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**DISPERSAL BEHAVIOUR AND ECOLOGY OF THE APPLE BLOSSOM
WEEVIL, *ANTHONOMUS POMORUM* (L.)**

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1. SUMMARY

Dispersal behaviour and habitat-related ecology of the apple blossom weevil, *Anthonomus pomorum* (L.) (Coleoptera: Curculionidae), and underlying mechanisms were investigated.

To characterise the spatial and temporal patterns of orchard colonisation in spring, mark-release-recapture experiments and capture-monitoring of immigrating weevils were undertaken in two apple orchards in northern Switzerland over four years. Weevils marked with enamel lacquer points were released from adjacent hibernation sites, *i.e.* from mixed forests. Spatial analyses of recapture data by means of circular statistics attested an orientated dispersal of weevils from the forest border towards the centre of orchards, irrespective of the angle of tree rows to forest borders or of climatic conditions. The distance moved by the weevil populations averaged 19 m. One third of the population remained on the first tree that the weevils encountered if blossom buds were available. The remainder of the population moved short distances, mainly following the direction of tree rows. Thus the ability of *A. pomorum* to disperse and to expand distribution within orchards seems to be limited.

The temporal pattern of spring dispersal and orchard colonisation by postdiapaused weevils was correlated with climatic factors. The timing was found to depend on the prevailing temperature during the spring season. In northern Switzerland, the Celsius degree-days (DD) required for a population of *A. pomorum* overwintering outside to colonise an orchard were 161 ± 27 , calculated from January 1 at a temperature above 0°C, and 10 ± 1 , from March 1 at a temperature above 6°C. This colonising dispersal started at a mean daily temperature of 7 to 9°C, which is regarded as a threshold temperature. This temperature occurred mostly in the second week of March. The observed start of mass colonisation into orchards took place at a mean of 210 ± 26 DD, calculated from January 1 at a temperature above 0°C. The mean daily threshold temperature for mass colonisation was 8 to 11°C. This temperature occurred mostly around March 24. The daily dispersal speed of moving individual weevils was estimated as 6.8 ± 7 m during the first 40 days. This dispersal speed was positively correlated with the mean and maximum daily temperatures and with the temperature between 6:00 p.m. and 10:00 p.m. when the weevils have their activity peak.

Furthermore, behavioural patterns in spring were established in relation to climatic factors by means of observations in field cages to gain information on the

physiological demands of *A. pomorum* and to validate previous laboratory results (Duan *et al.*, 1996). Data analyses showed that temperature played a major role in determining crepuscular activities of *A. pomorum* on apple trees. These include crawling, feeding, mating and oviposition. Air humidity had a significant effect, showing an optimal range for crawling, feeding and mating activities, and a negative correlation with the dispersal speed. Rainfall negatively influenced the weevils' crepuscular activity on apple trees. However, rainfall had no measurable effect on spring dispersal, neither did wind speed and wind direction. Light intensity had a positive influence on dispersal speed. In particular, the day-long full sunshine significantly increased crepuscular activities.

Further studies focused on the hibernation site selection in summer/autumn and its subsequent influence on the infestation phenology of apple trees in spring. The dispersal of prediapausing *A. pomorum* was investigated in two consecutive years by means of mark-release-recapture experiments. About 47 and 64 % of the weevils remained in the vicinity of the release sites, namely in an area of dwarf smooth-bark apple trees and older rough-bark apple trees, respectively. The dispersing weevils moved over an average distance of 5.5 m in the smooth-bark tree area, as compared to 3.8 m in the rough-bark tree area. The prevalent direction of dispersal was along tree rows in both areas. Some weevils displayed, after release in mid-July, a directional dispersal to the adjacent forests. Others, released in the smooth-bark tree area, dispersed towards the rough-bark tree area. Generally, autumn dispersal was less intensive and less directed than spring dispersal. The flight proclivity was investigated under laboratory conditions. Results showed that the flight proclivity of newly emerged weevils of the summer generation was significantly higher in June/July than in August/September. This corresponds to dispersal behaviour in the field, indicating an entry into aestivo-hibernation already in summer. The re-colonisation of orchards was investigated the following spring. Data analyses showed that the hibernation site in addition to climatic conditions influenced the spatial distribution of the apple blossom weevil. A greater abundance of weevils was recorded in the vicinity of hibernation sites, *e.g.* at edges of orchards, on high stem trees or around autumn release points. The timing of spring colonisation of apple trees was similar for weevils overwintering within the orchard and for those from outside. However, the gonad development was faster in females that overwintered within the orchard. Immigrating weevils fully matured their gonads 24 ± 3 days after start of dispersal, *i.e.* in the beginning of April.

Various potential hibernation substrates were compared for the weevil's preference in multiple choice tests in climatic chambers. Results demonstrated that the litter of dry leaves was the most preferred overwintering shelter, yielding also a relatively high survival rate. Branches with rough bark ranked second, while branches with smooth bark, grass and pure soil were not suitable for overwintering. These results suggest that dwarf apple orchards offer unfavourable conditions for overwintering, and that the relatively small proportion of weevils successfully reaching the adjacent forests find optimal hibernation sites in the leaf litter there. This led to high population densities of the pest at orchard edges adjoining forests.

The preference of *A. pomorum* for different bud growth stages was examined in multiple choice tests in climatic chambers. The weevils significantly preferred the most developed bud stage (*Malus domestica* Borkh. var. Boskoop) for feeding, which was the pink bud stage E(57) or balloon stage E2(59), over stages A(00), B(52), C(53) and D(55) (scale after Fleckinger, 1948; BBCH scale after Anonymous, 1992). Oviposition was mostly recorded in the mouse ear stage C3(54), in the tight cluster of green bud D(55) and in the pink buds E(57). The bud growth stage also had a significant influence on the mating and resting behaviour of *A. pomorum* on apple trees, as observed in field cages in spring. Females fed on all bud stages, though the most important stage for females' feeding in the field was the slightly silvery green tip stage, B(52). Stage E(57) was frequently fed upon by both males and females. Oviposition was recorded in buds of stage D(55) or E(57). However, the start of spring dispersal was not significantly synchronised with a single bud growth stage of trees in three orchards studied in four years.

The analysis of feeding of *A. pomorum* on the six most common apple varieties, *i.e.* Golden Delicious, Jonagold, Idared, Gala, Maigold and Gloster 69, showed no consistent preference for any one of the varieties under laboratory conditions. Thus, the bud stage preference of *A. pomorum* might lead to an increase in weevil population in areas with accelerated blooming of the apple trees, and this would consequently increase the risk of economic damage.

In conclusion, the population of *A. pomorum* performed directional dispersal for colonisation of orchards in early spring and, to a less degree, for hibernation habitats in summer/autumn seasons. Climatic conditions and interactions between the weevils and its host trees were the key factors behind the spring dispersal process. The pattern of spring dispersal can be predicted using the threshold temperature and the degree-day model.

2. ZUSAMMENFASSUNG

Das Ausbreitungsverhalten und die Ökologie des Apfelblütenstechers, *Anthonomus pomorum* (L.) (Coleoptera: Curculionidae), wurden samt den bestimmenden biotischen und abiotischen Einflussgrößen untersucht.

