Ecology of the larvae of the stiletto-flies *Cliorismia rustica* and *Spiriverpa lunulata* (Diptera, Therevidae)

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Summary

Identification of therevid larvae
Cast larval skins of five species of therevids in four genera were examined at high power. There were few differences between them, and none that were considered to be reliable for identification of preserved larvae. *Cliorismia* and *Spiriverpa* were least reliably separated, whereas most *Thereva nobilitata* and *Acrosathe* could be distinguished. Future field-work on larval ecology will have to rely on rearing final-instar larvae where *Cliorismia* and *Spiriverpa* occur together.

Ecology of BAP-listed therevids
Therevid larvae were sampled in 188 quadrats at two sites on the Usk, and one on each of the Bollin and Rother. Smaller larvae were preserved in the field and larger ones kept for rearing. Just over half 244 larvae collected live were reared to adults. Most were *Cliorismia*, four were *Spiriverpa* and six were *Thereva nobilitata*.

Mean densities of larvae varied widely between transects from zero to 37m^{-2}.

The relationship of environmental variables with the numbers of larvae was examined using profile plots of the transects, stepwise multiple regression and correlation of individual environmental variables with numbers of therevid larvae. It was clear that *Cliorismia* was most abundant away from or well above the river's edge on soft sandy sediment among tall herb or under its shade. It avoided tight grassy swards on consolidated soil, larger areas of open bare sand and gritty to stony sediments.

Cliorismia is a riverine species dependent upon the same hydrological processes that generate ERS but is not itself an ERS species. Management needs to allow natural river process. Trampling by stock is probably not a concern.

Few results were obtained for *Spiriverpa* which appears to be more tolerant than *Cliorismia* of wetter substrate but is confined to fine unconsolidated sediments.

Contents

Tables

Figures

Introduction

The study was initiated to take forward actions for the two stiletto-flies, *Cliorismia rustica* and *Spiriverpa lunulata* (Therevidae), listed in the UK Biodiversity Action Plan (UK Biodiversity Group, 1999a, b). These species, together with several beetles, were added to BAP not only because they are under threat but as flagship species for exposed riverine sediments (ERS). This report covers the larval taxonomy and ecology which form Projects 2 and 3 of a wider study of the flies using sandy ERS. The other projects were: Project 1 - Survey of BAP-listed flies and fly assemblages using ERS (reported by Drake *et al*., 2007) and Project 4 - Ecology of *Rhabdomastix laeta* (reported by Godfrey, 2007).

Both therevids are found next to rivers with notably sandy substrates. Such conditions are found where rivers flow on sandy floodplains or where sand is deposited as the river drops its load in foothill situations. Neither condition is common in Britain and this partly accounts of the rarity of both therevids which have RDB3 status. Although targeted survey in the accompanying project increased the number of sites for both species, they remain peculiarly restricted to these narrow ecological conditions (Drake *et al*., 2007).

An earlier study of the ecology of *Cliorismia rustica* and *Spiriverpa lunulata* was undertaken on the Usk and Monnow in Wales (Drake, 2004). It was established that *Cliorismia* larvae appeared to have a preference for areas with some open sand and with little tall herbaceous vegetation nearby, although larvae were frequently found under scrubby vegetation and in sand shaded by trees. In contrast, *Spiriverpa* larvae appeared to be more restricted to completely open areas of fine sand with sparse vegetation consisting at most of beds of nettles and thistles. Both species were found in dry sand well away from the river's margin and well above water level of normal spring to autumn flow.

This intial work was based on rearing larvae since they were undescribed at the time of the study. Using a stereo binocular microscope with magnification up to x100, no useful consistent differences could be found between cast larval skins of either species, with the possible exception of the maxillary palp of *Thereva* being proportionally slightly longer than that of the other two genera. The chaetotaxy of the body segments was identical. However, by analogy with the progress made with chironomid larvae when examined at high magnification, it was suggested that the head capsules should be re-examined at high magnification. This was done using the same reared material from the Welsh study, together with that of *Acrosathe annulata*.

The work undertaken for the Buglife project in 2006 used a similar approach to that of the earlier study but was extended to the Rother in West Sussex and Bollin in Cheshire. The Rother and Bollin sites were chosen since both appeared to support large populations of *Cliorismia* in 2005 and had different river morphologies to those of the Usk and Monnow; the Rother and Bollin flow in sandy floodplains whereas the Usk is sandy as a result of sediment deposited in a piedmont situation. The populations were also widely separated and, before recent discoveries in Cumbria and Perthshire, were thought to be at the extremes of the species' range. It was hoped to work on *Spiriverpa* at three sites on the Usk where it had been previously found but, as described later, none were found so further work was undertaken on *Cliorismia* here.

The main aim of the ecological study was to determine the small-scale habitat requirements of the larvae as this was thought to be most useful in understanding what management would benefit the species. Other aspects, such as feeding preferences and adult behaviour, were not covered although they deserve consideration if the work is extended.

Project 2. Identification of therevid larvae

Methods

Larval skins of specimens reared from the CCW study undertaken on the Usk and Monnow were soaked in warm potassium hydroxide solution for several minutes. The head capsule was mounted in DMFH (dimethyl hydantoin formaldehyde) between coverslips on a slip of card with a hole punched in it, which could then be staged with the rest of the specimen. Some heads were dismembered into the main capsule, the postmentum (the ventral sclerite) and both halves of mandibular complex, which can be easily separated from the central prolongation (labrum) of the head capsule. Seven specimens of all but *Thereva bipunctata* (one specimen) were mounted.

Drawings were made at x100 or x400 using a drawing tube on a high power microscope using transmitted light. The drawings shown here are computer-sharpened images of the original pencil drawings, hence the fine double line. They include a few confusing superfluous lines.

Results

Head morphology

The names used here for the components of the mouthparts may be incorrect, as the accounts by Teskey (1981) and Irwin & Lyneborg (1981) in the Nearctic Catalogue do not appear to agree. Three main parts are fused or articulate with the basal mandibular sclerite: the sickle-shaped mandible, which is flanked by the maxilla (or labrum?), and the stipes (?). The maxilla has extensive clear membrane on both its inner and outer sides, and which bears on its outer surface an obvious maxillary palp and three small simple ventral palps that are here labeled V1, V2 and V3 (V for ventral). The largest one, V2, is called the labial palp by Irwin & Lyneborg (1981). The hind edge of the maxilla on its outer surface, just in front of the suture of the capsule, carries three more small simple ‘palps’. These are here called L1 (L for lateral) and D1 and D2 for the pair close together in a dorso-lateral position. The inner surface of the maxilla is covered in ranks of very fine combs, an untidy row of coarse spines close to the mandible, and an apical brush of fine hairs that is just visible externally. The maxilla membrane also supports a long transparent process (as long as the rest of the mouthparts) terminating in three lanceolate spines, and which appear to also be joined to the fused labial palps. They appear to reach backwards into the oral cavity. The labial palps at the bottom of the head are fused into an egg-shaped component carrying three pairs of small spines that are clearly visible in side view. The antennae are placed laterally close to the front edge of the capsule, and consist of a squat cone and even shorter cylinder just below it. Of these small projections, only the antennae and V2 (larger labial palp) can be discerned with a stereo microscope.

The head bears three pairs of large setae and fine punctures on top and near the rear of the capsule whose positions do not vary between species. Internally a large central keel drops from the top of the capsule (the tentorium). Articulating with its rear end is a pair of apodemes. The hind edge of the capsule ends in a long metacephalic rod passing back into the body. It is flanked at its articulation with the capsule by a pair of small S-shaped sclerites that I call side appendages.

Comparison of species

Whole head capsules of different species were indistinguishable in dorsal or ventral view at x100 magnification in transmitted light, confirming the conclusion reached using reflected light and a stereo microscope. There were few differences between the genera in the mouthparts. Since the specimens were exuviae, some appendages may not have been in life-like condition, although those of one whole unreared larva of *Spiriverpa* (taken in the company of many other reared *Spiriverpa*) were not markedly different. The features listed in Table 1 and shown in Figures 1 and 2 may be consistently different. Some apparent differences shown in the drawings are merely the result of slightly different orientation of the parts; it was not easy to get this identical in a mount that has to be laid flat on the microscope stage. The relationship of some features, notably the maxillary combs and spines and the transparent memebrane, were not fully appreciated in early drawings, so may be slightly mis-represented.

However, these features are difficult to appreciate and therefore are of limited value in identification. The utility of features thought to differentiate the species was tested by attempting to identify the species in the 29 mounted capsules without looking at the label. The identifications were disappointingly unreliable. *Thereva nobilitata* was the most easily separated but occasional specimens of other species were confused with it. *Acrosathe* was also moderately distinct. But *Cliorismia* and *Spiriverpa* looked alike.

Conclusion

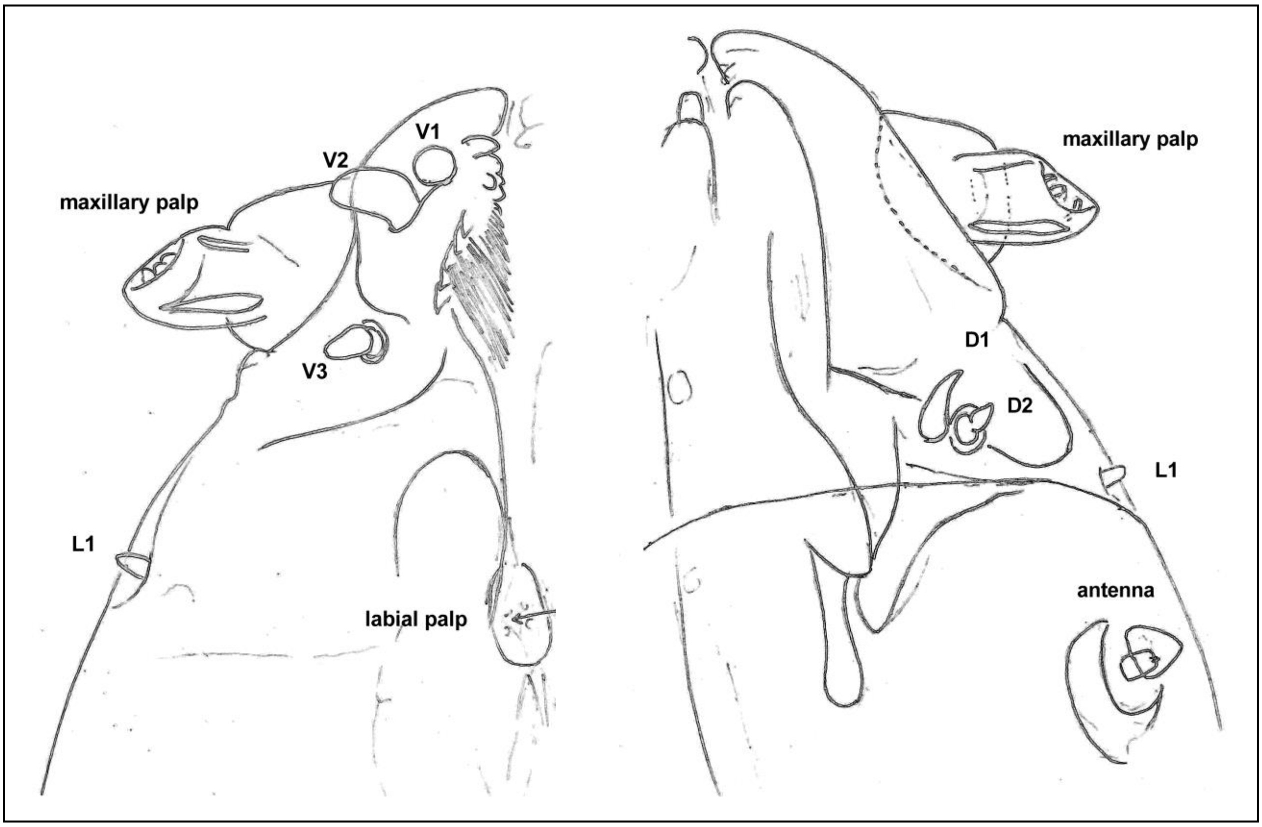
The apparent lack of reliable characters to separate therevid larvae limits the scope of ecological studies on larvae since preserved material takes considerable time in preparation for possibly unreliable identification. The only reliable way to identify individuals remains rearing large final-instar larvae to at least pupa which can usually be identified to species using the provisional keys and figures in Skidmore (2001) and Drake (2004).

