optimally developed in rather narrow structures, like hedges, which are pruned every year. Here, brambles and herbs alike can grow with and under the shrubs, facilitated by the light that reaches large parts of the ground. Where the economic base of hedges perishes, they are not longer maintained, and the shrubs can grow out to their natural proportions. This changes the amount of light reaching the surface in the inner parts of the thicket, changing the competition between the species. The brambles as well as the herbs are displaced to the outer edges of the scrub, and the vegetation “dissociates” in a high-growing scrub, a fore-mantle (“cuff”) with brambles, and a fringe with perennial herbs. These elements can hardly ever be assigned to the *Pruno-Rubion* anymore.

The *Pruno-Rubion sprengelii* in optima forma is a scrub in which the three elements (shrubs, brambles, and herbs) grow closely intertwined. This is rarely found in natural landscapes, and thus the alliance is a typical element of the old farmer landscape. What is more: the typical species of the alliance, like *Rubus nemoralis* and *R. polyanthemus*, could only evolve after the landscape was opened by farmers in the last six millennia (Matzke-Hajek 1997), giving way to *Rubus ulmifolius* to expand its distribution area. This caused an explosion of hybrids which stabilised through apomixis into the wealth of *Rubus* species inhibiting the West European landscape nowadays (Sochor et al. 2015). Many of these species have their original home in a man-made landscape. Therefore, the *Pruno-Rubion sprengelii* can be characterised as a “farmers alliance” pur sang.

Key Words agricultural landscape, management, *Pruno-Rubion sprengelii*, *Rhamno-Prunetea*, vegetation

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*In Scotland’s realm, where trees are few,
Nor even shrubs abound,
But where, however bleak the view,
Some better things are found,*

*For Husband there, and Wife may boast
Their union undefil’d,
And false ones are as rare almost
As hedge-rows in the wild*

*First strophes of “A Tale”
William Cowper, June 1793*

Introduction

In Europe, hedge landscapes are found in a rather broad zone along the coasts from Denmark to Portugal, including Great Britain and Ireland (Jessen 1937). In essence, hedges are linear, cultivated scrubs, so a vegetation dominated by shrubby phanerophytes. Most hedges in the more oceanic climate region are planted (Hartke 1951, Reif 1983/1985, Weber 1997, Weber 2003, Müller 2013), at least the dominant species, amongst which hawthorn (*Crataegus monogyna*) is the most important and abundant one, at least from an over-regional perspective. After planting, with the passage of time, the number of species in the hedge increases, both in the shrub layer (Hooper 1970) and the field layer (Litza & Diekmann 2019). Usually, thorny species, especially from the *Rosaceae*, make up the largest part of the shrub layer in hedges (see e.g. French & Cummins 2001): they are promoted, what can be brought back to the hedge’s function as livestock barrier. Where hedges are actually fulfilling this function, they are pruned annually in order to restrict the space which is taken by the hedge as non-productive structure (in some areas up to almost half the total agricultural area, Hartke 1951), as well as the promotion of the dense habit of the shrubs, to keep the animals in – or out.

Where hedges lose their function and economical value they are often cleared; barbed wire takes up less space, its maintenance is much easier and less time consuming, and it requires less traditional and less local knowledge. Whenever they are preserved, for instance in the framework of landscape or nature conservation, there is no need for the laborious traditional maintenance, even more so because it presumes specific and often region-specific knowledge (Aertssen & Gielen 2020, Aertssen et al. 2021), so it is often ceased (Fig. 1). It is to be expected that the change of use and management will be obvious from the species composition of the hedge vegetation. The vegetation is the synthetic expression of all working factors after all, so not only the physical and chemical soil factors, but also use and management (see e.g. Tüxen 1970b, a)



Fig. 1. A functional hedge (right) and a former, shot through and derelict hedge (left) either side of a wide, semi-paved path near Dailly, South Ayrshire. Where the function of the hedge lapses, its management becomes too costly. By abandoning functional management, the species in the hedge shoot through and a dense scrub is formed. To keep the path open, the scrub in the photo is pruned on the walkable side, creating an open thicket. Photo: R. Haveman.