Charakterisiert wurden das räumliche und zeitliche Ausbreitungsmuster dieses Käfers sowie die Besiedlung der Wirtsbäume, *Malus domestica* Borkh. Dies erfolgte mittels Freilassungs- und Wiederfang-Experimenten sowie der Überwachung einfliegender Käfer der Wildpopulationen in zwei Obstanlagen der Nordschweiz über vier Jahre. Mit Hilfe zirkularer Statistik konnte auf allen untersuchten Flächen eine orientierte und gerichtete Bewegung der Käfer von angrenzenden Habitaten in Richtung Obstanlagen gezeigt werden. Diese Bewegung war unabhängig von der Pflanzrichtung der Apfelbaumreihen und unabhängig von den Klimabedingungen. Die Distanz, welche eine Käferpopulation im Frühjahr zurücklegte, lag durchschnittlich um 19 m. Rund ein Drittel der Käfer verblieb am ersten knospenbesetzten Apfelbaum, den sie erreichten. Der Rest bewegte sich über kürzere Strecken und meist innerhalb der Apfelbaumreihen. Schlussfolgernd ist die Ausbreitungs- und Besiedlungsfähigkeit des Käfers im Frühjahr gering.

Klimatische Bedingungen waren Haupteinflussfaktoren für das Ausbreitungsverhalten des Käfers im Frühjahr. Das zeitliche Besiedlungsmuster der Obstanlage durch *A. pomorum* hing vor allem vom Temperaturverlauf im zeitigen Frühjahr ab. Eine Temperatursumme von 161 ± 27 Tagesgraden, summiert für Tagesmittel über 0°C ab dem 1. Januar, war für den Beginn der Besiedlung der Obstanlagen erforderlich. 10 Tagesgrade über 0°C war die nötige Temperatursumme, berechnet ab dem 1. März. Die Schwelltemperatur für den Beginn der Besiedlung war 7 bis 9°C im Tagesmittel, was meist in der zweiten Märzwoche eintraf. Der Masseneinflug der Käfer in die Obstanlagen fand ab einer Temperatursumme von 210 ± 26 Tagesgraden, summiert für Tagesmittel über 0°C ab dem 1. Januar, statt. Die dafür nötige Schwelltemperatur lag zwischen 8 und 11°C im März oder April. Die immigrierenden Käfer breiteten sich in den ersten 40 Tagen nach Einflugbeginn mit einer mittleren Geschwindigkeit von 6.8 ± 7 m pro Tag aus. Die Ausbreitungsgeschwindigkeit war positiv korreliert mit der mittleren und maximalen Tagestemperatur und mit der Temperatur zwischen 18 und 22 Uhr, wenn die Käfer die größte Aktivität zeigten.

Um die Autökologie des Käfers im Feld zu analysieren und mit Laborbefunden (Duan *et al.*, 1996) zu vergleichen, wurde sein Verhaltensmuster in Abhängigkeit von

klimatischen Faktoren direkt am Apfelbaum in Beobachtungskäfigen untersucht. Die Ergebnisse zeigten den signifikanten Einfluss der Umgebungstemperatur auf das abendliche Verhaltensmuster von *A. pomorum*. Dies bezog sich auf Verhaltensformen wie Laufen, Fraß, Kopulation und Eiablage. Unter verschiedenen gemessenen Klimafaktoren hatte zusätzlich vor allem die Luftfeuchtigkeit Einfluss auf Laufen, Fraß und Kopulation von *A. pomorum*. Die Ausbreitungsgeschwindigkeit war negativ korreliert zur steigenden Luftfeuchtigkeit. Regen beeinflusste das Verhalten der einzelnen Käfer am Baum signifikant. Einen messbaren Effekt des Regens auf die Ausbreitung der Käfer in der Obstanlage wurde jedoch nicht gefunden. Genauso wenig spielten Windstärke und Windrichtung eine Rolle. Die Lichtstärke hatte einen positiven Einfluss auf die Ausbreitungsgeschwindigkeit des Käfers. Insbesondere sehr sonnige Tage erhöhten die Aktivität der Käfer am Abend.

Weitere Untersuchungen konzentrierten sich auf die Suche des Käfers nach Überwinterungsplätzen im Sommer und Herbst und auf den Einfluss dieser Ausbreitung auf die Phänologie des Befalls im folgenden Frühjahr. Die Ausbreitungsaktivität der neuen Generation vor der Diapause im Sommer oder Herbst wurde mit Hilfe von Freilassungs- und Wiederfangexperimenten in zwei Jahren untersucht. Ein Großteil der freigelassenen Käfer blieb in der Nähe der Freilassungskästen, nämlich 47% der Käfer in Niederstammanlagen und 64% der Käfer in älteren Hochstammanlagen. Im Spätsommer und Herbst bewegten sich die Käfer durchschnittlich 5.5 m in Niederstammanlagen und 3.8 m in Hochstammanlagen. Die Hauptbewegung der freigelassenen Käfer fand entlang der Apfelbaumreihen statt. Einige Käfer orientierten sich in Richtung angrenzender Wälder und ein Teil in Richtung älterer hochstämmiger Apfelbäume. Zusammenfassend war die Herbstbewegung geringer und weniger gerichtet als die Frühjahrsausbreitung. Die gemessene Flugaktivität der Käfer im Labor war im Juni/Juli höher als im August/September, was mit der gefundenen Ausbreitungsaktivität im Feld übereinstimmt. Die Daten der Wiederbesiedlung von Obstanlagen im nächsten Frühjahr zeigten, dass neben den klimatischen Bedingungen auch der Überwinterungsplatz des Käfers das räumliche Besiedlungsmuster der Obstanlagen im Frühjahr beeinflusst. Große Abundanzen von Käfern wurde nahe der Überwinterungsplätze gefunden, beispielsweise an den Rändern der Obstanlage, an Hochstammbäumen oder in der Nähe der Herbstfreilassungspunkte. Im Gegensatz dazu war das zeitliche Erscheinen der Käfer unabhängig vom Überwinterungsort in oder ausserhalb der Obstanlage. Allerdings zeigten die Käfer in der Obstanlage eine frühere Gonadenentwicklung als solche, die von außen einflogen, was auch eine

frühere Eiablage vermuten lässt. Laborexperimente, die verschiedene Überwinterungsorte in Mehrfachwahltests simulierten, zeigten deutlich, dass trockenes Laub das bedeutendste Überwinterungssubstrat des Käfers war. Auch wurde darin eine höhere Überlebensrate festgestellt. Zweitwichtigste Überwinterungsmöglichkeit war rauhe und dicke Rinde, während dünne Rinde, Gras und freier Boden wenig geeignet waren. Generell zeigte sich, dass in modernen Niederstammanlagen ungünstige Überwinterungsbedingungen herrschen, und dass der Anteil an Käfern, der andere Habitate zur Überwinterung erreicht, bessere Überlebenschancen hat. Dies wiederum führt zu einem Randeffect im Befallsmuster der Obstanlagen.

