WalliesDeVries, M. (2006): Larval habitat quality and its significance for the conservation of *Melitaea cinxia* in northwestern Europe. – In: Fartmann, T. & G. Hermann (Hrsg.) (2006): Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. Abhandlungen aus dem Westfälischen Museum für Naturkunde. Heft 68 (3/4): 281–294.

Larval habitat quality and its significance for the conservation of *Melitaea cinxia* in northwestern Europe

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Abstract

The Glanville fritillary, *Melitaea cinxia*, is an endangered species in northwestern Europe and characteristic for dry low-productive grasslands. This paper presents the results of various recent studies in Belgium and The Netherlands on the ecology and conservation of the species. It highlights the importance of larval habitat quality in determining the overall suitability of sites for *M. cinxia*. Low-productive vegetation with an open and diverse structure and an abundance of the host plant *Plantago lanceolata* emerge as the main factors determining larval habitat quality. Such sites offer the warm microclimates required by this species at the cool thermal edge of its range. Warm microclimates are threatened nowadays by a combination of climatic warming, excessive nitrogen deposition and changes in land use. However, appropriate measures to restore and maintain habitats may counter these negative trends. Grazing, rotational mowing and top-soil removal in eutrophic sites offer suitable tools to achieve this purpose. Recent developments suggest that efforts in conservation management may prove successful in re-establishing a population of *M. cinxia* in Limburg, The Netherlands.

Zusammenfassung

Larvalhabitatqualität und ihre Bedeutung für den Schutz von *Melitaea cinxia* in Nordwest-Europa.

Der Wegerich-Scheckenfalter, *Melitaea cinxia*, gilt in Nordwest-Europa als gefährdete Art und ist charakteristisch für trockenes Magergrünland. In diesem Artikel werden die Ergebnisse verschiedener aktueller Studien aus Belgien und den Niederlanden zur Ökologie und zum Management der Art vorgestellt. Es wird die Bedeutung der Larvalhabitatqualität als entscheidender Faktor für die Eignung von Flächen für *M. cinxia* betont. Magergrünland mit offenen und heterogenen Strukturen und eine hohe Deckung der Wirtspflanze *Plantago lanceolata* sind die Hauptfaktoren, die die Larvalhabitatqualität bestimmen. Die Habitate an der nördlichen Verbreitungsgrenze weisen ein warmes Mikroklima auf. Warme Mikrohabitate sind gegenwärtig gefährdet durch Klimaerwärmung, übermäßige Stickstoffdepositionen und Veränderungen in der Landnutzung. Geeignete Maßnahmen zur Wiederherstellungen oder Erhaltung der Habitate müssen diesen negativen Entwicklungen entgegenwirken. Beispiele hierfür sind Beweidung, Rotationsmahd und Oberbodenabtrag auf nährstoffreichen Flächen. Aktuelle Beobachtungen aus Limburg (Niederlande) deuten eine erfolgreiche Wiederansiedlung einer Population von *M. cinxia* aufgrund der durchgeführten Naturschutzmaßnamen an.

1 Introduction

The development of metapopulation theory (HANSKI 1999) has generated a tremendous research effort to reveal the impact of spatial factors on the persistence and extinction of butterfly populations. Patch size and connectivity are the main variables in these studies. However, several studies have shown that the role of habitat quality should be regarded as at least as important as spatial factors (DENNIS & EALES 1997, THOMAS et al. 2001, WALLISDEVRIES 2004). Habitat quality is especially important for the larval stages of butterflies (THOMAS et al. 1998, 2001; BOURN & THOMAS 2002). Therefore, larval habitat quality deserves to be a focus for the conservation management of butterfly habitats.

From the aforementioned studies, it appears that the structure of the vegetation is one of the main factors determining larval habitat quality, next to host plant availability. It has been argued convincingly that the warm microclimates in short vegetation explain the significance of vegetation structure for larval habitat quality (THOMAS et al. 1998, 2001; BOURN & THOMAS 2002, ROY & THOMAS 2003). Unfortunately, microclimatic conditions are mostly inferred from vegetation structure, whereas actual measurements of the microclimate are extremely scarce (but see LORAM et al. 2003).