Method

Relevés are made according to the standard Braun-Blanquet method (Dierschke 1994, Westhoff et al. 1995). Visually homogeneous parts of the hedges were selected, measuring 30 to 40 m²; the complete width of the hedges was sampled. All species were noted, separately for all layers, and their abundance was estimated using a slightly modified version of the Braun-Blanquet scale in which the 2 was divided in 2m (< 5 % cover, > 100 specimens), 2a (5–12.5 % cover), and 2b (12.5–25% cover). Nomenclature follows Duistermaat (2020) for the vascular plants except the brambles, Edees & Newton (1988) for *Rubus*, and Siebel & During (2006) for the mosses. The relevés are compared to the vegetation units which are described in literature, and abductively interpreted (Weber 1920/1921, Gehlken 2000, Haveman & de Ronde 2021).

Results

Species composition

Table 1. Four relevés of managed hedgerows in South Ayrshire, Scotland. Management consists of annual pruning or shearing of the hedgerows. Species abundances according to the 9-scale modified Braun-Blanquet code (Westhoff et al. 1995).

Relevé number	1	2	3	4
Area (m ²)	30	30	40	30
Exposition	N	-	-	N
Inclination (degrees)	20	.	.	20
Cover shrub layer (%)	100	100	100	100
Cover herb layer (%)	70	60	90	40
Cover moss layer (%)	40	0	0	0
Height shrub layer (m)	1.5	1.8	1.8	0.7
Height herb layer (cm)	80	80	80	30
Max height herb layer (cm)	120	120	120	60
Total species number	21	22	22	23

Phanerophytes shrub layer

<i>Crataegus monogyna</i>	4	4	5	5
<i>Prunus spinosa</i>	2a	2a	.	.
<i>Acer pseudoplatanus</i>	4	2a	.	.
<i>Rosa canina s.l.</i>	.	2a	2b	.
<i>Fraxinus excelsior</i>	.	2a	2a	.
<i>Hedera helix</i>	.	.	+	2b
<i>Sambucus nigra</i>	2a	.	.	.
<i>Quercus robur</i>	.	+	.	.

Brambles shrub layer

<i>Rubus nemoralis</i>	2a	2b	2b	+
<i>Rubus raduloides</i>	2b	.	2a	.
<i>Rubus polyanthemus</i>	2b	.	.	2a
<i>Rubus latifolius</i>	+	.	.	.
<i>Rubus dummoniense</i>	.	2a	.	.
<i>Rubus idaeus</i>	.	.	2a	.

Herb layer

<i>Hedera helix</i>	3	2b	4	2b
<i>Urtica dioica</i>	2a	2a	1	1
<i>Galium aparine</i>	2m	2m	2m	+
<i>Silene dioica</i>	+	+	+	+
<i>Ranunculus repens</i>	+	1	r	.
<i>Holcus lanatus</i>	+	+	+	.
<i>Heracleum sphondylium</i>	.	2a	r	+
<i>Festuca rubra</i>	.	1	2m	2b
<i>Vicia sepium</i>	.	+	2m	+
<i>Aegopodium podagraria</i>	+	+	.	.
<i>Poa nemoralis</i>	+	.	2m	.
<i>Dryopteris filix-mas</i>	+	.	+	.
<i>Dactylis glomerata</i>	.	2b	.	+
<i>Stellaria holostea</i>	.	1	.	2m
<i>Achillea millefolium</i>	.	+	.	+
<i>Poa pratensis</i>	.	.	.	2m

Moss layer

<i>Brachythecium rutabulum</i>	2b	.	.	+
<i>Kindbergia praelonga</i>	2b	.	.	.

Addenda: once noted species with a maximum abundance of + or r: *Elytrigia repens*, *Dryopteris dilatata* (1), *Ranunculus acris*, *Athyrium filix-femina* (2), *Torilis japonica*, *Claytonia sibirica*, *Rumex obtusifolius*, *Cirsium vulgare* (3), *Stellaria graminea*, *Agrostis gigantea*, *Viccia cracca*, *Lapsana communis*, *Anthriscus sylvestris*, *Polypodium vulgare*, *Lathyrus pratensis* (4).

Table 1 shows the four relevés. They can unambiguously be attributed to the *Prunetalia spinosae*, with *Crataegus monogyna* as the main vegetation-forming species, as well as *Rosa canina*, *Prunus spinosa* and *Sambucus nigra*. *Hedera* in the shrub layer concerns high-growing flowering branches, which behave bushily and attract wasps, bees and flies in autumn. There are also several species in the hedges that, if they could grow out, would form real trees: *Acer pseudoplatanus*, *Fraxinus excelsior* and *Quercus robur*. Also notable are the brambles in the hedges, as most of the species growing in the hedges in this region are also found in the Netherlands.