Table 1. Features of the head that differ slightly between species.

Feature	*Acrosathe annulata*	*Cliorismia rustica*	*Spiriverpa lunulata*	*Thereva nobilitata*, *bipunctata*
maxillary palp	short, its internal dark walls not higher than the greatest external width.	intermediate length, dark walls equal to greatest external width.	clearly longer than wide, its internal dark walls about 1.25 times the greatest external width.	clearly longer than wide, its internal dark walls about 1.25 - 1.8 times the greatest external width.
V2	swollen and medium-length to long	swollen and long	swollen and long	relatively small, about the same length as V3 (but wider)
V3	short	long	short	long
L1	short	short	short	moderate length (L=3xW)
D1	small to moderate length (up to twice length of D2)	moderate length	short or moderate	long and narrow
D2	present	present	slender and short or absent	present
mandible - blunt points on its outer edge (N=1 per species)	c. 12	c. 9	c. 8	c. 7-9
tentorium in dorsal view		sides usually straight	sides usually slightly sinuous	
metacephalic rod side appendages		tips clubbed	tips curved but not wider than its shaft	

Figure 1. Front of head. Ventral (left) and dorsal (right).

Acrosathe annulata



Cliorismia rustica

Spiriverpa lunulata

Thereva nobilitata

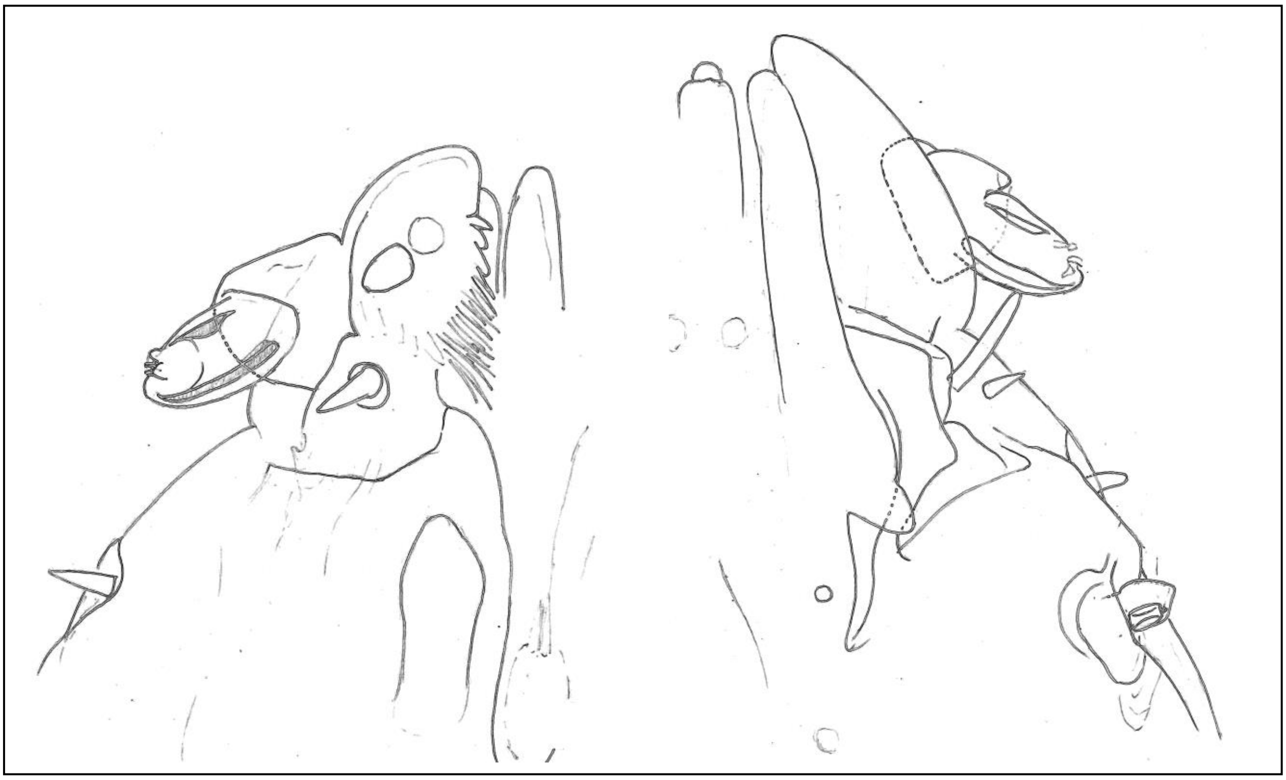
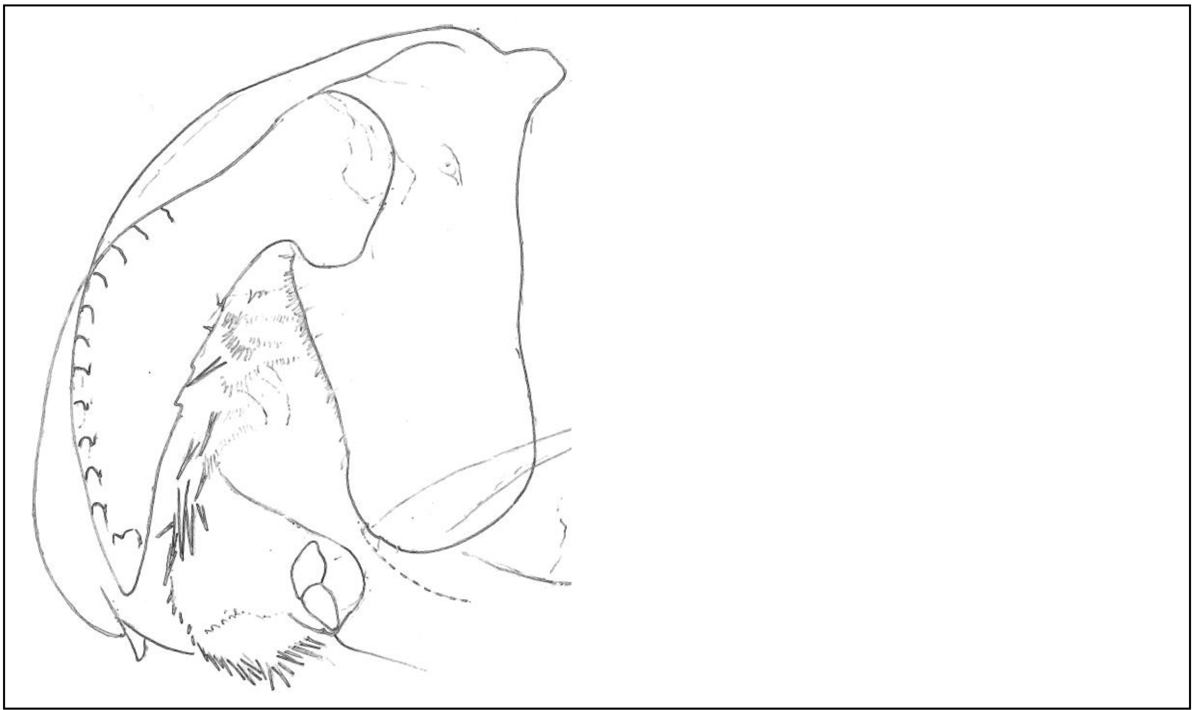


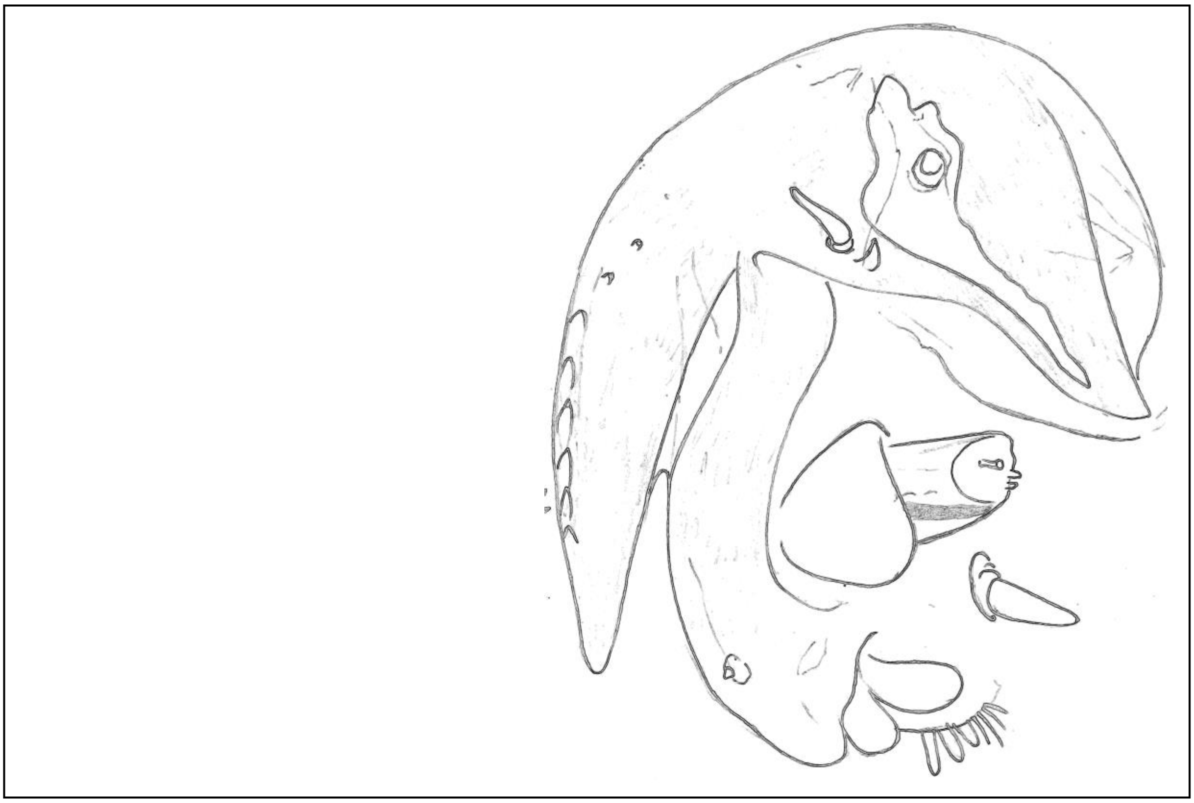
Figure 2. Mouthparts. Inner side (left), outer side (right).