In this paper, I describe the larval habitat of the Glanville fritillary *Melitaea cinxia* (Linnaeus, 1758), an endangered species in northwestern Europe, where it reaches the cold thermal limit of its distribution (WALLISDEVRIES 2001a). Temperature measurements are used to establish a link between vegetation characteristics and microclimate. The ensuing properties of larval habitat quality are then used to rate the suitability of actual or potential sites for *M. cinxia* and to formulate guidelines for conservation management.

2 Distribution and life history of *Melitaea cinxia*

The Glanville fritillary is a butterfly from dry grasslands with a diverse structure and an abundance of flowering plants (Fig. 1). The species has a large Eurasian distribution (BINK

Figure 1: At the landscape scale, the habitat of *Melitaea cinxia* often consists of dry grassland with pioneer vegetation and surrounded by scrub or forest (photograph of Zutendaal site by M.F. WallisDeVries).

1992). In Europe its northern limit coincides with a July isotherm of 16.5–17.0 °C. In The Netherlands, *M. cinxia* was found beyond this thermal limit in the dunes before 1950 (most records date from the period 1847–1919; DE VLINDERSTICHTING n.p.). It is likely that the warm microclimate of the dry and hilly dune environment, with abundant pioneer vegetation, explains this anomaly.

Despite recent climatic warming, *M. cinxia* shows a decline in all of northwestern Europe. In Great Britain the species has disappeared from the mainland since the 1860s, but it survives on the Isle of Wight (and neighbouring Hampshire) where its status currently appears stable (THOMAS & LEWINGTON 1991, ASHER et al. 2001). The decline of *M. cinxia* has been especially pronounced in The Netherlands and Belgium (VAN SWAAY & WARREN 1999; Fig. 2). In The Netherlands, the species was classified as extinct since 1995, which has led to a species protection plan aiming at its re-establishment by recolonisation from neighbouring populations in Belgium (WALLISDEVRIES 2001a).

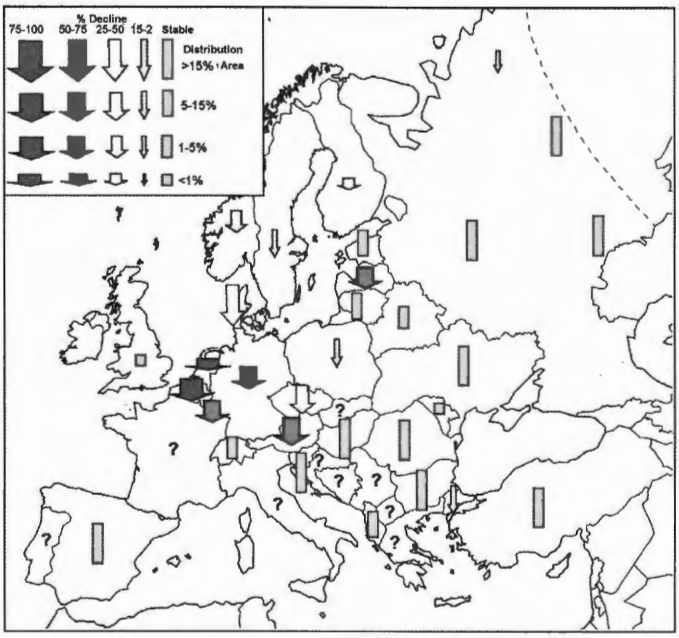

Figure 2. Distribution and status of *Melitaea cinxia* in Europe (after VAN SWAAY & WARREN 1999). The species is present in countries with a question mark, but the change in distribution over the last 25 years within that country is unknown.