Fig. 2 *Rubus nemoralis* is the most common bramble species in hedgerows in the Straiton and Dailly area. Blackberries grow in such maintained hedges within the hedge, but can easily colonise the surrounding vegetation with their primocanes. Where their tip touches the ground, they take root and form fronds ("cuffs") on the outside of the hedge in the following year. This only happens if the hedge is not pruned on time and the grassland in the verge is not mowed. Photo: R. Haveman.

The most common species in this area are *Rubus nemoralis* and *Rubus polyanthemus*, followed by *Rubus latifolius*. *Rubus radulooides* is clearly less common and in the Straiton area, and I was able to get one relevé with *Rubus dumnoniense*. Not recorded, but occasionally found in the hedgerows are further *Rubus nessensis*, *Rubus plicatus* and *Rubus lindebergii*. Common in all kinds of woodlands around Straiton is *Rubus dasyphyllus*, but in the hedgerows this species is less common, though not completely absent; no relevés are made with it. Of the listed species, *R. latifolius* and *R. dumnoniense* do not occur in the Netherlands: the former is an in Scotland widely distributed species from the sect. *Corylifolii*, the latter is a species without a clear distributional focus in the British-Irish Isles (Edees & Newton 1988, Newton & Randall 2004). *Rubus lindebergii* and *R. dasyphyllus* are rare in the Netherlands, while the latter is widespread in the UK. Noteworthy

is the absence of *Rubus ulmifolius* in the relevés of these hedgerows: it is a common species in England which is restricted to a very narrow strip along the Irish Sea in this part of Scotland and completely absent further north.

The herb layer in the recorded hedgerows is well developed with a cover of 40–90 (mean 65) % and an average of 15 (11–18) species. In all four relevés, *Hedera helix* is the species with the highest cover in the herb layer. *Urtica dioica*, *Galium aparine* and *Silene dioica*, plants of eutrophic forest fringes, were also noted in all four relevés. Furthermore, the undergrowth consists mainly of grassland plants, such as *Festuca rubra*, *Ranunculus repens*, *Holcus lanatus* and *Achillea millefolium*, and forest (fringe) plants, like *Poa nemoralis*, *Stellaria holostea* and *Dryopteris filix-mas*.

Discussion

Phytosociological assignment

The phytosociology of bramble scrubs of the *Prunetalia spinosae* is rather complex, as was sketched before by Haveman (2017) and Haveman & de Ronde (2019); recent studies make plausible that at least three alliances should be distinguished for temperate western and central Europe. The basis for the phytosociology of bramble scrubs was laid by the late prof. Heinrich Weber (1932–2020) in a several publications (e.g. Weber 1967, 1974, 1981, 1997, 1999). His ideas developed over time, but in his later studies he recognised only two alliances, viz. the *Pruno-Rubion ulmifolii* Bolós 1954 for the thermophilic Atlantic scrubs, ranging from Portugal to France, Belgium and the UK, and the temperate *Pruno-Rubion radulae* Weber 1974 in Central-Europe as well as the Netherlands. In the revised overview of the Dutch vegetation types, Haveman et al. (2017) distinguished between the Central-European *Pruno-Rubion radulae* and the Northwest-European *Pruno-Rubion sprengelii* Weber 1974, based on the occurrence of the alleged occurrence of almost mutually exclusive *Rubus* species. A justification for this, with a comparison of tables published in literature, was provided by Haveman & de Ronde (2019). Neither the southern and northern boundaries of the *Pruno-Rubion sprengelii*, nor the northern boundary of the *Pruno-Rubion ulmifolii* are clear (Haveman et al. 2016, Haveman & de Ronde 2019). Related to this is the uncertainty about the phytosociological position of the bramble scrubs in the northern part of the UK (Haveman & de Ronde 2019).

The relevés presented here at least shine some light on the latter question. The similarity of the shrub vegetation of the hedgerows in South-Ayrshire to the Dutch bramble-rich *Prunetalia* scrubs is striking: undoubtedly they belong to the same alliance (i.e. the *Pruno-Rubion sprengelii*). *Rubus polyanthemus* (Fig. 3) and *R. radulooides* are considered as character species and *R. nemoralis* as differential species of this alliance (Haveman et al. 2017). Considering the wide distribution of *R. polyanthemus* and *R. nemoralis* in North-England and Scotland (Edees & Newton 1988; Newton & Randall 2004), it is plausible that the *Pruno-Rubion sprengelii* is not restricted to the North German Plain and the Netherlands as assumed by Haveman & de Ronde (2019), but has also a wide distribution in Scotland.