Acrosathe annulata



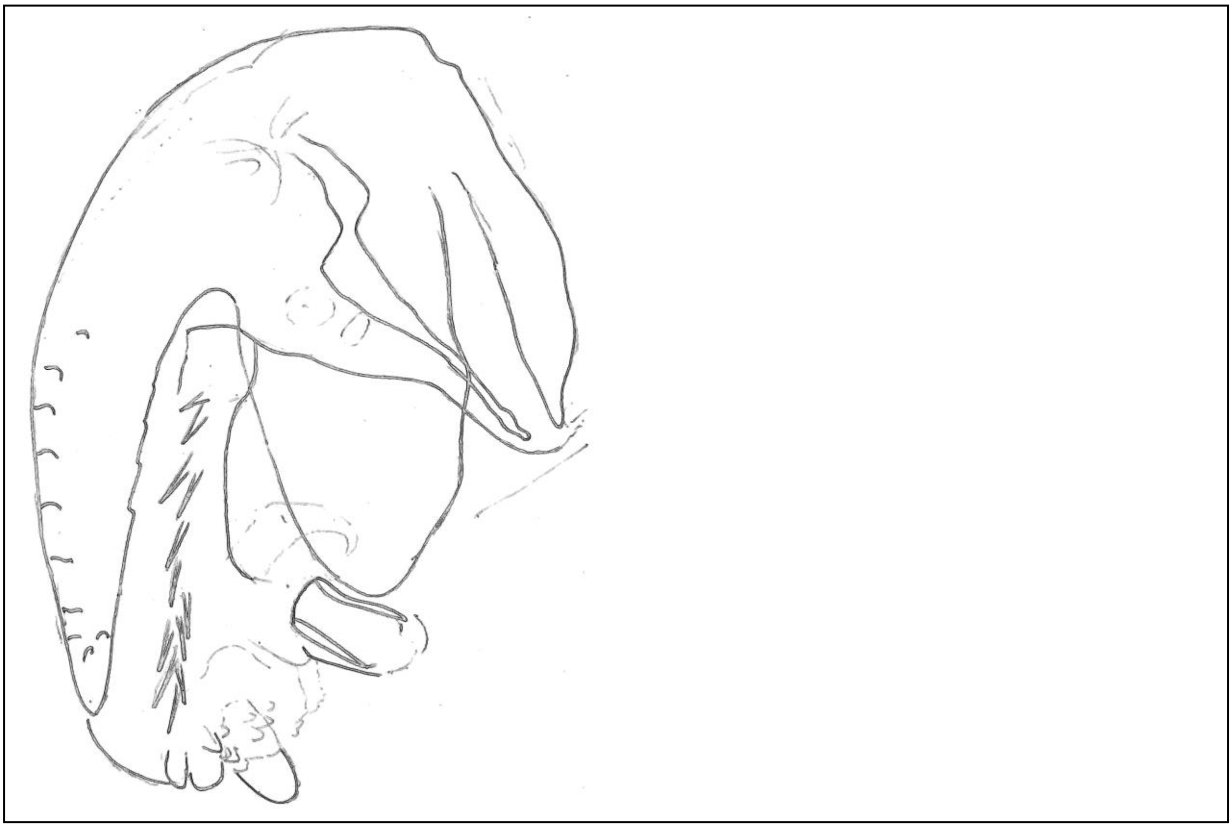
Cliorismia rustica

Spiriverpa lunulata



Thereva nobilitata

Thereva bipunctata



Project 3. Ecology of the BAP therevids

Methods

Field methods

As reported for Project 2, no characters could be found to reliably separate the larvae of different genera of therevids. It was therefore necessary to rear larvae to establish their identity.

Samples were taken along transects running either at right-angles or parallel to the rivers along a zone that appeared to be most suitable for larvae of *Cliorismia*. At each sampling point, the soil was quickly removed using a small shovel from a quadrat 32x32cm in area (~0.1m^2) down to a depth of about 5cm, and placed on a polythene sheet. It was passed through a coarse sieve (5mm mesh) in small quantities so that, as the 'rain' of material fell onto the sheet, larvae could be seen. This method differed from that used in the 2004 study when a fine-meshed sieve was used to retain larvae, but the new method had to be adopted since the sand was damp so would not pass through a fine sieve (the weather in 2004 had been dry so that the soil was dry to several centimetres depth). It was later found that carefully but quickly scooping the material aside on an advancing face about 2cm deep worked effectively and was slightly quicker than sieving the large quantity of sand removed using the shovel. Both methods worked well even in light rain. To supplement rearing results, large larvae were occasionally sought casually in promising-looking patches of habitat.

Transects varied in length and in the spacing between samples. On steep banks with rapidly changing conditions, samples were taken at 1m intervals (sometimes less), whereas those from transects parallel to the river were sometimes spaced up to 5m apart.

Environmental variables were noted on a form (Table 2) Variables were measured directly (distances), estimated as percentages (vegetation cover, shade, particle size by volume) or on simple scales (volume of roots, twigs and dead leaves, likelihood of flooding), or as presence/absence (topography type, soil compaction and wetness, presence of large animals).

Horizontal distances were measured using a tape measure; the vertical distance above river level was estimated using a 1m marked pole, although this incurred some inaccuracy. However, as river level was itself variable, the exact height was probably of less importance than the relative height. For instance, on one day, the level of the Usk dropped by about 50cm during the day's work, after heavy rain had stopped.

To supplement the measured variables, a photograph of each sampling point was taken from about 1m above the ground, pointing vertically downwards. A file of these images was deposited with Buglife.

Large and medium-sized larvae were kept live in separate tubes. Previous experience had shown that small larvae almost invariably died in captivity, so nearly all small individuals (less than about 15mm long) were preserved immediately in the field.

Invertebrates that may have been prey items of the therevids were noted, although only to a crude level of identification.

Laboratory methods
In the laboratory, larvae were kept individually in small pots (5 x 6 cm) with about 10mm of finely sieved sand. They were fed every 7-10 days on *Calliphora vomitoria* (blow-fly) and *Musca domestica* (house-fly) larvae sold as fishing bait. The sand was watered using rain-water every few days, and allowed to dry out between watering. The tubs were left exposed without tops and inspected weekly for pupae. As the pupal period is well over a week, this procedure allowed maximum air circulation (to prevent mould forming) with no loss of flies. The pupae and last larval skin were put into smaller tubes which were stopped using tissue paper. Some flies did escape at this stage as I underestimated their ability to push past tissue placed too loosely in the mouth of the tubes, but most specimens could still be identified to genus from the pupal exuviae.

All flies that emerged were preserved dry with their pupal and larval exuviae in tubes. As about 100 were reared, and about 60 had already been mounted from previous work, there was no need to mount this material. It is available should any other worker wish to use it.

The length of larvae collected from the Rother and Bollin was measured by restraining the larvae in the sharp fold of a piece of graph paper. Those from the Usk were estimated into crude size classes large or medium, corresponding to the last and penultimate instars.

Statistical analysis
Parametric statistics were used to test for the important environmental variables that influenced the distribution of larvae, although the method of sampling may contravene the requirement of random sampling. Variables were correlated with the numbers of larvae using Pearson correlation. This was useful in identifying possibly influential variables, but could not indicate which were most important. The most important variables were therefore sought using forward stepwise multiple regression which indicates the variables accounting for most of the variation in larval numbers. This method takes each variable in turn and selects the one that explains most of the variance in the larval data (i.e. has the smallest residual variance in the regression). The tests for entering and retaining a factor is that its regression coefficient is significant at $p \leq 0.05$ for entering it and $p \leq 0.1$ for retaining it (the defaults in the software used). The process is repeated, adding the next best factor, until no factor passed the test for retaining it. Data from each river were treated separately since the rivers' morphologies were very different.

Table 2. Field form for environmental variables measured for Therevid larval study.

River	Site	Sample					Grid ref				
		1	2	3	4	5	6	7	8	9	10
distance to next											
height above river											
likelihood of flood											
topography	flat - gentle										
	slippage										
	cliff base										
	pasture										
distance from	river										
	tall herb										
	scrub										
	bare sand										
shade	trees										
	scrub										
	tall herb										
plant cover	grass sward										
	short herbs										
	tall herbs										
	scrub										
particle size	sand										
% volume	grit										
	pebble										
	stone										
	soil										
compaction	loose										
	surface pan										
	subsurface pan										
	solid										
comments	dry to ...cm										
on soil	damp										
roots etc	fine roots										
	twigs										
	leaves										
	dung										
animals	cattle										
	sheep										
	horse										
	rabbit										
invertebrates	therevids										
notes											
photo											
sketch											

Sites

River Bollin, Cheshire

The site was just downstream of the sewage works at Prestbury (SJ893788), and is described in Bates *et al*. (2006). The river here passes through sandy soils in a narrow floodplain less than 100m wide, bordered by steep but low valley into which the river has eroded sandy cliffs up to 5m high. Most of the river in this area runs through sheep and cattle pasture, or passes through woodland. At the sampling site, the land between the river and the valley side is open ungrazed rough vegetation superficially resembling heathland with some willow and alder scrub. The floodplain narrows at this point and this probably leads to flooding sufficiently severe to scour the land of vegetation. The river was about 8m wide and was easily crossed in wellington boots. Although the floodplain here is confined by steep sides, the floodplain itself is relatively flat and close to river level so that no sample was estimated to be more than 0.6m above river level. It is likely to flood often.

Five transects were taken, two close together on the right-hand bank in mainly open vegetation, and three on the left-hand bank, passing from open ERS into the willow and alder scrub. The site was visited on 13-14 May 2006.

River Rother, West Sussex

The river at Habin was surveyed for fly assemblages in the Buglife project in 2005. The wide floodplain here is composed of sand into which the river has eroded a deep, steep-sided channel about 5m deep. The river's banks fall suddenly from the flat cattle pasture, with a small 'cliff' usually about 1m high at the top and a steep pile of eroded material below that falls away into the water and is covered in dense rank vegetation with occasional bare areas caused by slippage or cattle trampling. It provided a strong contrast with the flat, sparsely vegetated banks of the Bollin and much of the Usk.

Transects were taken at four points along a 200m section. Four transects ran along the banks, and two down it. The site was visited on 9-10 May 2006.

River Usk, Gwent

Three main sites were investigated: Llanvihangel Gobion (SO3408), Great Hardwick (SO3010) and Scethrog (SO105243). The first two of these had been sampled for larvae in the 2003 CCW study and were known to support good populations of *Cliorismia* and, at Llanvihangel only, *Spiriverpa*. Scethrog was surveyed in the Buglife project in 2005 when *Spiriverpa* adults were found. It had similar characteristics to Llanvihangel so was chosen to provide a second site for studying *Spiriverpa*. The Usk is a broad river flowing through sandy deposits at these sites although the shore and bed are stony. Its banks are mostly steep with a small cliff at the top (usually about 1m high) dropping down from pasture, then a moderately steep slope of eroded material with varying amounts of vegetation cover. At both Llanvihangel and Scethrog there is a wide plain of ERS.