The flight period of *M. cinxia* peaks between mid-May and mid-June (THOMAS & LEWINGTON 1991, BINK 1992). The butterflies are fairly mobile with 20% covering more than 1 km (HANKSI et al. 1994, 1995). They are attracted by richly flowering grasslands (KUUSSAARI et al. 1996); in The Netherlands and Belgium *Centaurea jacea, Leucanthemum vulgare, Lotus corniculatus* and *Hypochaeris radicata* are main nectar sources (WALLIS DE VRIES 1998, GOFFART et al. 2001). Butterfly emigration is enhanced by a poor nectar supply and by open fields adjacent to habitat patches (KUUSSAARI et al. 1996). Oviposition typically occurs in clusters of 100–200 eggs on the underside of the leaves of its host plant, predominantly *Plantago lanceolata* in Great Britain, The Netherlands and Belgium (THOMAS & LEWINGTON 1991, BINK 1992). Larval habitat patches are typically small (median 300 m^2; HANSKI et al. 1995) and scattered over the landscape. The caterpillars live gregariously in a web on the host plant. They hibernate in a densely woven web, but the structure of the

vegetation in which hibernation takes place has not been well described. The larvae remain together in spring until the final instar. Their black colour and gregarious behaviour is regarded as an adaptation to meet thermal requirements and larvae are frequently seen basking on dead vegetation (WALLISDEVRIES 1998) (Fig. 3). South-facing slopes provide an even warmer and probably more preferred microclimate at the northern edge of the species' range (SIMCOX & THOMAS 1979). As the food requirement of a larval group continues to increase and larval mobility is limited to a few meters, the required *Plantago* density is high (Fig. 4); two independent estimates of the minimum density for an average nest of 44 larvae gave the same value of 7 small plants/m^2 (WALLISDEVRIES 1998). Kuussaari (pers. comm.) found an average density of 10.3 plants/m^2. At the final instar, caterpillars are more mobile and disperse to pupate in dense vegetation (THOMAS & LEWINGTON 1991).

Figure 3: The basking behaviour and black coloration of the caterpillars of *Melitaea cinxia* enable them to benefit from warm microclimates (photograph by M.F. WallisDeVries).

Figure 4: Larval microhabitats of *Melitaea cinxia* are characterised by an open and diverse vegetation structure and a high density of the host plant *Plantago lanceolata*. This picture shows a larval hibernation nest (photograph by M.F. WallisDeVries).

3 Methods

3.1 Habitat characteristics

Characteristics of habitat quality were investigated in three populations in Flanders near Zutendaal, Wezel and Meeuwen-Gruitrode during 1998 (with additional data collected in 2000). Those factors known or suspected to be of importance but not well described were given special attention (see also WALLISDEVRIES 1998): host plant density, vegetation height at hibernation sites and Ellenberg site indicator values.

Host plant density was estimated in a 1 m^2 square around the spring nests in the populations of Zutendaal and Meeuwen-Gruitrode. Vegetation height at and around each spring and autumn nests was determined in two crosswise 2 m-transects, in N-S and W-E directions, intersecting at the nest itself. Height measurements were carried out with a light tempex disc (8 g, 10 cm diameter) lowered gently along a wooden rod onto the vegetation.

Ellenberg indicator values have been used successfully by OOSTERMEIJER & VAN SWAAY (1998) to characterise abiotic conditions of butterfly habitats. Site indicator values on a scale from 1 to 9 were calculated for soil reaction (1 = acid, 9 = calcareous), productivity (also known as nitrogen value (1 = poor, 9 = rich) and moisture (1 = dry, 9 = wet) from plant species lists for 45 sites, excluding rare species. Of these sites, 15 had been occupied by *M. cinxia* in the 1990s (including the above populations, a site near Olmen in Flanders and along the Julianakanaal in The Netherlands) and 30 sites were chosen from dry grassland sites in the vicinity of these populations. In the calculation the contributions of individual species were averaged without weighting according to their cover. The same sites were surveyed for nectar plant abundance. All these sites were located on sandy to sandy-loamy soils. For comparison, 6 sites were surveyed on calcareous soils in the area of an introduced population near Lanaye, Belgium. Logistic regression was used, as in OOSTERMEIJER & VAN SWAAY (1998), to derive optimal values for occupied patches.