Um das optimale Knospenstadium für *A. pomorum* zu finden, wurde die Bevorzugung von Apfelknospen unterschiedlicher Entwicklung in Mehrfachwahltests in Klimakammern untersucht. *A. pomorum* nutzte Apfelknospen im fortgeschrittenen Entwicklungsstadium mehr zum Fraß als unterentwickelte Knospen. Dies waren das Rotknospenstadium E und das Ballonstadium E2. Im Feld kann das Knospenstadium ebenfalls einen signifikanten Einfluss auf das Verhalten des Käfers am Baum haben. Besonders weibliche Tiere können jedoch auch unterentwickelte Knospen (A, B oder C) zum Reifungsfraß nutzen, wobei besonders das Knospenschwellstadium B bedeutend war. Erst das Rotknospenstadium E wurde von männlichen und weiblichen Tieren gleichermaßen genutzt. Eine Eiablage wurde im Mausohrstadium C3, im Grünknospenstadium D und im Rotknospenstadium E im Labor und im Feld beobachtet. Trotz der Präferenzen für weiterentwickelte Knospenstadien war der Beginn des Einfluges der Käfer im Frühjahr in drei Obstanlagen in vier Jahren nicht mit einem bestimmten Knospenstadien korreliert. In Dreifachwahltests wurde das Fraßverhalten von *A. pomorum* an sechs weitverbreiteten Apfelsorten getestet, nämlich an Golden Delicious, Jonagold, Idared, Gala, Maigold und Gloster 69. Die Knospen dieser Sorten befanden sich im gleichen Entwicklungsstadium. Eine Bevorzugung einer bestimmten Sorte wurde nicht beobachtet. Jedoch könnte die Knospenstadien-präferenz bei *A. pomorum* zu einem erhöhten Befallsrisiko an frühblühenden Sorten oder Bäumen in einer Obstanlage führen.

Schlussfolgernd zeigt diese Forschungsarbeit, dass Populationen von *A. pomorum* zu gerichteter Ausbreitung zur Besiedlung von Obstanlagen im Frühjahr und zum Auffinden von Übersommerungs- oder Überwinterungsplätzen im Sommer oder Herbst fähig sind. Klimatische Bedingungen und die Beziehungen zwischen Käfer und Wirtsbaum sind Schlüsselfaktoren des Dispersionsprozesses. Der Besiedlungsprozess von Obstanlagen kann im Frühjahr mit Hilfe von

Temperatursummen und Schwelltemperaturen vorhergesagt werden, jedoch nicht mit Hilfe der Entwicklungsstadien der Blütenknospen.

3. GENERAL INTRODUCTION

Insect dispersal, especially in relation to movements between agricultural and surrounding non-agricultural habitats, is poorly understood. This is due, in large part, to ignorance of the basic population dynamics of pests, their dispersal and their relationship with host plants. The purpose of this project was to gain insight into the dispersal dynamics and habitat related ecology of the apple blossom weevil, *Anthonomus pomorum* (L.) (Coleoptera: Curculionidae), and into its early seasonal interactions with the apple tree, *Malus domestica* Borkh. *A. pomorum* was a well-known and widespread pest of apples in the last century (Omerod, 1890) and in the beginning of this century (Speyer, 1939). Then, it was suppressed over decades by broad-spectrum insecticides used to control *Cydia pomonella* and aphids. Nowadays, *A. pomorum* is re-gaining the pest status in Integrated Production and even more pronounced in biologically managed apple orchards in Europe (Niemczyk, 1989; Wildbolz, 1992; Blommers, 1994). Interventions against the weevil take place in early spring with disruptive broad-spectrum synthetic or natural products without any precise timing. Selective control methods are not yet available nor was the exact timing of interventions clarified.

The apple blossom weevil uses both agricultural and surrounding natural habitats as overwintering sites (Korchagin, 1978). These habitats are generally regarded as a critical factor in the diversity and abundance of pests in orchards (Szentkiralyi and Kozar, 1991). *A. pomorum* is known to overwinter under rough barks (Régnier, 1925; Trojtzky, 1928). This hibernation site is not commonly present in dwarf apple orchards. Consequently, it is assumed that the weevil overwinters in sheltered habitats outside the orchard, for example, nearby forests (Brown *et al.*, 1993). However, quantitative studies on preferred hibernation sites were not available.

Current knowledge on the biology of this pest species is limited, being often confined to anecdotal evidence and empirical statements without any statistical analysis, particularly in the older literature. Adults are characterised by a short period of spring activity (Duan *et al.*, 1996) followed by a long period of dormancy (or aestivo-hibernation, after Masaki, 1980), lasting from summer to early spring (Kostal and Simek, 1996). Ctvrticka and Zdarek (1992) have reported that following hibernation,

the weevils begin to colonise orchards in early spring when the mean daily temperature is above 6 °C. Male weevils have been reported to be sexually mature immediately after emergence from diapause (Ctvrtecka and Zdàrek, 1992), whereas female weevils need a period of feeding on the developing buds of its primary hosts, *Malus sp.* and *Pyrus sp.*, for egg maturation (Trojtzky, 1928). It was still unclear how long a feeding period is needed. Following fertilisation, females oviposit into the blossom buds where larval damage causes sterile and capped flowers. However, the details of the proper timing as well as the assessment of the impact of this damage on fruit production were empirical, contradictory and not related to the adult populations. The newly emerged adults feed on the apple leaves for about 6 weeks and then search for an aestivation or hibernation sites (Miles, 1923). A high population density of the emerged weevils may cause strong deformations on young fruits by feeding (Schaub, 1995).

For advancement of biological and integrated pest management in orchards, it is particularly important to address the biology and activity of early season pests. In the case of *A. pomorum* the most pressing needs are to discover its patterns of dispersal in space and time and the behavioural and ecological mechanisms underlying these patterns. All these are critical gaps of knowledge, impeding progress in integrating *A. pomorum* management into a more environmentally sound, system-oriented orchard management strategy. So far, there have been only two contributions dealing with spring dispersal of the weevil. Tret'yakov (1984) and Brown *et al.* (1993) showed that trees closer to a neighbouring forest were much more severely damaged than the more remote ones, thus demonstrating a strong edge effect. Research to exploit the parasitoids as biocontrol agents are considered to be of low priority (Cross *et al.*, 1999) *.

The stage of bud development seems to be a critical factor for successful weevil feeding, oviposition and larval maturation. The ideal growth stage for oviposition might last a very short time. Wiesmann (1928) found that the main oviposition period lasted only 4 days. However, under cold, wet spring conditions, the critical stage for oviposition may be extended to 4 weeks or more (Grison and Chevalier, 1963). Aggregations of *A. pomorum* on buds of certain apple varieties have been described by Brown *et al.* (1993), but the factors leading to this characteristic distribution pattern were not known.

* Quantified observations on natural antagonists of *A. pomorum* gained in the course of this study are included in Cross, J.V., M.G. Solomon, D. Babandriker, L. Blommers, M.A. Easterbrook, E.N. Jay, U. Kuhlmann, R. Lilly, E. Olivella, St. Toepfer, and S. Vidalis, 1999. Review: Biocontrol of pests of apples and pears in Northern and Central Europe: Parasitoids. *Biocontrol Science and Technology* 9: 277-314.

A better understanding of the pest dispersal dynamics and its interactions with habitat characteristics will enhance the prospects for sustainable agriculture. This research was thus concentrated on the following main goals for detailed investigation on key aspects of behaviour and ecology of *A. pomorum*:

1. The spring dispersal dynamics of the postdiapaused weevils.
2. The influence of climatic factors on the temporal pattern of spring dispersal and on the spring behaviour of the weevil.
3. The selection of overwintering sites and substrates by prediapausing weevils and the influence of hibernation sites on the colonisation process in the following spring.
4. The relationship between the phenology of host trees, especially the growth stages of the blossom buds, and the behaviour of the postdiapaused weevils.