Four transects were taken down the steep bank at both Llanvihangel and Great Hardwick, and one on the ERS plain at Llanvihangel. This last was abandoned after a while as no larvae were found in the quadrats, nor in casual searches across the area. Previously, larvae were quickly found by looking under dry cow pats but none were found in 2006 using this method. A transect was started at Scethrog but abandoned as no larvae were found, either in the transect quadrats or in extensive casual searches across the ERS. These two transects on flat ERS were expected to reveal *Spiriverpa*. In place of these, more transects were taken on the river banks where *Cliorismia* is found. The site was visited on 20, 29 and 30 May 2006.

Results

Rearing

A total of 188 quadrat samples were taken (52 on each of the Bollin and Rother, 84 on the Usk). These contained 288 therevid larvae, 74 of which were small and therefore preserved immediately (i.e. 26% of all seen). The remaining 214 larvae, along with about 30 larvae collected outside quadrats, were kept alive for rearing. *Cliorismia* adults were reared from 118 larvae (producing 61 males, 49 females and 8 that escaped), *Spiriverpa* from four larvae (two of each sex) and *Thereva nobilitata* from six larvae (4 females, 1 male, one escaped but identified from the pupal exuvia). Ten larvae were still alive and well at the time of writing (August 2006), but the remainder died. The success rate in rearing 128 adults from 244 live larvae was therefore 52%.

It was assumed that larvae that died and those that were preserved in the field were distributed among these three genera in the same proportion as those successfully reared, so that, to a rough approximation, all larvae belong to *Cliorismia*. This simplified interpretation of the quadrat counts but incurred a small error. The reared *Spiriverpa* were from Llanvihangel on the Usk, and comprised 8% of reared individuals from there. Five *Thereva* were from the Rother, comprising 14% of reared individuals, and one from the Usk. The error was therefore moderate for the Rother, small for the Usk and apparently not an issue for the Bollin. The real error may have been greater if the assumption that species are distributed in the proportion of reared adults was not true, but clearly this could not be checked.

Transect counts

The abundance of larvae was low in most quadrats. About 60% of all quadrats contained no larvae, and some transects included almost no larvae at all. The most found in one quadrat was 12 larvae. Mean density varied widely between transects, ranging from 5 – 30m^{-2} on the Bollin, 1 – 37m^{-2} on the Rother and 0 – 13.6m^{-2} on the Usk (Table 3). The quadrat area was 0.1m^2, so these densities are ten times the mean counts given in the table. The highest densities were therefore moderately similar between sites, despite the large intra-site variation.

Table 3. Mean and maximum numbers of therevid larvae in quadrat samples, and the number of quadrats containing no larvae.

River	Transect	Quadrats taken	Zero cells	Mean number	Maximum count
Bollin	A	8	2	0.5	2
	B	10	5	1.2	4
	C	14	6	1.86	6
	D	15	8	3.0	12
	E	5	0	2.0	3
	all	52	21	1.87	
Rother	A	10	8	0.6	5
	B	10	9	0.1	1
	C	10	7	0.6	3
	D	10	3	3.7	9
	Dx	5	2	1.8	7
	E	7	2	2.43	7
	all	52	31	1.46	
Usk	A	12	10	0.25	2
	B	10	8	0.3	2
	C	14	3	1.36	3
	F	6	6	0	0
	G	6	4	0.33	1
	H	6	5	0.17	1
	I	10	4	2	5
	J	10	4	0.2	5
	K	10	9	0.2	2
	all	84	53	0.83	

Representative transects
Bollin

Three transects are shown (Fig. 3) Transects C and D were taken 20m apart. The land was flat and low-lying relative to the river, as shown by the profiles (Figs. 4, 5 & 6). The bank fell sharply into the river at the edge of B, but more gradually at C and D where the shore was wet ERS. Therevids (which were probably all *Cliorismia*) became more frequent away from the river. The dips in numbers on the landward side of all transects coincided with damp depressions with more silty conditions.

The percentage cover of short and tall herbs is shown for all three transects. The occurrence of larvae showed no particularly strong association with cover of these larger plants, but it was clear that tall herbs did not suppress the numbers of larvae. The cover of grass is shown for transect B to demonstrate that high cover of grass did not necessarily depress the numbers of larvae. The grass was in loose tussocks rather than close-cropped sward, so there was abundant loose sand below the aerial parts of the plants.

Shade cast by willow and alder scrub also was no deterrent to the larvae, and on the contrary it is thought that light shade is a requirement of the larvae.

Figure 3. Bollin showing the positions of transects B, C and D, and the view along each of these transects.

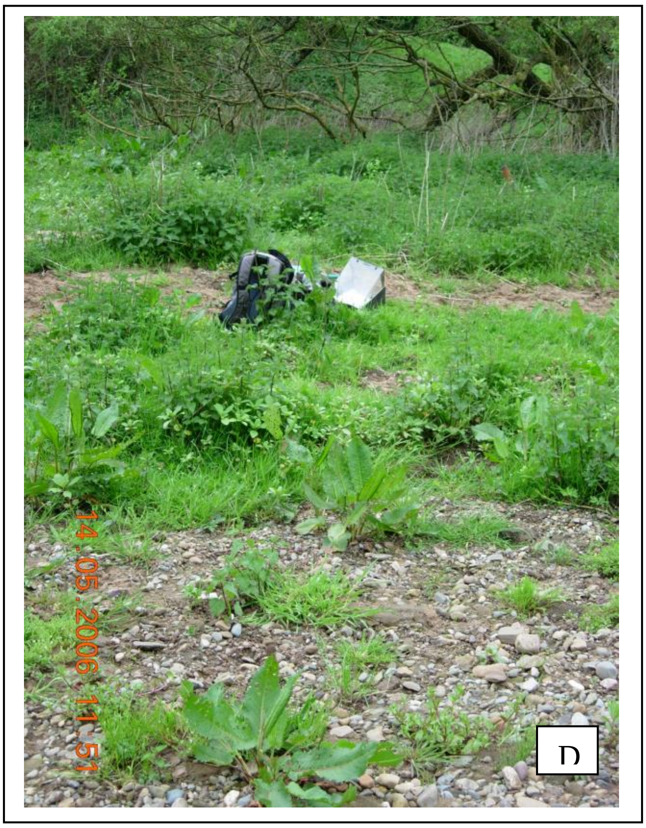


Figure 4. Bollin transect B.

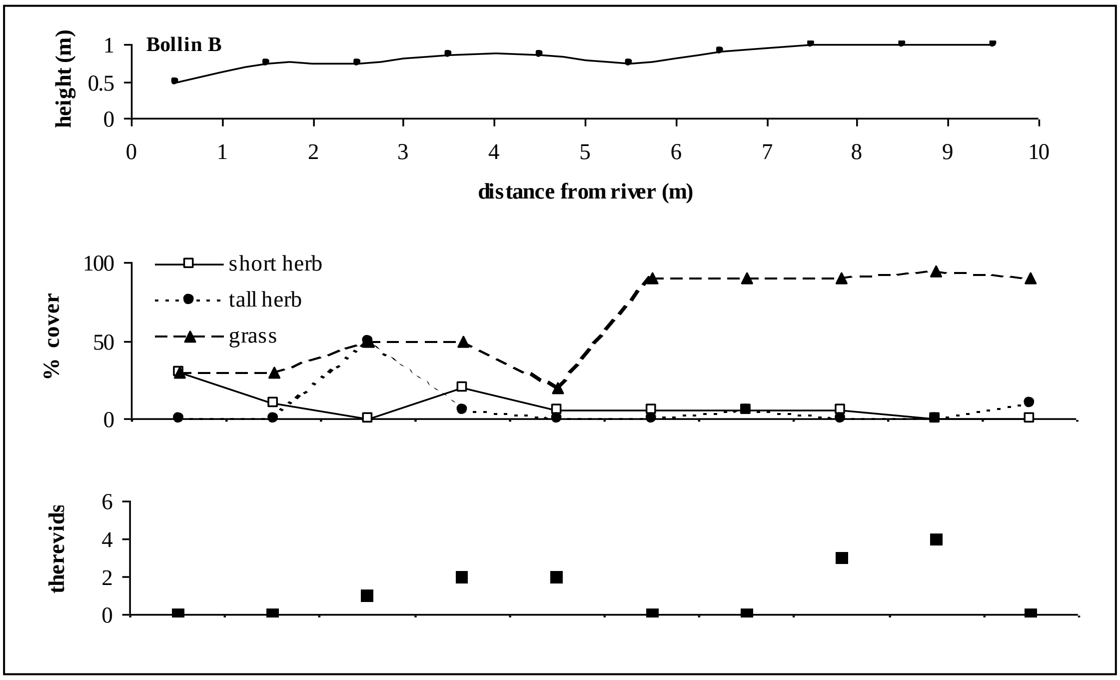


Figure 5. Bollin transect C.