3.2 Microclimatic measurements

Microclimatic measurements were made at the site of Wezel, Belgium, during sunny days in late summer (31st August 2000) and in spring (28th March 2002). Substrate and larval temperatures were measured at each location using a handheld infra-red thermometer (OS530 L). Ambient air temperature was measured with a digital thermometer at a fixed point in the shade at 1.3 m height. In 2000 the temperature of 13 different larval nests and their surroundings were measured once during the day, between 10.00 AM and 16.00 PM. In 2002 eight different larval sites in sunny locations were followed at 30-minute intervals between 9.30 AM and 16.00 PM. For the analysis of the data for 2000, comparisons between substrate temperatures were made, using location number to correct for variation in temperatures during the day. Repeated measures for each location were averaged over the day prior to analysis for 2002.

3.3 Habitat quality index

A habitat quality index was designed to classify various components of habitat patches in terms of low, moderate or high quality (Table 1). The importance of all factors has been shown either in the above-mentioned studies or in the present study, although the factors 'sun' and 'shelter' are merely surmised from general microclimatic considerations. The index is calculated as the sum of the values for the various quality components, with –2 for 'low', 0 for 'moderate' and 1 for 'high'. Thus, low quality weighs heavy but a cut-off point

for complete unsuitability was not included. Boundary values were derived from field data and from other studies. Topography has not been presented in the data and index values, as only a few areas showed any relief. A preliminary test of the predictive power of the habitat quality index was performed at a scale of 50 × 50 m, which lowered the number of sites to 40 (with 8 recently occupied), by logistic regression of the index on actual or recent occupancy.

Table 1. Factors included in the habitat quality index for *Melitaea cinxia* and their values for low, moderate or high quality habitat; the respective index values for low, moderate and high quality are –2 , 0 and 1. Variation in (micro)topography was so low in the study areas that this factor was left out of the final index.

Characteristic	**Quality**		
	Low	**Moderate**	**High**
Primary factors			
%Cover standing dead vegetation	< 5	5–25	> 25
Ellenberg soil reaction value	< 3.8	3.8–4.5	≥ 4.6
Scale of structural diversity (m)	> 50	10–50	< 10
Ellenberg productivity value	> 5.7	5.2–5.7	≤ 5.1
Area with high *Plantago* density (m^2)[1]	10–100	100–1000	> 1000
Open field border (%)	> 75	50–75	< 50
Secondary factors			
%Cover short vegetation (< 5 cm)	< 5	5–15	> 15
Nectar abundance (flowers/m^2)	< 0.01	0.01–1	> 1
Ellenberg moisture value	> 5.8	5.4–5.8	≤ 5.3
Sun	Shady	Some shade	Sunny
Shelter	None	Some	Secluded
(Micro)topography	None	Some	Abundant

[1] In the first test of the index, a *Plantago* density measure was used instead of this criterion (with values for low: < 1, moderate: 1–10, and high quality: > 10 plants/m^2)

In a practical application of the habitat quality index in Limburg (The Netherlands), sites were chosen on the basis of the occurrence of *Plantago* concentrations (> 10 plants/m^2 on > 10 m^2) instead of selecting dry grasslands. This provides a more practical and less ambiguous selection criterion in field surveys. Consequently, the host plant density criterion in the index was replaced by an area criterion (based on HANSKI 1994): low quality 10–100 m^2, moderate quality 100–1,000 m^2 and high quality > 1,000 m^2 of high *Plantago* density.

4 Results

4.1 General site characteristics

At a scale of 50 × 50 m habitat patches were secluded with only 33 ± 17% (± 95% confidence interval) of the perimeter bordering open fields. The vegetation showed affinity with *Violion*, *Thero-Airion* and, locally, *Bromion* communities. Occupied patches showed a high frequency of occurrence (> 60%) for the following plant species: *Plantago lanceolata*, *Achillea millefolium*, *Festuca rubra*, *Vicia hirsuta*, *Hypericum perforatum*, *Holcus lanatus*, *Vicia sativa* ssp. *angustifolia*, *Trifolium dubium* and the main nectar plant *Centaurea jacea*. Significant positive associations (chi-square test, $P < 0.05$) of plant species with the occur-

rence of *M. cinxia* were found for *Achillea millefolium*, *Hypochaeris radicata*, *Rumex acetosella* and *Vicia sativa* ssp. *angustifolia*, whereas *Rumex obtusifolius*, *Ranunculus acris* and *Alopecurus pratensis* were more frequent in unoccupied patches. Host plant densities around larval nests in spring averaged 29.0 ± 14.6 per m^2 ($N = 9$) in Meeuwen-Gruitrode and 23.7 ± 12.0 per m^2 ($N = 16$) in Zutendaal, which is well above the calculated minimum density. Nectar abundance in occupied patches typically ranged in the order of 1–10 flowers/m^2.