To answer these research questions a combination of field experiments in apple orchards and laboratory experiments in climatic chambers were carried out.

The results of this project are being published or have been submitted for publication, as presented in this and the following chapters. In the appendix, additional figures and tables comprising further results are presented. The general discussion covers the main findings of this study, the implications of these findings for pest management and presents an outlook for future research work.

4. SPRING COLONISATION OF ORCHARDS BY *ANTHONOMUS POMORUM* FROM ADJACENT FOREST BORDERS *

4.1 Abstract

The early-season dispersal of *Anthonomus pomorum* (L.), is a crucial stage in the colonisation of dwarf apple orchards adjacent to forests. Release-recapture studies were conducted with 1700 to 4000 marked weevils at two orchard sites in Switzerland over two years to characterise the spatial and temporal pattern of the dispersal process. The dispersal and colonisation of orchards in spring by overwintered weevils was dependent upon the prevailing temperature.

An orientated dispersal from the forest border to the centre of the orchard was observed consistently, irrespective of the angle of the apple tree rows with respect to the forest border or of climatic conditions. The average dispersal distance of the weevil populations was 19 m. Approximately one third of the weevil population remained on the first tree encountered, the remainder of the population moved over short distances mainly along the tree rows. This dispersal pattern led to a strong "edge effect" with higher numbers of weevils occurring at the edges adjoining the forests as compared to the centre of orchards. The relevance of these findings to population dynamics and management of the pest is discussed.

4.2 Introduction

The apple blossom weevil, *Anthonomus pomorum* (L.) is a widespread univoltine herbivore in apple orchards in Europe. In the past four decades this weevil has been a minor pest of apple, *Malus domestica* Borkh. Although the use of broad-spectrum insecticides to control other pests has provided adequate control previously (Blommers, 1994), the importance of this pest has increased recently. For example in Lithuania, the percentage of damaged apple-blossoms can reach 60%, and in more extreme circumstances can reach 90% (Vyangelyauskaite, 1992).

* Based on publication: Toepfer, St., Gu, H., Dorn, S. 1999. Spring colonisation of orchards by *Anthonomus pomorum* from adjacent forest borders. *Entomologia exp. et appl.* 93: 131-139

Included: Toepfer, St., Gu, H., Dorn, S. 1999. How does *Anthonomus pomorum* (Col.: Curculionidae) colonize apple orchards in early spring? IOBC.WPRS. (in press).

In several European countries, population densities of this weevil often increase to economically unacceptable levels (Wildbolz, 1992; Blommers, 1994). This new pest status poses new challenges to the IPM systems currently in use, as the biology and population ecology of this weevil is poorly documented (Weber, 1994).

The apple blossom weevil uses both agricultural and surrounding natural habitats as overwintering sites (Korchagin, 1978). These habitats are generally regarded as a critical factor in the diversity and abundance of pests in orchards (Szentkiralyi & Kozar, 1991). Although *A. pomorum* overwinters in ground litter and rough bark, these overwintering sites are generally not present in dwarf apple orchards. Consequently the weevil overwinters in sheltered habitats outside the orchard, for example, nearby forests (Brown *et al.*, 1993). Cvrtecka & Zdàrek (1992) have reported that following hibernation, the weevils begin to colonise an orchard in early spring when the mean daily temperature is above 6 °C. Female weevils have been reported to need a period of feeding on the developing buds of its primary host, *Malus sp.* and *Pyrus sp.*, to allow egg maturation (Trojtzky, 1928). Following fertilisation, they oviposit in the blossom buds where larval damage causes sterile and capped flowers.

Our recent studies investigated the spatial and temporal patterns of these post-overwintering activities. Information from such studies is essential for developing monitoring and management programmes for this pest. The temporal pattern of various behaviours and their relationship with temperature of *A. pomorum* have been documented previously (Duan *et al.*, 1996). This paper describes the colonisation of orchards from forest borders and the subsequent within-orchard dispersal by overwintered weevils. The results reported here were obtained from release-recapture experiments in the field in 1996 and 1997.

4.3 Materials and methods

Experimental orchards. The release-recapture experiments were done in two apple orchards in northern Switzerland in 1996 and 1997, referred to as orchard A and B respectively. No pesticide treatments were applied during the experimental period, in the “Integrated Pest Management” (orchard A) or “organic regime” (orchard B).

Orchard A, 1 ha large, was located in Zürich (47 °N, 8 °E, elevation 509 m) and had rows of trees running parallel to the adjacent forest (Fig.A.1 & A.4.1). Rows consisted of dwarf apple trees, 2.5 m high, with a 3.5 m space between rows, with five

different varieties: Primerouge, Gravensteiner, RubINETTE, Arlet and Gala. The orchard was bordered along the east side by an old mixed forest, along the south and north sides by residential buildings and along the west side by a road. An area of 0.6 ha with 1800 trees was used for sampling and experimental observations.

Orchard B, 0.9 ha large, was situated in Niederwil (47 °N, 8 °E, elevation 440 m) and had rows of trees perpendicular to the adjacent forest (4 m row spacing, Fig.A.2 & A.4.3). It comprised two parts: an area of dwarf apple trees with smooth bark and an area of old high-stem apple trees (4 m high) with rough bark. The orchard contained 11 apple varieties: Alkmene, Retina, Idared, Florina, Liberty, Priam, Jonathan, Vista Bella, Spartan, Summerred and Roter Marlet. The experiment was conducted in a 0.5 ha part of the orchard with 600 trees, which was bordered to the north by a mixed forest (ca. 20 m high), to the south and west by apple trees and to the east by fallow land.

Mark-release-recapture of weevils. The capped brown blossoms bearing *A. pomorum* pupae were collected in the spring-summer of previous years in northern Switzerland. They were kept in plastic boxes until adult emergence, which were fed with fresh apple leaves until the onset of hibernation. Then they were overwintered outdoors under semi-natural conditions in plastic boxes together with several leaves and pieces of corrugated cardboard as shelter and sprayed with water at weekly intervals. In early spring, the overwintered weevils were marked with one colour dot of enamel lacquer. The use of different colour codes at five different positions on the elytra and pronotum enabled us to administer over 1200 combinations of individual markings on the captured weevils.

Approximately 4000 marked individuals were released in orchard A in 1996 and 1700 in orchard A and in orchard B each in 1997. In each case, two open plastic release boxes were installed on stems of portable apple trees at a height of 1m, situated at the orchard's border directly adjacent to the forest (Fig.A.4.1 & A.4.5). The portable apple tree allowed the weevils to leave the release point voluntarily. The weevils were kept in the boxes for at least 2 days, so that they could acclimatise to field conditions. Then they were released at a temperature of ca. 10 °C between 4 p.m. and 6 p.m. when the mean daily temperature had reached 6°C. The release dates differed slightly owing to differences in temperature between replicates. For orchard A, release dates were 18 March 1996 and 11 March 1997; for orchard B the release date was 12 March 1997.

Following release, weevils were recaptured with the limb-jarring method (Lafleur & Hill, 1987) every 2 to 3 days in the orchards and adjacent bushes and in

small trees of the mixed forest until mid May (Tab.A.1, A.2, A.4). Each whole tree was beaten three times a with wooden stick and the dropped weevils were caught on white sheets under trees (2 x 20 m) on dry, sunny afternoons. This method was preferred because of its high efficiency, compared to other methods: for example shelter traps of corrugated paper packages on trunks of trees and sticky window traps of 1.5x1.5 m. The limb-jarring method yielded a recapture rate of $75 \pm 19\%$ (mean \pm s.d., $n=34$) in dry and sunny days. The recapture rates of *A. pomorum* with the two alternative methods were considerably lower (0-3%). Higher within-orchard movement of weevils disturbed by the sampling was not observed.