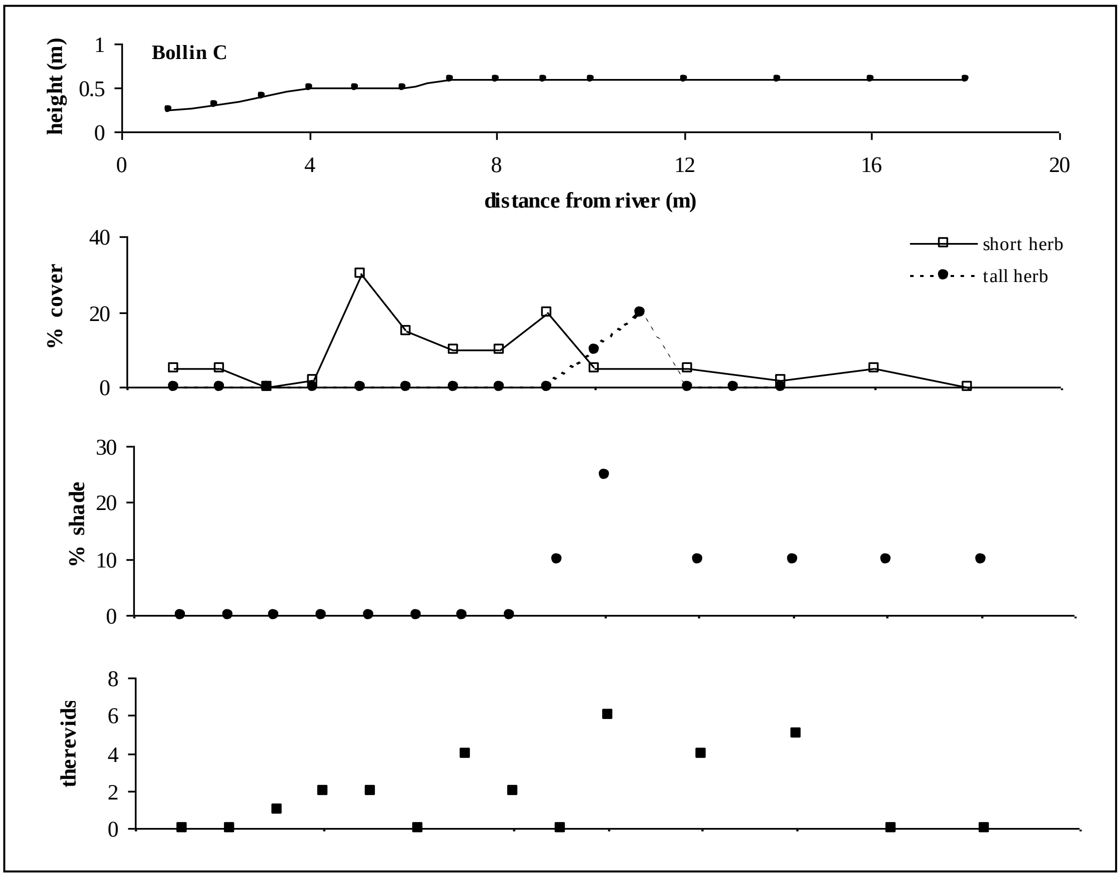
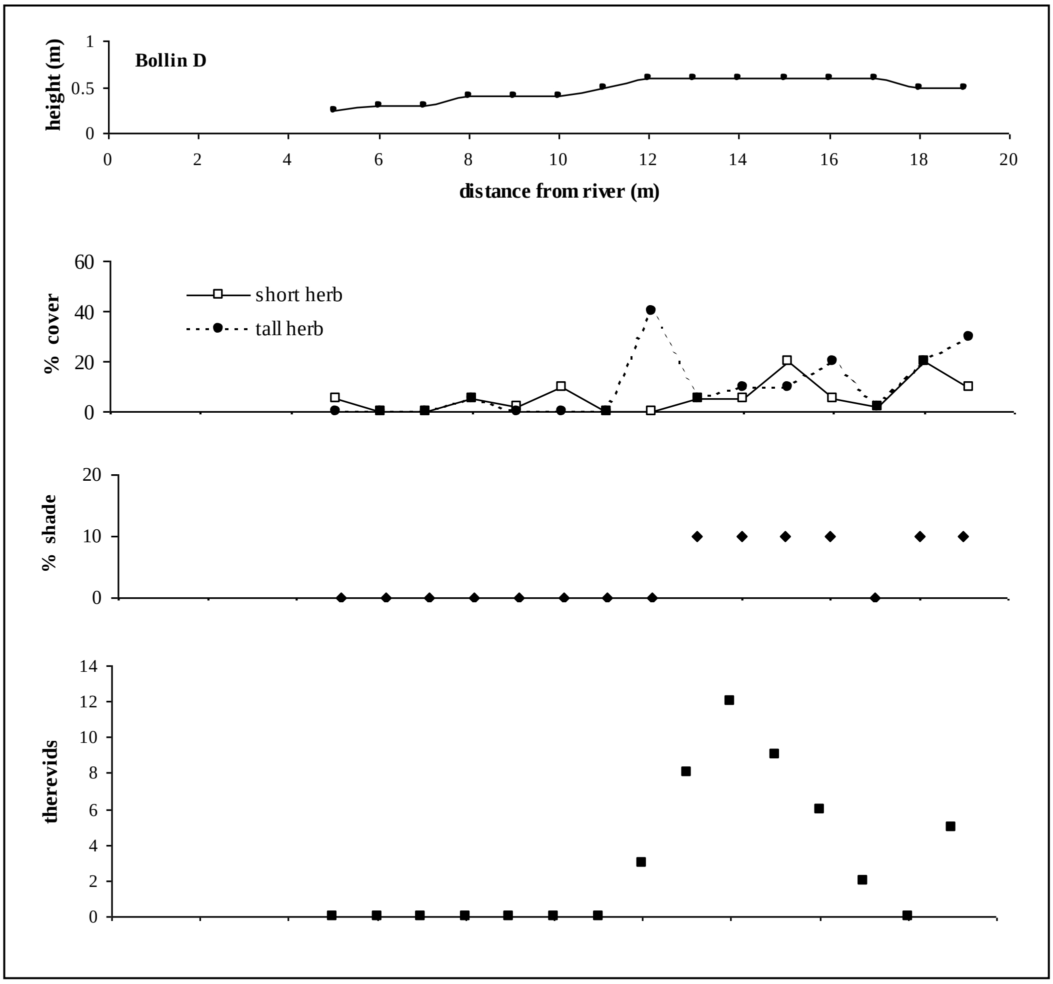


Figure 6. Bollin transect D.

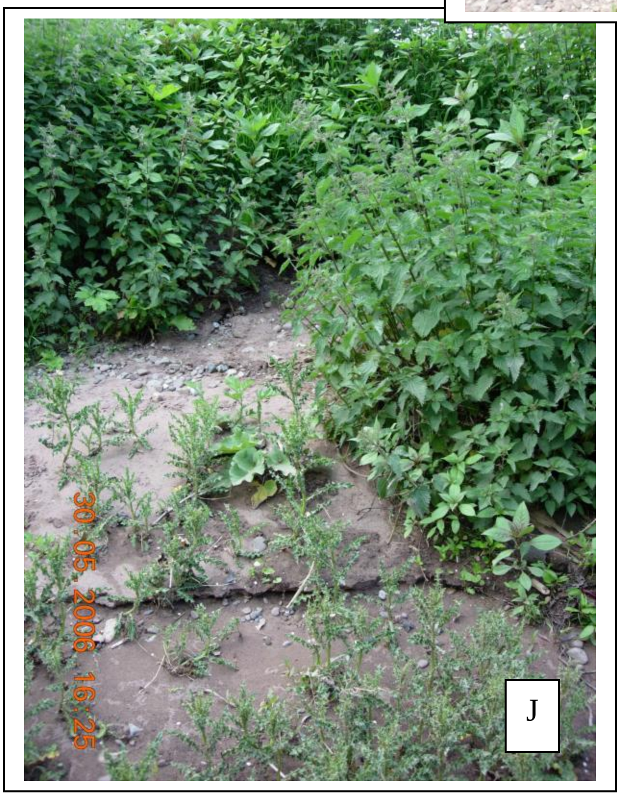


Usk

Three transects at Great Hardwick are shown as these demonstrated marked differences in the abundance of larvae over a short stretch of bank (Fig. 7). Transect I passed from the stony shore up the bank through willow scrub over Himalayan balsam on loose sand. Transect J, just outside this scrub, passed from a wet sand shore through dense nettles and Himalayan balsam with associated leaf litter on loose sand. Transect K ran from wet shore across bare sand (not visible in the photographs) then across tight sward grazed by sheep. The distance between each transect was about 15m. All transects stopped at the tightly grazed sheep pasture.

Larvae were absent on the damp sand and gravel of the lower parts of all transects by the river but number rose quickly on higher ground where the sand was loose in transects I and J (Figs. 8 & 9). Numbers declined again at the top of these two transects as the sand was replaced by compacted sandy soil where grass sward became dominant. All the productive quadrats of both transects I and J were under the shade of willow, Himalayan balsam or nettles. In contrast, the exposed grass sward of transect K was extremely unproductive and only two larvae were found in one of ten quadrats (Fig. 10).

Figure 7. Usk at Great Hardwick, with positions of transects I, J and K.



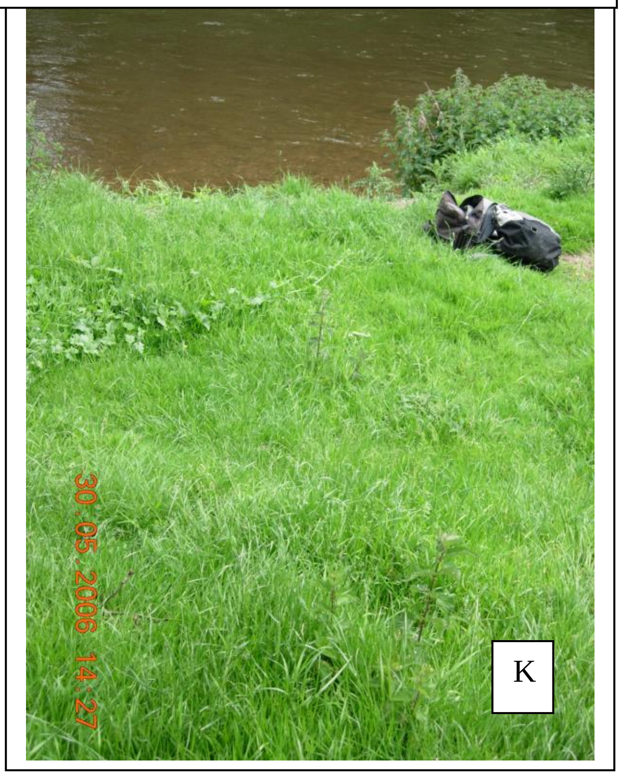


Figure 8. Usk transect I.

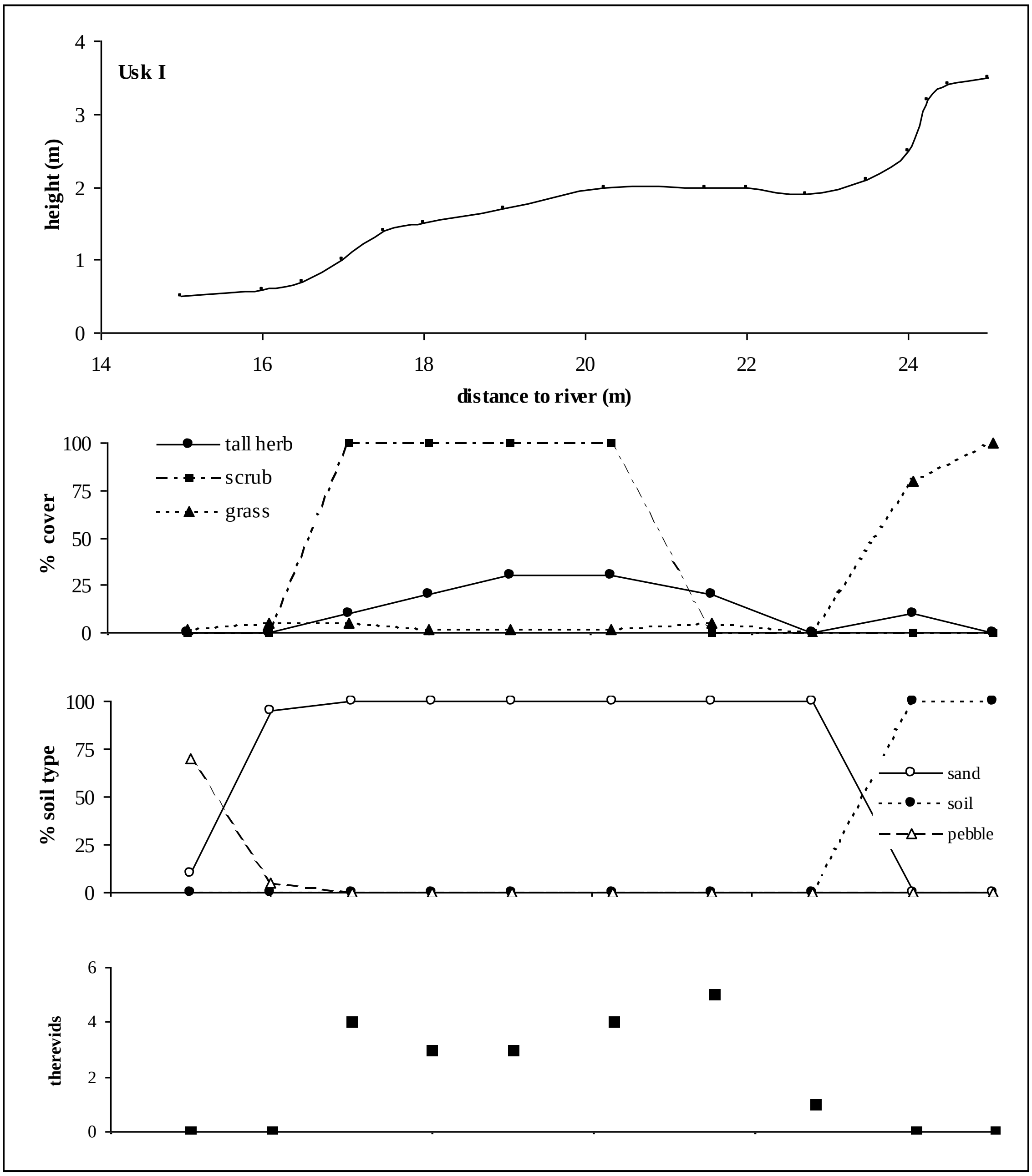


Figure 9. Usk transect J.