On sandy soils, occupied patches were located on sites of intermediate soil reaction and productivity. On these soils soil reaction and productivity values are significantly correlated (Pearson correlation, r = +0.89, $P < 0.0001$, $N = 40$). The optimal soil reaction value was 4.9 with a tolerance of 0.5 and a maximum probability of occurrence of 0.60 (logistic regression, $P = 0.0003$, $N = 40$). The optimal productivity value was 4.8 with a tolerance of 0.5 and a maximum probability of occurrence of 0.61 (logistic regression, $P = 0.004$, $N = 40$). No relation was found between occupancy and moisture value, but this was probably due to the narrow range of conditions sampled in this respect. The average moisture value of occupied patches was 4.8 ± 0.5 (± 95% confidence interval). The sites on calcareous soils showed that *M. cinxia* may also occur at high soil reaction values in combination with low productivity values.

4.2 Vegetation structure

In April, 70–85% of the vegetation on larval sites from four populations was less than 15 cm high, with 20% less than 5 cm. This confirms the open nature of the vegetation structure of caterpillar feeding sites. In contrast, hibernation nests were located in comparatively tall vegetation in late summer: 20.9 ± 10.6 cm ($N = 19$) in Zutendaal and 13.7 ± 5.2 cm ($N = 18$) in Wezel. This vegetation typically consisted of standing dead grasses. The nests themselves were always suspended at some height above ground level, with a respective median of 8 and 5 cm for the two populations (Fig. 5).

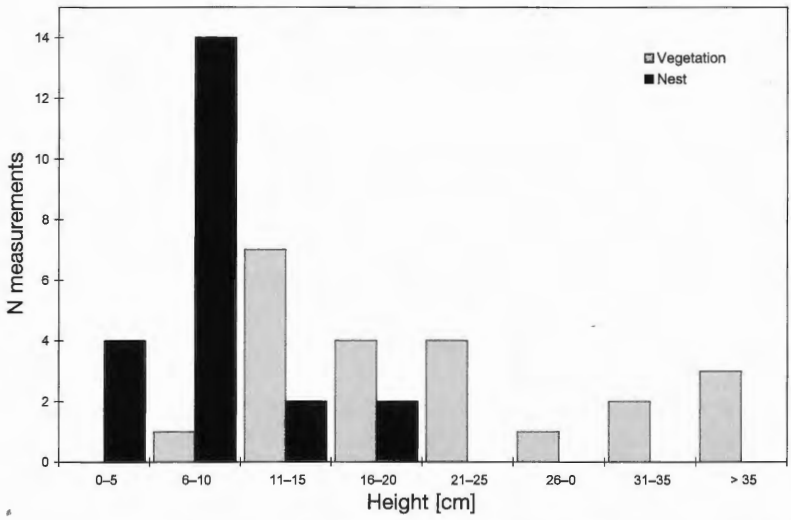

Figure 5. Distribution of the vegetation height above larval nests of *Melitaea cinxia* and of the larval nests themselves in late summer ($N = 22$ nests).