In addition, within-orchard movement of weevils was also determined. I marked the captured weevils, including those of the native population, with 5 different colour-position combinations indicating capture location and date, and released them immediately at the capture site.

Analysis of recapture data. For each recaptured weevil, the distance between the recapture and release points and the dispersal direction were recorded along with the recapture and release dates. The dispersal direction of each weevil from the release point were used to calculate the co-ordinates of the vector of displacement $\left\{ \begin{bmatrix} X \\ Y \end{bmatrix} \right\}$, ($x_i = \cos \varphi_i$; $y_i = \sin \varphi_i$). These co-ordinates for different recaptured weevils were averaged in intervals of 15° $\left\{ \begin{bmatrix} X \\ Y \end{bmatrix} \right\}$, of an interval, ($X = 1/n * (\cos \varphi_1 + \dots + \cos \varphi_n$; $Y = 1/n * (\sin \varphi_1 + \dots + \sin \varphi_n)$). The resultant vectors of dispersal (R), *i.e.* the product of mean vector lengths ($r = \sqrt{X^2 + Y^2}$) at the chosen intervals of 15° and the number of weevils (n) moving in this direction were calculated and are illustrated in Fig.2.,3.& 4. Mean vector lengths close to 1 indicates the highest level of concentration. To test significance of mean vector's length (r), a Rayleigh-Test was used (Batschelet, 1981) (see Tab.1.). This statistic describes whether the population from which the sample was drawn differs significantly from randomness or whether there is statistical evidence of one-sidedness or directness. Finally, the mean average angle of dispersal of the dispersing population (φ_{all}) was calculated with the main average vector $\{\varphi_{all} = \arctan(Y_{all}/X_{all})$ if $X_{all} > 0$ or $= 180^\circ + \arctan(Y_{all}/X_{all})$ if $X_{all} < 0\}$. The confidence ellipse (Hotelling's ellipse) was calculated as a bivariate statistical description of population centres with a probability of $Q = 95\%$ (Batschelet, 1981, Fig.A.4.1, A.4.2 & A.4.3). To determine differences between main angles of dispersal in different years, the Watson-Williams-test was applied (Zar, 1984).

4.4 Results

Recapture profiles. The percentage of the marked weevils that dispersed from the release points was 75 % and 90% for 1996 and 1997 in orchard A, and 95% for 1997 in orchard B respectively. Examples of the general recapture profiles of released weevils in the two experiments are shown in Fig. 1a & 1b (see also Tab. A.1,2,4). In 1996 the period of highest recapture of both released and native weevils started 21 days after release in orchard A (8 April). In 1997 it occurred around the March 12, *i.e.* one day after release in both orchards A and B. In 1996 the temperature increased slower during spring (see Fig.1a). 9% and 15% marked weevils were recaptured from orchard A in 1996 and 1997 respectively (281 and 262 weevils for 1996 and 1997 respectively). 13% marked weevils were recaptured from orchard B in 1997 (174). Some individuals were recaptured up to 5 times and the mean cumulative number of recaptures and the standard deviation in each case were 340 and 85 ($n=3$).

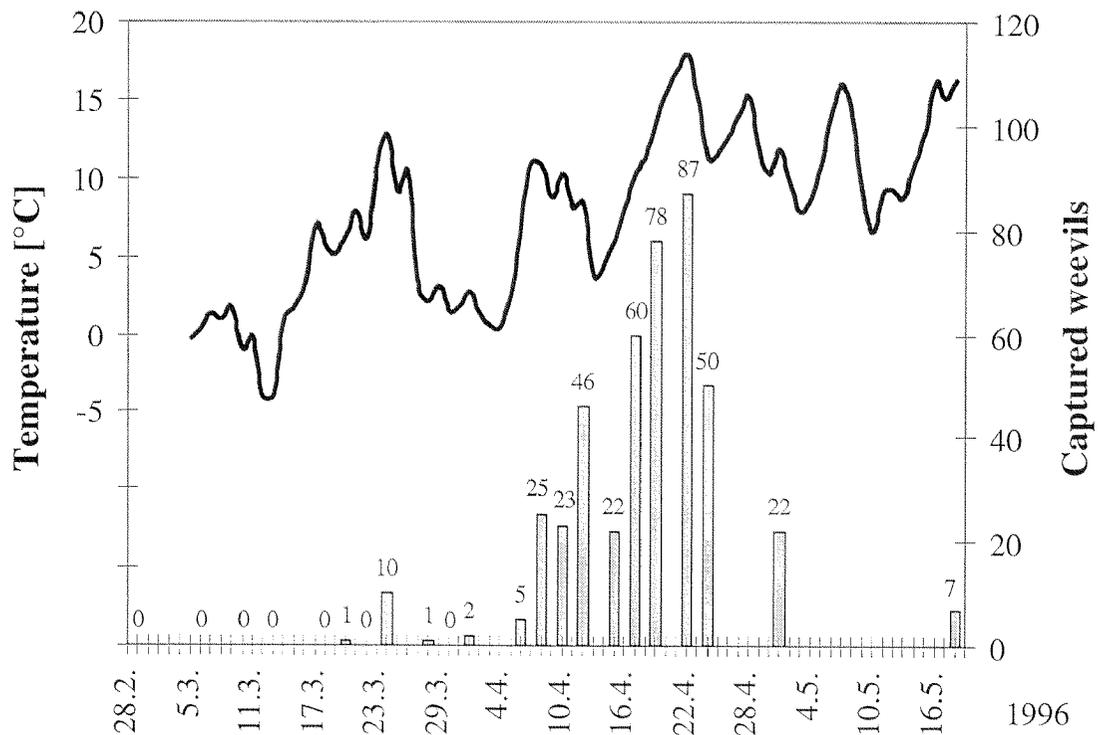


Fig. 1a. Recaptured *A. pomorum* (bars) and mean temperature at height of 1 m (line) in orchard A in spring 1996 (the numbers above bars present the recaptures on each sampling day).