Although *Rubus nemoralis* is considered a species of the *Pruno-Rubetum sprengelii* (as far as its occurrence in *Prunetalia* vegetation in the agricultural landscape is considered), the presented relevés form too narrow a basis to conclude that the vegetation of hedgerows in South Ayrshire should also be included in this association. The occurrence of *R. latifolius*, *R. dasyphyllus* and *R. dumnoniense* could be an indication that we are dealing here with a distinct, endemic association, but much more relevés from a much wider distribution area, namely from large parts of Scotland, are needed to clarify this.

The *Pruno-Rubion sprengelii*: an alliance of the agricultural landscape

The recorded Ayrshire hedgerows are managed and used in a traditional way, so as livestock fencing, and their appearance is far from natural scrubs: they are layed, neatly sheared, usually less than a metre wide, and only between 80 and 150 cm high (Fig. 4). The relatively restricted dimensions of these hedges – free-growing hawthorns easily reach a height of 5 m and a width of 3 m – clearly influences their species composition. This is evident when we compare the hedge with the *Pruno-Rubion* scrubs we often encounter in the Netherlands (Fig. 5). In most of the hedgerows of South Ayrshire, the brambles cannot be disentangled from the rest of the vegeta-



Fig. 3. *Rubus polyanthemus* is a character species of the *Pruno-Rubion sprengelii*. Here it grows together with *Rosa canina* (agg.) and *Crataegus monogyna* in a hedge northeast of Dailly, South Ayrshire. Photo: R. Haveman

tion: they are an integral part of it. It is easy to see that this is the effect of the restricted dimensions of the hedges and the resulting light climate. The long primocanes of the brambles growing in the hedges easily cover its height and width, and they stick out on all sides. In other words, there is no competition for light between the shrub species and the brambles. Were the dominant phanerogams, like *Crataegus* and *Prunus spinosa*, allowed to show their natural habit, they would form a dark scrub in which brambles could only survive at the outer edge. The cause of the intricate co-existence of phanerophytes (the shrubs) and pseudo-phanerophytes (the brambles) in the Ayrshire hedges thus is the effect of the specific use and associated management.

In places with apparent overdue management and the hedges are starting to grow out, as is often the case with the Dutch-hedges, the vegetation dissociates: in front of the hedge, a narrow bramble cloak is formed, probably originating from the rooting primocanes of the previous year(s). This is further promoted if the grassland directly alongside the hedge is not managed due to extensivation or even abandonment: in the absence of mowing and/or grazing, the brambles have plenty of opportunity to take root at the tops (Fig. 2).



Fig. 4. The *Pruno-Rubion sprengelii* is optimally developed in narrow structures, such as those in managed hedges. Here, enough light penetrates the centre of the scrub for the growth of brambles and herbs through and under the thorny bushes. Photo: R. Haveman.

As a result, a completely closed bramble vegetation can develop within one or two years, like a furrow surrounding the hedge. In the Dutch landscape, the situation is often a little further developed: because the hedges have lost their (agricultural) function completely, they alter, not only in appearance, but also in species composition and they grow completely into closed, high-rising thickets, often shaded by shot-out trees. Because not enough light penetrates in the centre, brambles are absent from the inner parts of these scrubs, and they often form a mantle at the outer edge of the thicket, or they are missing altogether. Here, the dissociation is complete, and the phytosociological researcher should appreciate this by making two separate (homogeneous) relevés: one with high-growing shrubs without brambles, and another one for the zone with lower-growing brambles, without high-growing shrubs. At the boundary between the two, where

both shrubs and vines grow, a third relevé could possibly be made, but this zone is usually very narrow.

What applies to brambles is, *mutatis mutandis*, also applicable to the herb layer. In closed thickets, often hardly any undergrowth of herbs is present, due to the lack of light. Where herbs do occur, it is often in the outer decimetres, and we speak of a fringe, which often is no more than half a metre. On the contrary, the South Ayrshire hedges show a different pattern, which especially can be observed in the older hedgerows: enough light penetrates the surface to allow a herb layer to develop across the entire width of the hedge. In fact, the hedge can be seen as two edges that meet in the middle of the hedge. Here, three structures thus interlock, as a result of the characteristic use: the higher-rising thicket, the bramble-rich fronds and the herbaceous fringe.