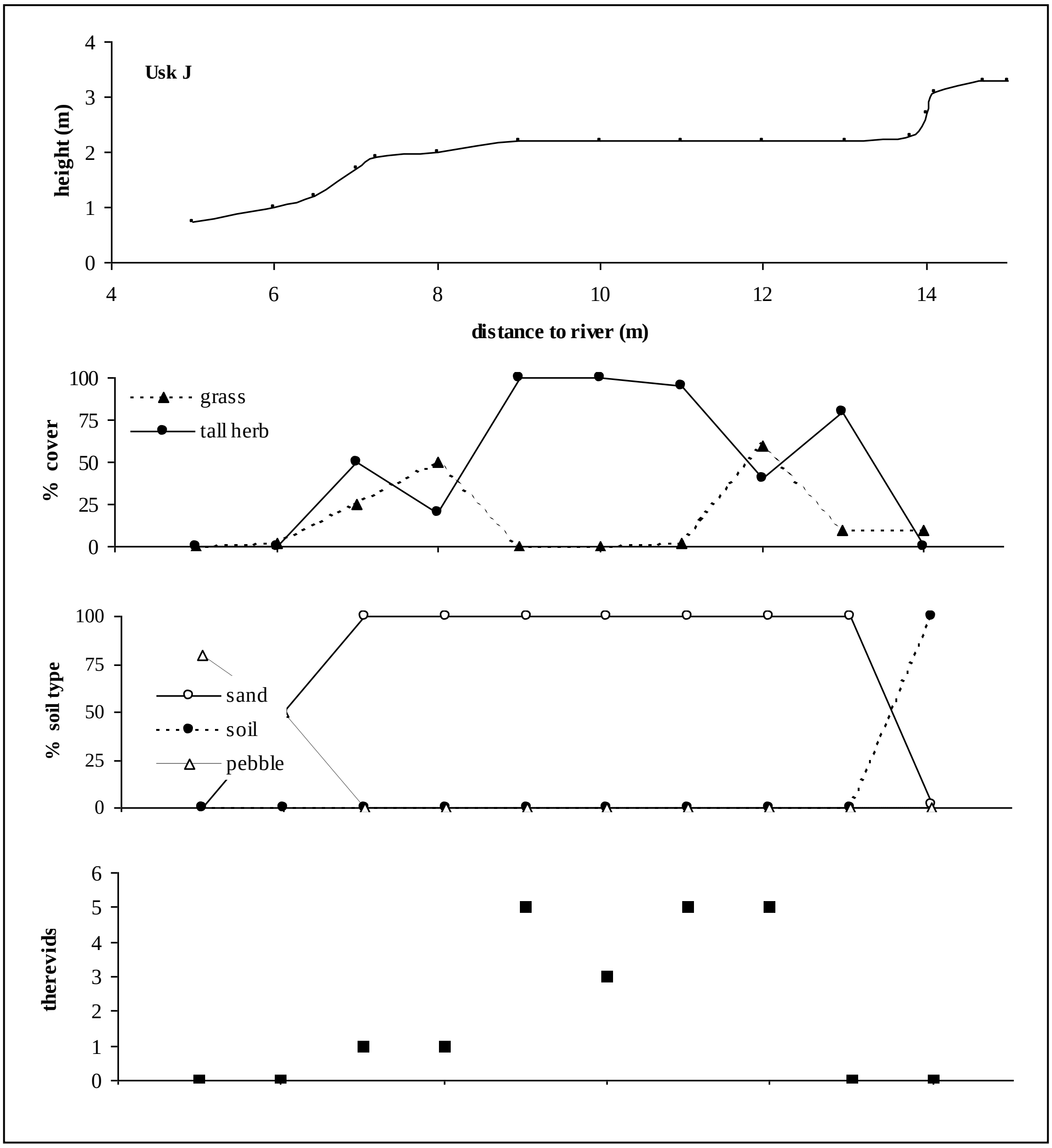


Figure 10. Usk transect K.

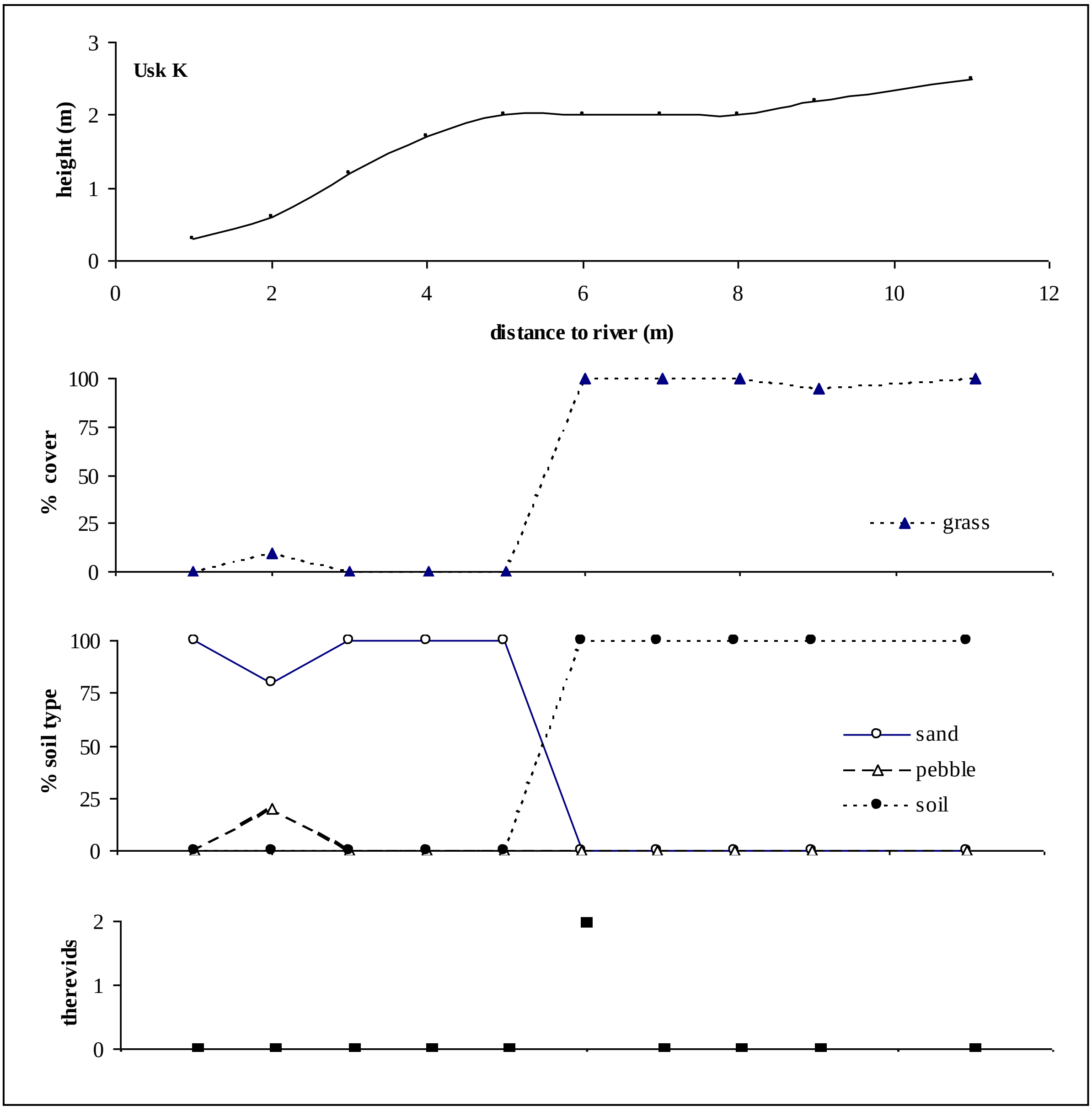


Fig. 11. Rother transects Dx and E, showing level plateau and steep drop to river (D, above and left), and dense tall herb at the top of E and running down the slope (below).

Figure 12. Rother transect Dx.