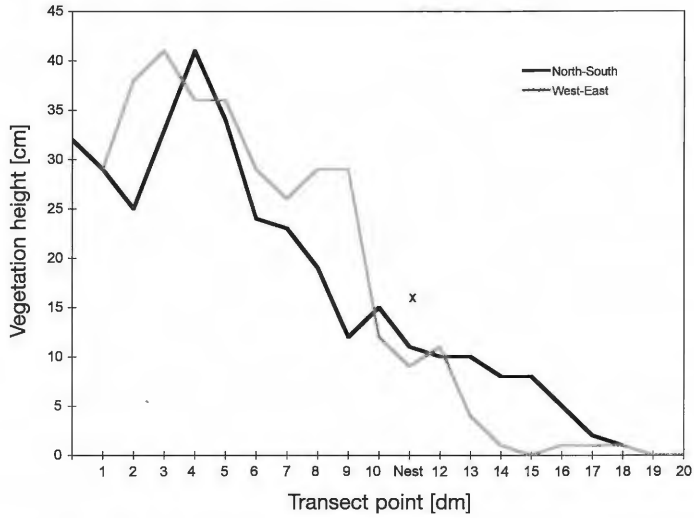

Figure 6. Example of the change in vegetation height around larval nests of *Melitaea cinxia* in late summer along a North-South and West-East oriented transect; the position of the larval nest is indicated by the cross.

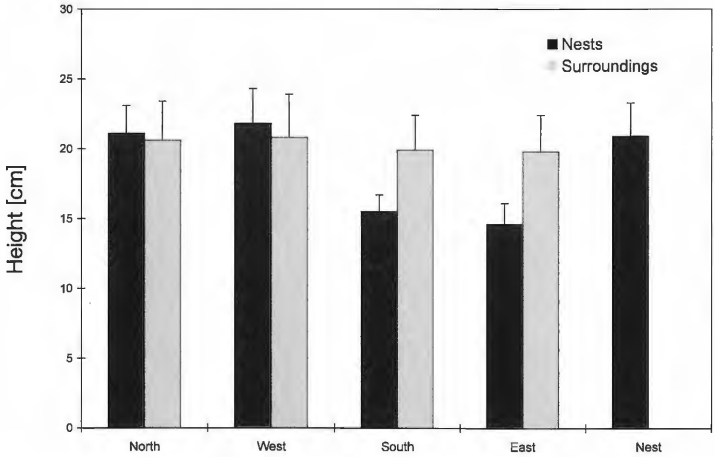

Figure 7. Mean vegetation height (± s.e.) in transects laid out in four directions around larval nests of *Melitaea cinxia*, and mean vegetation height at the larval nests in late summer ($N = 19$ nests).

In Wezel, all the surrounding vegetation was shorter (9.7 ± 3.3 cm; Wilcoxon test, $P = 0.0005$, $N = 18$), whereas in Zutendaal only the vegetation on the sun-facing southern and eastern sides was shorter (15.0 ± 5.8 cm; Wilcoxon test, $P = 0.004$, $N = 19$; Fig. 6 and 7). In other words, the vegetation around larvae nests showed structural diversity with short vegetation adjacent to tall vegetation.

4.3 Microclimate

Microclimatic measurements in late summer and in spring showed that solar irradiation substantially raises surface temperatures of larval nests and larvae of *M. cinxia* above those of green plants and air temperature (Fig. 8). The surface temperature of green plants in the sun does not get much higher than ambient air temperature due to evaporation. Dead plants and sandy soil, however, have a low moisture content, and thus readily heat up 10–18 °C higher than air temperature. The caterpillars bask on these warm substrates and, in combination with their black coloration, also achieve body temperatures 10–16 °C higher than air temperature.

4.4 Habitat quality index

The full index explained 61.1% of the variation in patch occupancy; the lowest value for an occupied site was 5. However, some components of the index rather decreased than raised the proportion of explained variation. A stepwise regression approach identified six primary factors out of the original 11 factors, which explained 72.7% of patch occupancy (Table 1; also see WALLISDEVRIES 2001b). All but one of the primary factors were associated with larval habitat quality. Only the proportion of the location perimeter with open field is associated with adult habitat quality.