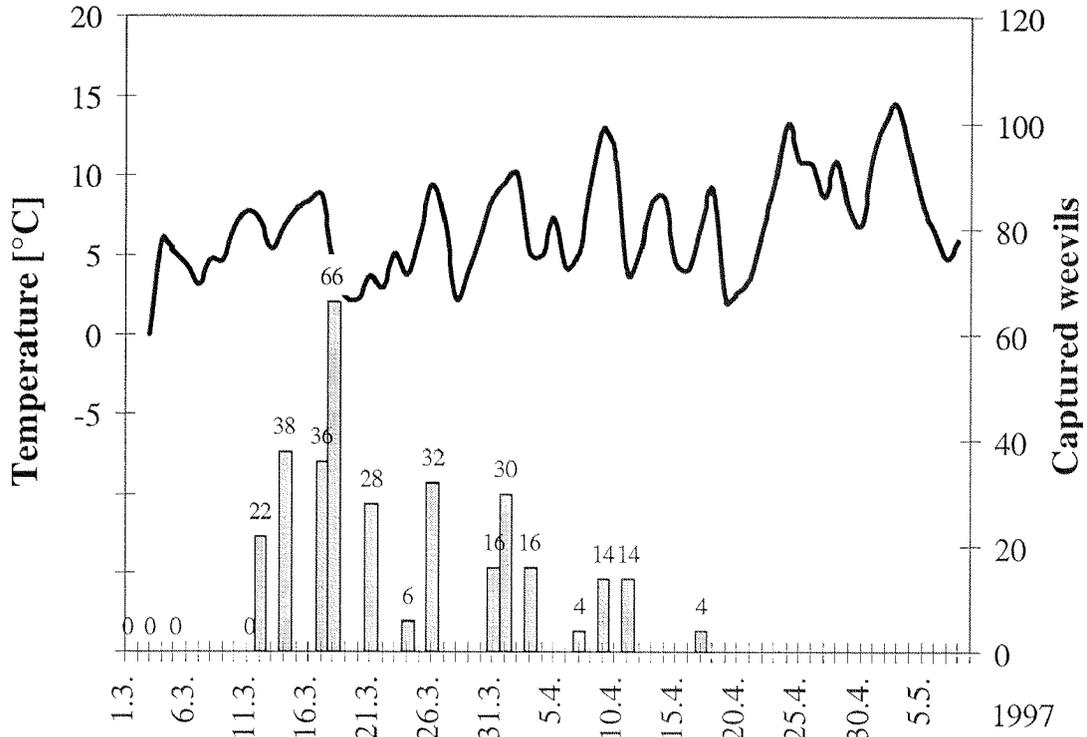


Fig. 1b. Recaptured *A. pomorum* (bars) and mean temperature at height of 1 m (line) in orchard A in spring 1997 (numbers above bars present the recaptures on each sampling day).

Orientated dispersal. In each experiment, most of the released *A. pomorum* migrated from the release point into the orchard (Fig.A.4.3 and Fig.4&5). Only a few weevils were found to move towards the forest ($1.5 \pm 0.5\%$). The overall dispersal pattern of released weevils are shown in Fig. 2a, 3a and 4a for each orchard and year. The vectors of dispersal are shown, along with the number of recaptured weevils and the concentrations of dispersal directions indicated by their lengths. The average main vector describes the overall direction of dispersal, specified by the large arrow head in Fig. 2a, 3a and 4a. Mean direction and the standard angular deviation were calculated as $\varphi_{\text{all}} = 280 \pm 34.8^\circ$ in 1996 and $287 \pm 51.2^\circ$ in 1997 for orchard A and $148 \pm 41.4^\circ$ in 1997 for orchard B. The estimate of the mean vector length (r) for these cases equalled 0.8, 0.6 and 0.74 respectively. The dispersal angle between the two years were not significantly different in orchard A (Watson-Williams-test, $P > 0.05$, Tab.A.4.1). Each of these angles corresponds to the respective direction from the release point to the centre of the apple orchard. Generally, the direction of dispersal did not vary during the whole colonisation period with the released weevils moving into the orchard (Tab.1&A.4.2). The direction of apple tree rows did not seem to influence the direction of dispersal, because the principal direction of movement in orchard A and orchard B

was comparable, irrespective of the different direction of tree rows corresponding to the adjacent forest (Fig. 3a and 4a).

Tab. 1. Vectors of dispersal in relation to days after release, based on recapture of marked *A. pomorum* in orchard A in spring 1996 & 1997 (orchard is 270° relative to release point, wind direction $181 \pm 34^\circ$), φ_{all} = mean direction of displacement, s.d.= standard angular dev., n= recap. number, r_{all} = length of main vector as a measure of concentration.

Days after release	φ_{all} [°]	s.d. [°]	n	r_{all}
10	286.5	61.1	77	0.4
20	279.0	40.2	67	0.8
30	288.0	46.5	158	0.7
40	281.5	43.8	161	0.7
50	288.0	32.4	18	0.8
Mean	283.5	43.0	543	0.7

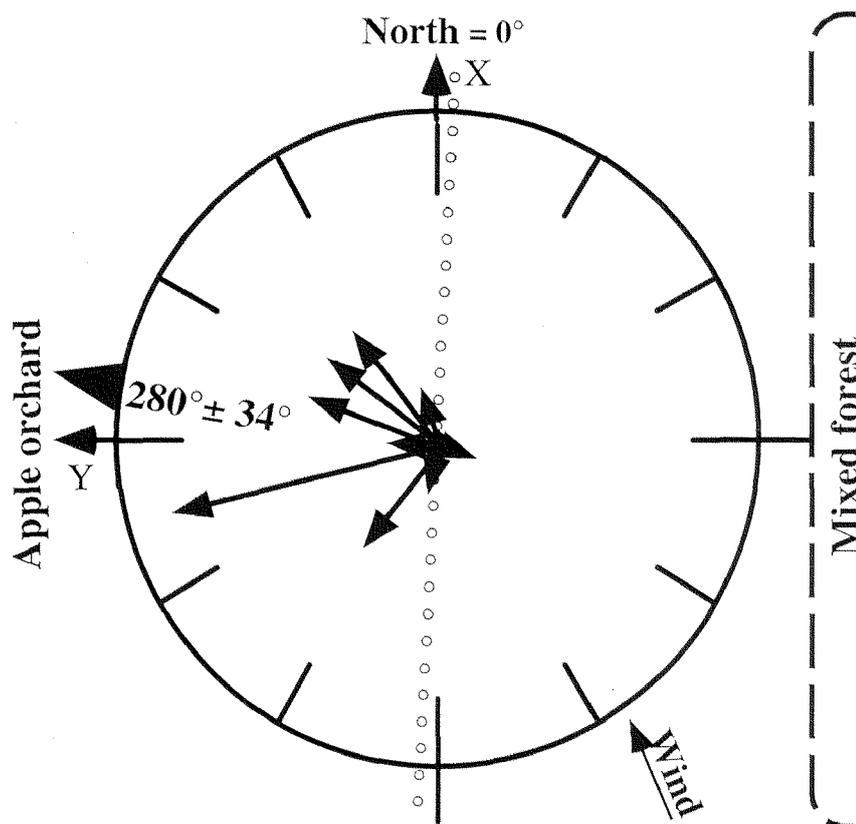


Fig. 2a. Dispersal of marked *A. pomorum* from release point in orchard A in spring 1996 (281 individual recaptures). Arrows represent the sum of vectors in a sector of 15° . The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and their concentration (r). The arrow on the outline of circle shows the main average direction of dispersal ($\varphi_{all} = 280 \pm 34^\circ$, $r_{all} = 0.8$ indicates a high level of concentration at $P < 0.005$, Rayleigh-test). The dotted line shows the direction of the tree rows in the orchard.