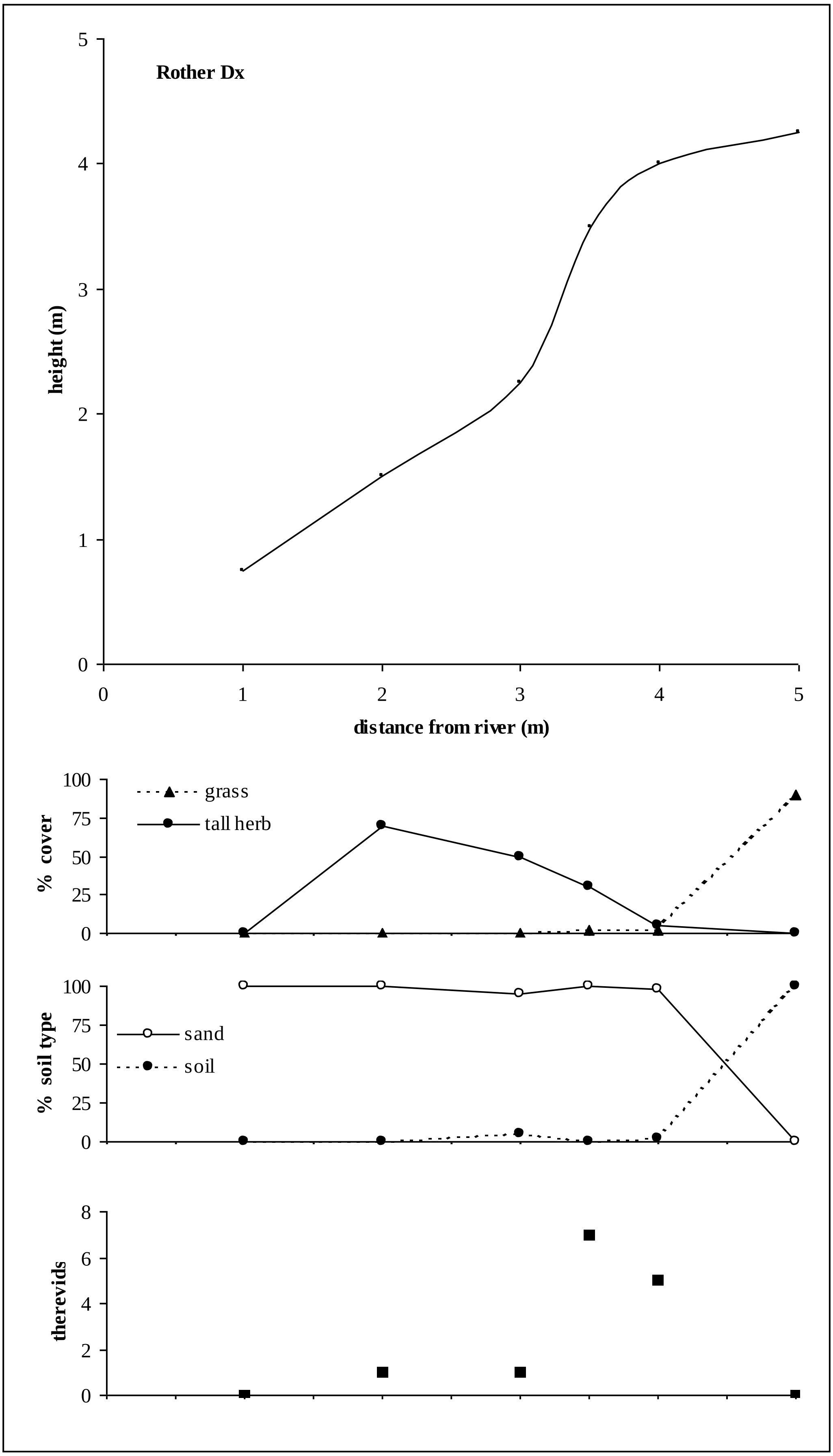
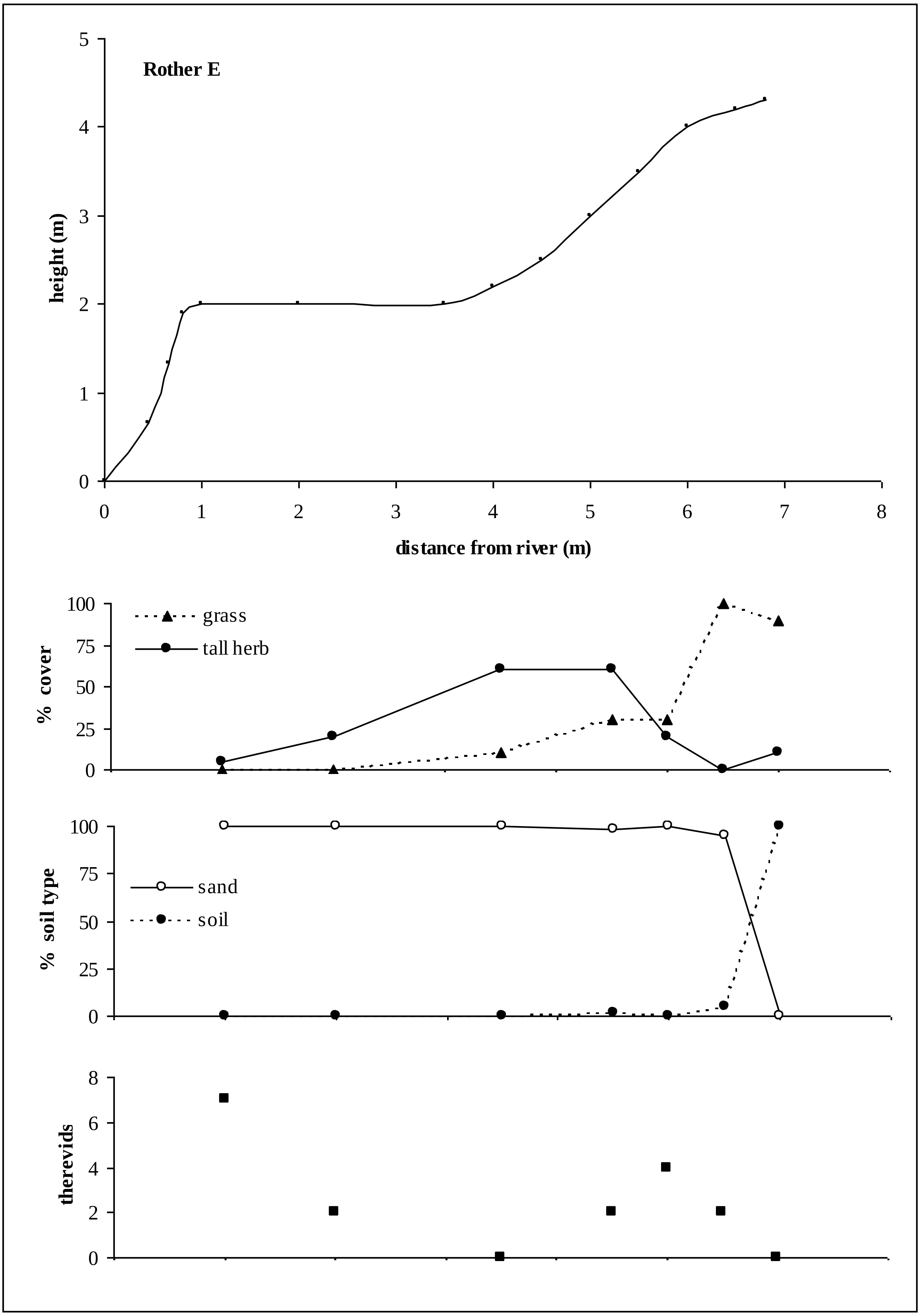


Figure 13. Rother transect E



Rother

The Rother banks were even steeper than those of the Usk at Great Hardwick (Figs. 11, 12 & 13). Therevid larvae were usually absent at the damper foot of the steep slope; occasional individuals were found in the loose sand and had probably fallen down to this level over their life-time. Numbers were moderately high on more level areas under tall herb (nettles, Himalayan balsam, cleavers, dock) and became scarce as the grass sward closed over towards the top of the slope where the substrate changed from loose sand to compacted sandy soil.

Highest numbers were clearly associated with the loose sand in the zone above the damp foot of the slope and below the closed grass sward of the pasture. Few were found in almost completely bare patches of sand, and most were clearly associated with light shade under tall herbs.

Strongly associated variables

Multiple regression

As might be expected, multiple regression did not select all the same variables on the three river (Table 4). On the Bollin, the initial run with all variables suggested that only two variables contributed significantly to explaining the numbers of larvae, which increased with the percentage of shade cast by tall herbs and decreased the further away from bare sand. The latter was considered to be a poor variable since the few samples far from bare sand were devoid of larvae, and all quadrats with larvae were within 2m of bare sand, and showed no relationship at this small scale. This variable was therefore excluded. The model then selected shade cast by tall herb and trees (which had been separately scored) and dampness. Together these accounted for 42% of the variation in larval numbers. When scrutinised in isolation, these variables appeared to correlate with numbers of larvae, although clearly there was considerable scatter of point. The small range in the values of all these variables resulted in most points lying in only two or three clusters when plotted against the numbers of larvae, so graphical presentation added little to the understanding.

On the Rother, five variables had a significant effect on the distribution of larvae, and together accounted for nearly half the variation in larval numbers ($r^2 = 0.462$). Numbers of larvae increased with the height above and distance from the river, and with increasing cover of tall herb, but decreased as the amount of soil increased in the substrate or when at the cliff base. The explanatory power of each of these variables individually was poor, with the exception of height above river. This is illustrated by some examples of linear regression plots of variables against numbers of therevid larvae (Figure 14). These graphs show the regression line and its 95% confidence limit (the curved lines), and also the limits within which new data points may lie. These outer lines are very widely spaced, indicating the these single regressions had poor predictive power. The proportion of variation explained (r^2) was also minute. Therefore, although the multiple regression picked out these five variables as explaining most of the variation in therevid numbers, only height above the river appears to be a particularly strong explanatory variable. The others cannot be dismissed, since not only does the multiple regression model select them, but they were among the features that appeared to be important in the field.

The initial run for the Usk with all variables selected six that fitted the selection tests, but three of these had only 3 or 4 non-zero values out of 84 quadrats (cover of scrub, abundance of twigs, presence of slippage). They were excluded and the regression run again. Two of the original variables were again selected (percentage shading by tall herbs, abundance of leaves) but the ordinal variable gentle/flat (referring to topography) was not selected in the second run. Thus the number of larvae appeared to be greater in the shade of tall herbs and inversely related to the abundance of tree leaves in the substrate. There appeared to be a conflict in conclusions here since larger amounts of leaf litter were often found under stands of tall herbs.

Correlation
The variables were tested one-by-one against the numbers of larvae using Pearson correlation. The usual significance level of $p \leq 0.05$ was relaxed, and values significant at $p \leq 0.1$ were also accepted. When the significance and sign of the correlation coefficients are compared across the three rivers, some factors recur and suggest trends that would help explain the abundance of larvae (Table 5).

Strong or consistent trends are that more larvae are found:

- higher above the river, or in the case of the low-lying flat ERS at the Bolin further from the river's edge
- close to or under tall herb, and in its shade.

Weaker or less consistent trends show more larvae are found:

- in sandy sediment
- in loose substrate (not consolidated)
- in dry or damp sediment but avoiding wet areas
- where there were more earthworms.

Weak but always negative trends show fewer larvae are found:

- in grass swards and pasture
- in consolidated soily substrate
- in gritty, pebbly or stony sediment
- where there were fewer tipulid larvae.

Figure 14. Linear regressions of some example environmental variables on number of therevid larvae from the Rother.

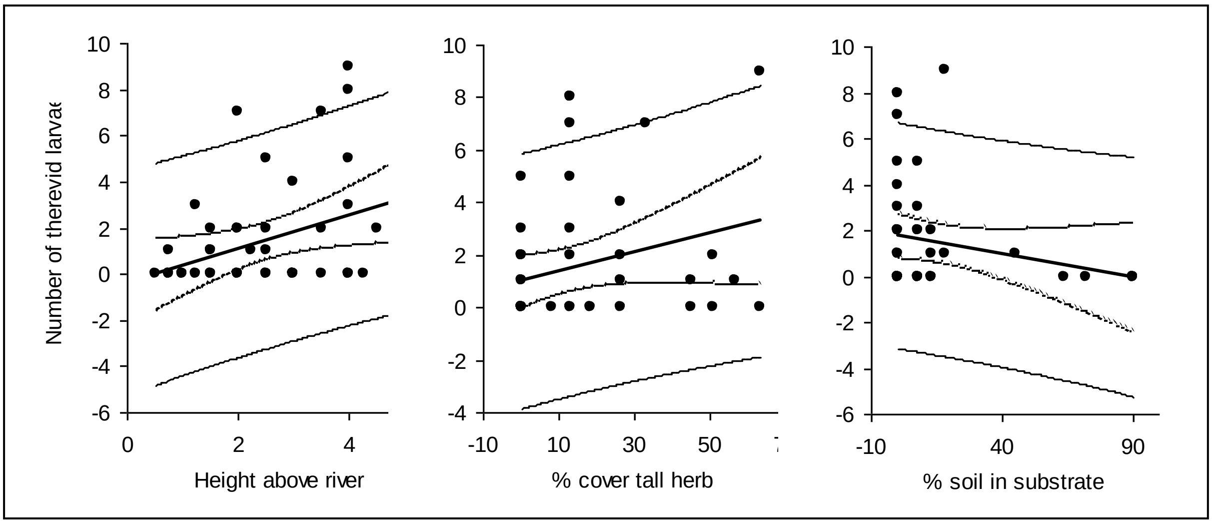


Table 4. Stepwise multiple regression of larvae against environmental variables for each river.