This is the *Pruno-Rubion sprengelii* in optima forma: a bramble-rich thicket with a well-developed herb layer. It is optimally developed in old hedgerows and narrow wooded banks which are traditionally managed, e.g. because they have a function in farming. This makes the vegetation type as dependent on human use as the traditionally recognised 'farmer associations' like the *Calthion palustris*, *Cynosurion cristati* and *Caucalidion platycarpi* which defined the face of the landscape at the time of the existential economy. Where the hedge loses its function and traditional management is discontinued, it disintegrates into different parts, which can often only partially be counted as *Pruno-Rubion* (Fig. 6). Moreover, if the bramble vegetation can be considered part of an association at all, they are often only fragmentarily developed. Similar developments were observed in formerly managed coppice woodlands after they fell fallow: the herbs are disappearing from the centres and they can only survive in margins, for instance along paths (Bijlsma et al. 2001, Bijlsma et al. 2002, Haveman & Schaminée 2005).



Fig. 5. A "hedge" in the Maasheggen area in 2010 during an excursion of the Dutch phytosociological society. Although these scrubs were once managed as hedges, this is hardly recognisable from their current habit. The woody species have grown out, completely changing the competitive relationships in the vegetation compared to the situation when it was still actually managed as a hedge. Photo: R. Haveman.

What about brambles in the natural vegetation?

The characterisation of the *Pruno-Rubion sprengelii* as a "farmer alliance" even goes one step further than what is discussed hitherto. In fact, the most characteristic species of the

alliance, the *Rubus* species, owe their origins to farming practice. The brambles in the *Pruno-Rubion sprengelii* originated as hybrid swarms of which *Rubus ulmifolius* is one of the parental species (Sochor et al. 2015, Haveman et al. 2016). After the retreat of the land ice, agriculture became an important factor in the landscape, and from about 6,000 years ago, increasingly large parts of the landscape were cleared of the forests that naturally occurred here, for the purpose of agriculture. *Rubus ulmifolius* expanded its range northwards along the Atlantic coast, hybridising with sexual species belonging to the series *Glandulosi* and *Rubus*, as well as *Rubus caesius*. Some of the resulting hybrids stabilised via polyploidisation and apomixis, creating the divergent group of blackberries that now populate Europe (Sochor et al. 2015). The brambles in the *Pruno-Rubion sprengelii* therefore have no "natural home" outside the man-made landscape (Matzke-Hajek 1997). Only the glandular species of the series *Glandulosi* and *Hystrix* are more restricted to woodlands and probably also populated the contiguous forests that once covered the European continent. At the other end of the spectrum, we find blackberries that are more like the primordial parent *Rubus ulmifolius* in characteristics, with large spines, leathery leaves and felt on the underside of the leaves. These typical "thamnophilous" brambles (Weber 1986) have their natural home in hedges and hedgerows of the *Pruno-Rubion sprengelii*.



Fig. 6 When hedges shoot through due to lack of management, dense thickets form in which brambles and herbs can only grow at the outer edges. As these thickets age, a linear, woody system emerges. On an earth wall with stones near Dailly, South Ayrshire, a tall, open woodland thicket has thus developed, including *Crataegus monogyna*, *Ilex aquifolium* and *Sorbus aucuparia*. Blackberries are largely absent, probably because along the path the amount of light is not sufficient for blackberry growth. On the outside, the grazing pressure is too high for the establishment of brambles. Noteworthy is the fence on the outer sides of the embankment, which has taken over the function of the former hedge. Photo: R. Haveman.

It is concluded that the *Pruno-Rubion sprengelii* therefore is to be considered one of the most characteristic alliances of the tradition agricultural landscape in (sub-)Atlantic Europe. Not only the co-occurrence of the species in this vegetation is a consequence human use, but also its character species have arisen in the wake of agriculture. What at first sight

might seem a deformed and probably impoverished form of a natural vegetation is in fact a highly antropogenic, cultural feature. Its high species density, caused by traditional management, might be higher than in related, more natural scrubs, but further research is needed to answer this question.

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