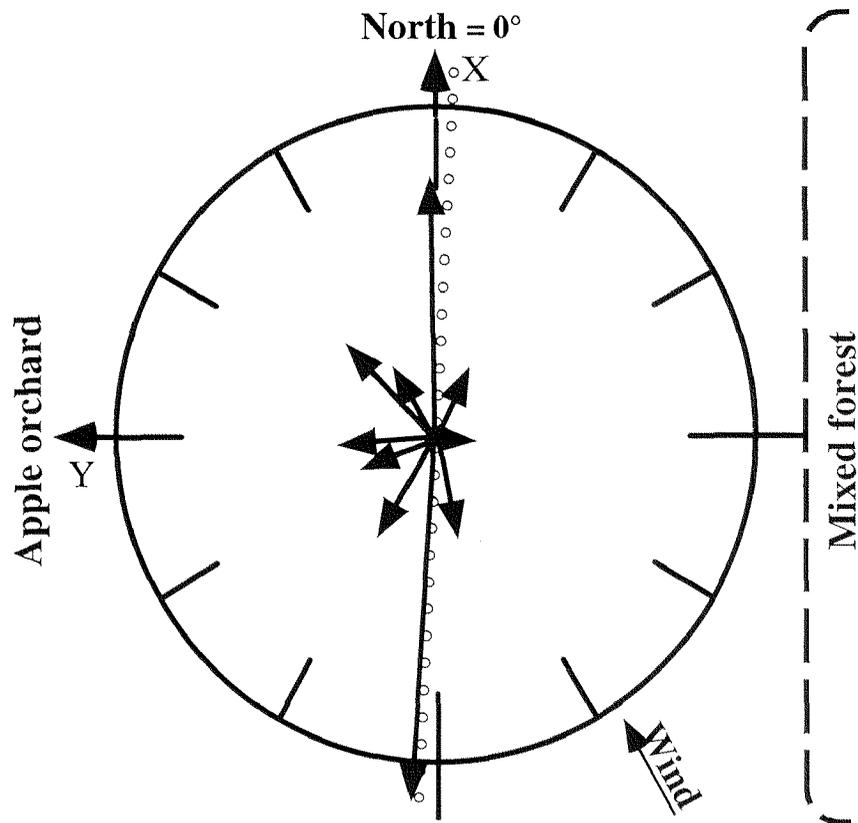


Fig. 2b. Within-orchard movement of *A. pomorum* following colonisation in orchard A in spring 1996 (123 repeated recaptures, excluding 40 weevils which did not move). Arrows are resultant vectors and represent the sum of vectors in a sector of 15° . The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and the concentration of the vector (r). X and Y are co-ordinates. The dotted line shows the direction of the tree rows in the orchard.

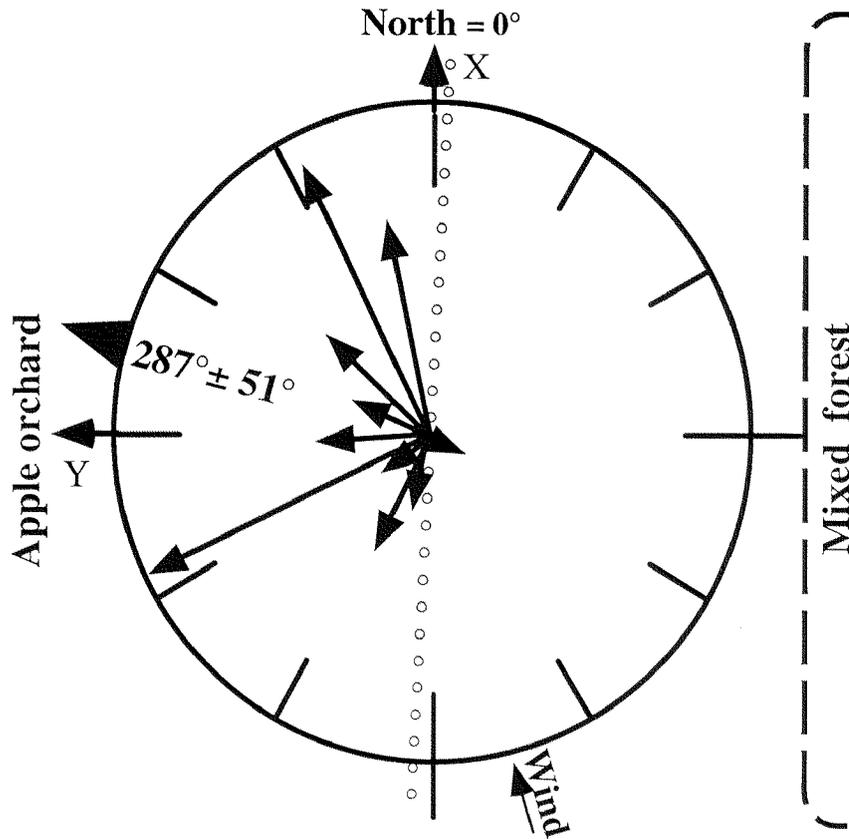


Fig. 3a. Dispersal of marked *A. pomorum* from release point in orchard A in spring 1997 (368 individual recaptures). Arrows are resultant vectors and represent the sum of vectors in a sector of 15° . The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and the concentration of the vector (r). The arrow on the outline of circle shows the main average direction of dispersal ($\phi_{all} = 287 \pm 51^{\circ}$, $r_{all} = 0.6$ indicates a high level of concentration at $P < 0.005$, Rayleigh-test). X and Y are co-ordinates. The dotted line shows the direction of the tree rows in the orchard.

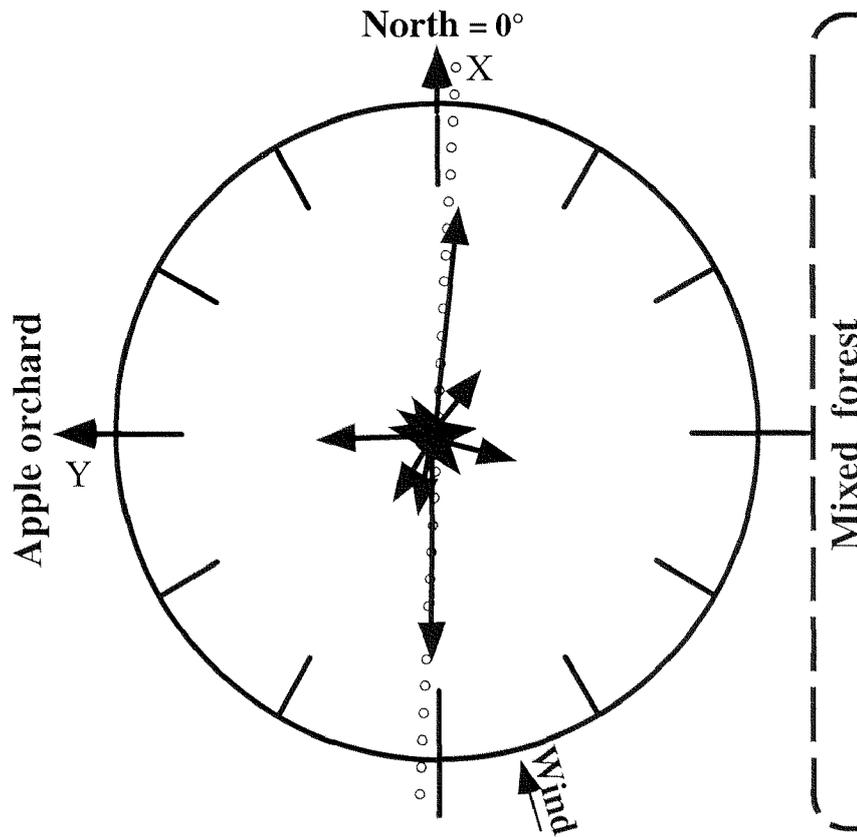


Fig. 3b. Within-orchard movement of *A. pomorum* following colonisation in orchard A in spring 1997 (110 repeated recaptures, excluding 44 weevils which did not move). Arrows are resultant vectors and represent the sum of vectors in a sector of 15° . The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and the concentration of the vector (r). X and Y are co-ordinates. The dotted line shows the direction of the tree rows in the orchard.