4.5 Application for species conservation

The habitat quality index has been used to rate potential and actual population sites for *M. cinxia* in Flanders, Belgium (WALLISDEVRIES 2001b, VANREUSEL et al. 2005), and in Limburg, The Netherlands (WALLISDEVRIES 2004). The index provides both insight in the quality of the sites and in the limitations that exist for the establishment of *M. cinxia*, excluding isolation. The limitations in habitat quality have been translated into recommen-

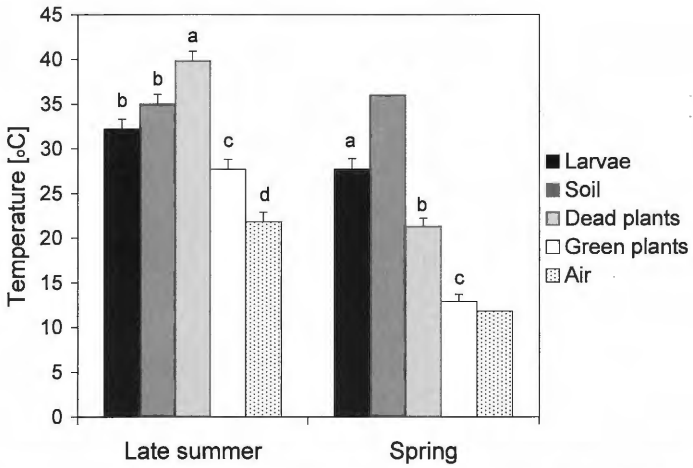

Figure 8. Mean temperatures (°C; least square means ± s.e.) of *M. cinxia* larvae (larval nests in late summer), substrates and ambient air temperature on sunny days in late summer (31st August 2000) and spring (28th March 2002). Different letters in the bar chart indicate significant differences ($P < 0.05$; Tukey HSD) between categories within the measurement period; soil and ambient air temperatures in spring were not replicated and were therefore not included in the statistical analysis.

Table 2: Recommendations for habitat management for *Melitaea cinxia* as a function of limitations in habitat quality.

Limitation	Recommendation
Uniform short or tall vegetation	Rotational mowing or extensive grazing
Eutrophic sites	Top-soil removal or mowing twice a year
Acidified soils	Sod-cutting ('plaggen') or liming
Small *Plantago* areas	enlargement by appropriate management
Insufficient shelter	Promote hedgerows or tree lines
Shade	Reduce by cutting trees or shrubs

dations for management (Table 2). In the framework of the species protection plan for *M. cinxia* (WALLISDEVRIES 2001b), these recommendations are integrated in management plans of government and conservation authorities in order to promote the re-establishment of *M. cinxia* in The Netherlands.

Recolonisation could become reality due to the presence of two small source populations in Belgium, Lanaye and Zutendaal, situated at 4 and 12 km, respectively, from potentially suitable habitat in The Netherlands. The Zutendaal population is now expanding due to, amongst other reasons, appropriate management. New sites have been colonised at 2 km from the source population (VANREUSEL et al. 2005). Despite the pessimistic predictions of Hanski's metapopulation models (Etienne n.p.), a first colonisation attempt has also occurred in The Netherlands in 2004. A female butterfly was seen in spring at the St. Pietersberg, later followed by a male, at 4 km from the source population near Lanaye (Fig. 9). In August a larval nest was found at the same location. The warm year of 2003 boosted the source population in Lanaye to an estimated size of 300–400 individuals. This may have been favourable for the colonisation attempt in the sunny spring of 2004. Several butterflies have again been observed in 2005 and 2006, but it is too early to conclude that a local population has now established.

Figure 9: This *Melitaea cinxia* butterfly was the first individual to be observed in The Netherlands during 2004, after an absence of nine years (photograph by R. Ketelaar).

5 Discussion

5.1 The significance of warm microclimates

The present data indicate that abiotic conditions (moderately acid to calcareous soils with low to intermediate productivity) and small-scale diversity in vegetation structure are important aspects of habitat quality for *Melitaea cinxia*. These aspects have not been quantified earlier, although abiotic conditions have been described earlier in qualitative terms (THOMAS & LEWINGTON 1991, BINK 1992). It appears, as expected, that habitat quality for the larval stages is more important in defining habitat characteristics for *M. cinxia* than quality aspects for the adult stage.