The important variables are shaded.

Rother

Analysis of Variance

Source	DF	SS	MS	F	Prob.>F
Regression	5	158.929	31.786	9.748	0
Residual	46	149.994	3.261		
Total	51	308.923			

Correlation

r	0.717
r^2	0.514
Adjusted r^2	0.462

Variables in Model

Variable	Coef.	SE	SD	t	Prob.>t	VIF	TOL
height above river	1.37	0.686	0.263	5.209	0	1.645	0.608
% soil in substrate	-0.04	-0.46	0.01	-3.969	0	1.273	0.785
distance to river	-0.468	-0.35	0.173	-2.709	0.009	1.581	0.633
quadrat at cliff base	-1.883	-0.315	0.626	-3.006	0.004	1.044	0.958
% cover tall herb	0.03	0.232	0.014	2.167	0.035	1.084	0.922

Constant	0.347

Bollin

Analysis of Variance

Source	DF	SS	MS	F	Prob.>F
Regression	3	157.181	52.394	13.039	0
Residual	48	192.877	4.018		

Total	51	350.058						

r	0.67
r^2	0.449
Adjusted r^2	0.415

Variables in Model

Variable	Coef.	SE	SD	t	Prob.>t	VIF	TOL
% shading by tall herb	0.265	0.68	0.048	5.565	0	1.299	0.77
% shading by trees	-0.208	-0.284	0.089	-2.342	0.023	1.282	0.78
dampness	-1.375	-0.233	0.638	-2.156	0.036	1.017	0.983
Constant	2.821						

Usk

Analysis of Variance

Source	DF	SS	MS	F	Prob.>F
Regression	2	84.727	42.363	44.599	0
Residual	81	76.94	0.95		
Total	83	161.667			

r	0.724
r^2	0.524
Adjusted r^2	0.512

Variables in Model

Variable	Coef.	SE	SD	t	Prob.>t	VIF	TOL
% shading by tall herb	0.066	0.928	0.009	7.588	0	2.545	0.393
abundance of leaves	-0.563	-0.292	0.236	-2.388	0.019	2.545	0.393
Constant	0.486						

Table 5. Pearson correlation coefficients of the number of larvae with each environmental variable.

Notes. The type of measurement is indicated for variables that were not either direct measurements or percentages. (1,2,3) indicates a 1 to 3 scale, +/- = present/absent. r = Pearson correlation coefficient, p = probability of its significance, signif. gives + for p≤0.05, ≈ for p≤0.1 and >0.05. Empty cells had no measurements for that river.

Variable	Usk			Rother			Bollin		
	r	p	signif.	r	p	signif.	r	p	signif.
number of tipulids	-0.063	0.570		-0.150	0.290		-0.017	0.910	
number of worms	0.180	0.093	≈	0.230	0.096	≈	0.250	0.078	≈
height above river	0.270	0.012	+	0.360	0.008	+	0.091	0.520	
likelihood of flood (1,2,3)	-0.310	0.004	+	-0.510	0.720		0.013	0.930	
distance to river	-0.072	0.520		-0.080	0.570		0.430	0.001	+
distance to tall herb				-0.290	0.040	+	-0.340	0.013	+
distance to scrub							-0.110	0.450	
distance to bare sand	-0.018	0.840		0.037	0.800		-0.270	0.054	≈
% shade by trees	0.028	0.800		-0.015	0.920		0.049	0.730	
% shade by scrub				-0.100	0.460		0.130	0.350	
% shade by tall herb	0.700	0.000	+	-0.004	0.980		0.580	0.000	+
% total shade	0.270	0.013	+	-0.079	0.580		0.470	0.001	+
% cover grass sward	-0.076	0.490		-0.180	0.200		-0.140	0.320	
% cover short herb	0.190	0.077	≈	0.130	0.350		0.081	0.570	
% cover tall herb	0.650	0.000	+	0.280	0.048	+	0.260	0.058	≈
% cover scrub	0.430	0.000	+						
% sand	0.270	0.013	+	0.230	0.100	≈	0.170	0.230	
% grit	-0.087	0.430					-0.220	0.110	
% pebble	-0.160	0.150					-0.240	0.088	≈
% stone	-0.120	0.270					-0.190	0.190	
% soil	-0.200	0.066	≈	-0.230	0.100	≈	-0.036	0.800	
loose particles (+/-)	0.260	0.016	+	0.200	0.160		0.240	0.086	≈
solidly compacted (+/-)	-0.270	0.014	+	-0.220	0.120		-0.130	0.340	
dampness (1,2,3)	-0.070	0.530		-0.150	0.290		-0.300	0.028	+
abundance of fine roots	0.047	0.670		0.068	0.630		-0.150	0.290	
abundance of twigs	-0.110	0.320		-0.068	0.630		0.290	0.035	+
abundance of leaves	0.430	0.000	+	0.130	0.370		0.083	0.560	
flat-gentle (+/-)	0.230	0.037	+	0.170	0.240				
slope (+/-)	-0.110	0.300							
slippage (+/-)	0.110	0.330		-0.180	0.210				
cliff base (or face) (+/-)	-0.170	0.130		-0.210	0.130				
pasture (+/-)	-0.190	0.091		-0.170	0.220				

Discussion

It seems likely that most of the larvae recorded in the field were *Cliorismia rustica*, based on the high proportion of this species among those successfully reared, so much of the following discussion is assumed to concern just this species.

Its preferences appear to be well demonstrated here. Both statistical techniques highlighted tall herbs and the shade they cast on all three rivers as the most important variable related to the abundance of therevid larvae. As shade was correlated with the cover of tall herb and scrub, it may be one of the factors mediating the effect of tall herb on the distribution of larvae. Alternatively, tall herbs suppress more tighly growing low plants, especially grass, and so make the substrate easier for the active larvae to move through.

The cover of grass expressed as a percentage was a misleading measure since loose tall lush growth and tight low sward were scored similar high percentage covers. These were very different habitats at soil level, as loose grass provided only a small amount of cover on the surface whereas a tight sward often had a thatch of rhizomes that bound the soil together. Larvae were often recorded below loose grass but far less often in tight swards. This effect was thought to be only partly due to the difficulty in retrieving larvae from the mass of roots as all sward was dismembered thoroughly during sampling.

There were less consistent trends suggesting a preference of drier, sandy substrate further from the river, and avoidance of hard-packed soily pasture and of sediments with particles larger than sand. Soil texture had a strong influence on the occurrence of larvae. It was obvious during sampling that larvae were most readily found in loose sand, even if the sand was only a thin surface layer (10mm) over more compacted soil. Larvae were often noted in the top few millimetres of sand, and rarely recorded at several centimetre depth, even on cool days with drizzle when the soil would be no warmer near the surface. They were rarely found in hard, compacted soil or soil with a crumb structure, which was the typical condition of the pasture's edge at bank top and often in the soil washed down to the foot of the low cliff at the pasture's edge. Careful measurement of the ease of penetration or looseness of the top 10mm of soil is likely to have provided a good correlate with larval abundance. This preference is interpreted as a need for sediment through which larvae can move easily in search of prey.

Coupling these conclusions with the distribution along individual transects, there is a clear preference for the narrow zone on the river banks above the permanently wet sand but below the closed sward of the pasture on top. This zone usually has softer sandier sediment, and may be either eroding, as on the Rother and Usk, or slightly stabilised ERS, as on the Bollin. Within this zone, the larvae prefer lightly to moderately shaded ground below tall herbs consisting often of nettles, creeping thistle and Himalayan balsam below which the vegetation at ground level has a low density. Larvae were also notably frequent under sallow and less so under alder where light shade allowed a profuse growth of tall herbs, usually Himalayan balsam. Open sandy areas were avoided.

It seems clear, therefore, that *Cliorismia* is not a species of exposed riverine sediment but the continuity of its habitat does depend upon the same hydrological conditions required by true ERS species.

Slightly different conclusions were drawn from the earlier study of therevid larvae (Drake, 2004) who suggested that *Cliorismia* larvae were not especially more frequent where tall herb was present within 5m of the quadrats. This result may have arisen from the cruder assessment of nearby tall herb and scrub. The preference for open or sparsely vegetated sand rather than tighter swards, and avoidance of coarser particles was shown in both studies. These trends suggested from the quadrat samples were sometimes contradicted by casual collecting along the banks where larvae were sometimes found very quickly in mole hills in sandy pasture, often several metres from the sloping bank. Conversely, larvae may congregate at molehills as they represent the only loose ground in otherwise tight sward, and perhaps reach them through the disturbed soil in mole tunnels. It is likely that the individuals in the pasture are supplemented by a much larger population on the river banks as it is difficult to imagine these large fast moving subterranean predators making much headway in tight closed swards.

Few useful results were obtained for *Spiriverpa* since only four were reared from three quadrats at Llanvihangel Gobion where a large population was recorded in 2004. However, three larvae were from wet sand very close to the river, and the fourth in sand that may have been submerged in floods that were subsiding as the work took place. Two of the quadrats were in light shade of large trees. In 2003, several *Spiriverpa* larvae were reared from this same stretch of riverbank where they had been collected in partial shade, although the samples' proximity to the river's edge had not been noted (Drake 2004). The wet river-edge habitat of the 2006 records was in strong contrast to the habitat where large numbers were found in 2003 on dry heavily trampled and grazed sandy ERS well away from the river. It seems that *Spiriverpa* may have a wider tolerance of wetness than does *Cliorismia*, but both are restricted to loose sandy sediments.

Management implications

The implications for river management are clear. River banks must be allowed to erode and expanses of sandy ERS to continue being deposited so that the sediment remains unconsolidated and fairly free of organic matter that would lead to a closed grass sward. Conversely, some development of tall herbs or even light willow scrub appears to be particularly important to *Cliorismia*, but apparently not to *Spiriverpa*. The species of herbs is irrelevant; it is perhaps unfortunate that Himalayan balsam happens to produce good conditions for *Cliorismia*. Stabilising banks to the extent that trees cast dense shade may be detrimental. No larvae have been found in such situations in the course of work on the therevids.

Trampling by grazing stock is probably a minor issue. Steep eroding banks, such as those of the Rother and parts of the Usk, are largely avoided by animals even where not fenced. The animals do make narrow churned tracks on these steep banks but these are a small proportion of the area, and larvae were found in them. More gentle slopes where the pasture grades into river bank, such as at Great Hardwick, may be more susceptible since grazing may be responsible for making the tight sward of low value to *Cliorismia*. Nevertheless, the intervening scrubby areas with sheep tracks were among the richest for larva.

Spiriverpa may have little susceptibility to trampling as large numbers were found in the previous study of the heavily trampled and churned Llanvihangel Gobion site on the Usk. Pupal exuviae were also found on the lightly trampled site of Sharperton on the Coquet, and males were seen swarming over a sheep-trampled bank at Bewick Bridge on the Till in 2006.

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