Both the geographical distribution and the characteristics of its microhabitat indicate that, in an oceanic temperate climate, *Melitaea cinxia* is a thermophilous species depending on warm microclimates. This study has identified several factors confirming this hypothesis. The main factors appear to be a low productivity, an open vegetation structure, with sufficient standing dead vegetation over winter. The sunny exposition of the vegetation fringes with hibernation nests in Zutendaal suggests an even more subtle influence of microclimate on the selection of microhabitats. The importance of standing dead vegetation for hibernation nests seems implied by SIMCOX & THOMAS (1979) on the Isle of Wight, but hibernation apparently takes place mainly in low vegetation in Finland (Singer & Kuussaari pers. comm.). It may be that the protection offered by standing dead vegetation is more important with the greater humidity and essentially snow-free winters of the oceanic climate in Western Europe. Although of lesser importance in Flanders and The Netherlands, a sunny exposition of topography undoubtedly is a potentially important additional factor contributing to a warm microclimate for *M. cinxia* (SIMCOX & THOMAS 1979). Indeed, Fartmann (pers. comm.) recently observed on the Isle of Wight that larval development was more advanced in sunny expositions than on more shady, westerly or northerly exposed locations.

There seems to be a paradox between the thermal requirements of *Melitaea cinxia* and the general decline of the species in northwestern Europe during a period of climatic warming, WALLISDEVRIES & VAN SWAAY (2006) have suggested a solution for this paradox by highlighting the discrepancy between changes in macro- and microclimates. While the macroclimate has warmed during the last decades, microclimates have rather become cooler in early spring, at the time of the larval development of species such as *M. cinxia*. The reasons for this microclimatic cooling are found in the advancing start of the plant growing season in combination with increased levels of atmospheric nitrogen deposition. Both lead to taller and greener vegetation, and, hence, a cooler vegetation. Warm microclimates have also disappeared due to changes in land use, leading either to intensification (more productive environments) or abandonment (cooler tall environment) (BIGNAL & MCCRACKEN 1996). This is likely to have caused the disappearance of *M. cinxia* from the Diemeltal in northwestern Germany (FARTMANN 2004; last record from 1926) and possibly also from the dunes in The Netherlands (see section 2; the disappearance from mainland Britain may have been a true effect of macroclimatic cooling during the latter part of the 19th century, comparable to the effect on *Pararge aegeria* (ASHER et al. 2001).

5.2 Conservation management for butterflies

The suggested process of microclimatic cooling poses a severe threat for thermophilous species such as *Melitaea cinxia*. Range expansions driven by climatic warming only appear to occur in butterflies when suitable microclimates are present (WALLISDEVRIES & VAN SWAAY 2006). Appropriate management may overcome this limitation to a significant

extent. Warm microclimates can be promoted by reducing the nutrient status in the soil and by promoting an open and diverse vegetation structure. Grazing, rotational mowing and top-soil removal in eutrophic sites offer suitable tools to achieve this purpose (BOURN & THOMAS 2002, WALLISDEVRIES 2001a, 2004).

6 Conclusion

Studying the ecology of *Melitaea cinxia* has contributed both to insights in the role of metapopulation dynamics (HANSKI 1999) and in the importance of habitat quality (THOMAS et al. 2001, WALLISDEVRIES 2001b and this study). This study emphasises the crucial role of larval habitat quality, and warm microclimates in particular. Improving habitat quality through appropriate management may overcome the growing threat of microclimatic cooling for species such as *M. cinxia*. The recent recolonisation attempt of the species in the Netherlands, mentioned above, suggests that serious efforts in habitat restoration may, to a certain extent, even overcome problems of isolation by boosting local population sizes and increasing the availability of suitable habitat. This gives hope for a permanent re-establishment of *M. cinxia* in The Netherlands and, in a wider perspective, also presents a major challenge for conservation management in northwestern Europe!

Acknowledgements

The studies underlying this paper were carried out with financial support of the Dutch Ministry of Agriculture, Nature and Food Quality, the Vlaamse Landmaatschappij and the Province of Limburg. Nicoliene Peet, Sicco Ens, Ivo Raemakers, Tineke de Groot and Margreet van der Veen kindly contributed to the field work. Dirk Maes' help in introducing me to the Flemish sites is much appreciated. Finally, thanks are due to Chris Van Swaay for many fruitful discussions on butterfly research, trends and conservation.

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