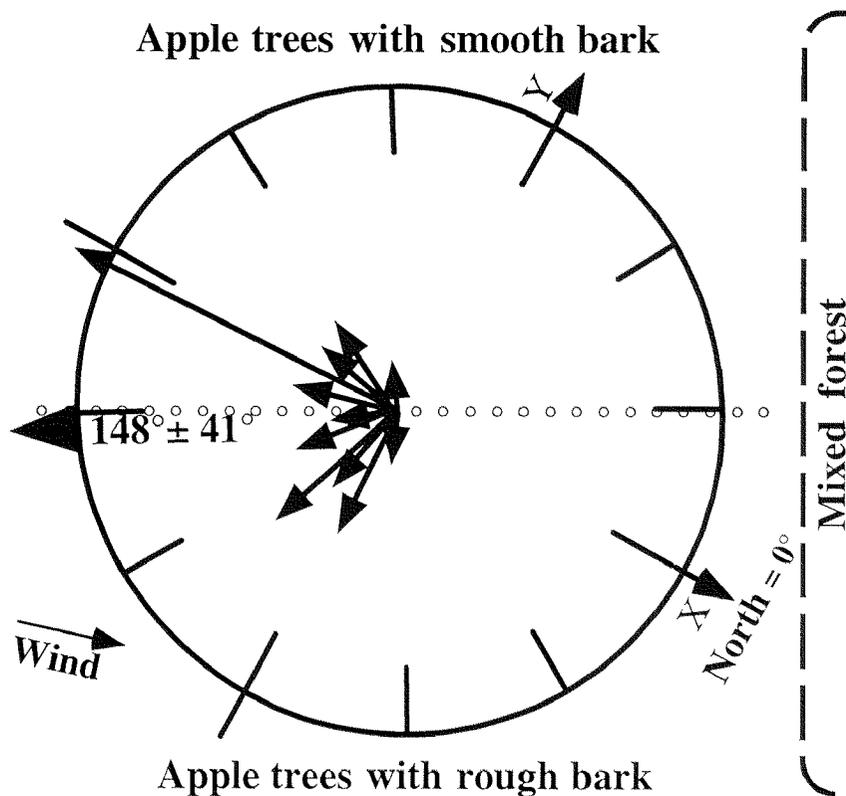


Fig. 4a. Dispersal of marked *A. pomorum* from release point in orchard B in spring 1997 (240 individual recaptures). Arrows are resultant vectors and represent the sum of vectors in a sector of 15°. The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and the concentration of the vector (r). The arrow on the outline of circle shows the main average direction of dispersal ($\varphi_{\text{all}} = 148 \pm 41^\circ$, $r_{\text{all}} = 0.74$ indicates a high level of concentration at $P < 0.005$, Rayleigh-test). X and Y are co-ordinates. The dotted line shows the direction of the tree rows in the orchard.

Dispersal distance. In each experiment, a substantial proportion ($38 \pm 6.5\%$) of the released population remained in 10 m of the release point. After two to three weeks, the released weevils were only slightly more widely distributed (Fig. 5). These weevils were usually found to move 5-25m during the first 30 days following the start of colonisation, with a mean distance of $17 \pm 12.8\text{m}$, though a small proportion of released weevils ($6 \pm 1\%$) dispersed over 40m, a few moving 30 to 40m in a single day even up to a maximum distance of 90m during 30 days (Fig.6, Tab.A.4.3)). The centre of population as described by the Hotelling's confidence ellipse was within a $19 \pm 2\text{m}$ distance from the release point and forest border ($Q=95\%$). Due to the relatively limited dispersal range in each situation, only a limited part of the experimental orchards was colonised by the released weevils ($0.29 \pm 0.05\text{ha} \approx 30\text{-}50\%$). Even within this range, the density of marked weevils decreased with increasing distance from the forest (Fig. 5 and 6), described by the Cauchy distribution (Johnson & Kotz, 1970).

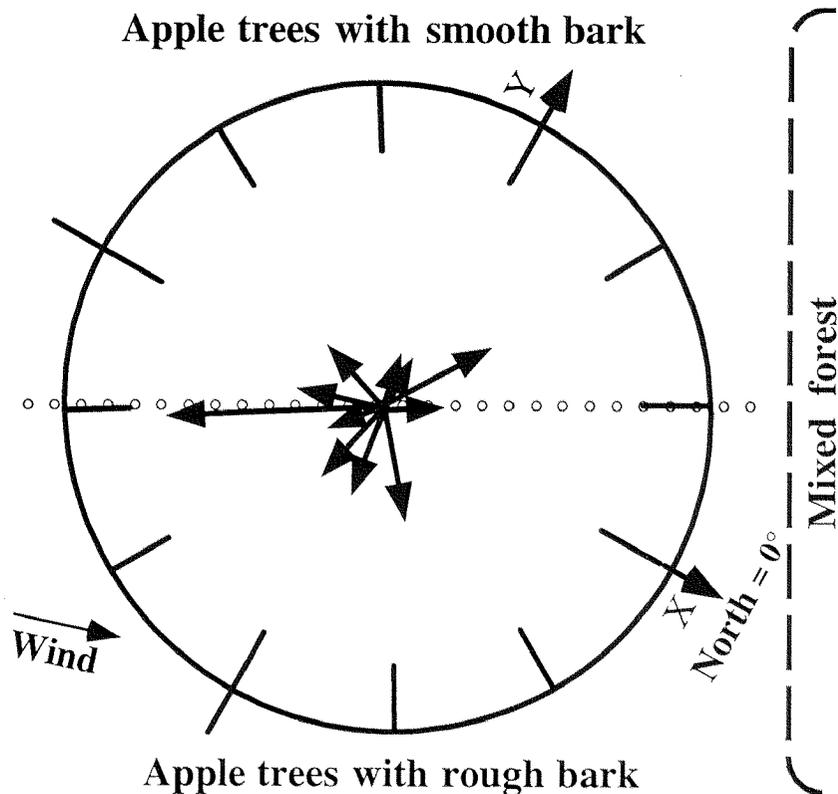


Fig. 4b. Within-orchard movement of *A. pomorum* following colonisation in orchard B in spring 1997 (77 repeated recaptures, excluding 18 weevils which did not move). Arrows are resultant vectors and represent the sum of vectors in a sector of 15° . The length of the resultant vectors (R) is the multiple of the weevils (n) dispersing in the sectors direction and the concentration of the vector (r). X and Y are co-ordinates. The dotted line shows the direction of the tree rows in the orchard.

The direction of apple tree rows had a minor impact on the dispersal distance, as indicated by a comparison of data from the differently structured orchards used in this study. The standard deviation of the dispersal distances of released populations was only 2 m in distance from the adjacent forests. Also, the areas with old high-stem apple trees with rough bark or with modern dwarf apple trees with smooth bark did not have different effects on spring dispersal of *A. pomorum* (Fig. 4a, b). After moving into the orchard, about $33.5 \pm 8\%$ of weevils remained on the trees where they first arrived. The rest moved mainly following the rows of apple trees over distances of 11 ± 5 m, (Fig. 2b, 3b and 4b). The variety of apple and the direction from the release point or the surrounding forest had little effect on this trend.

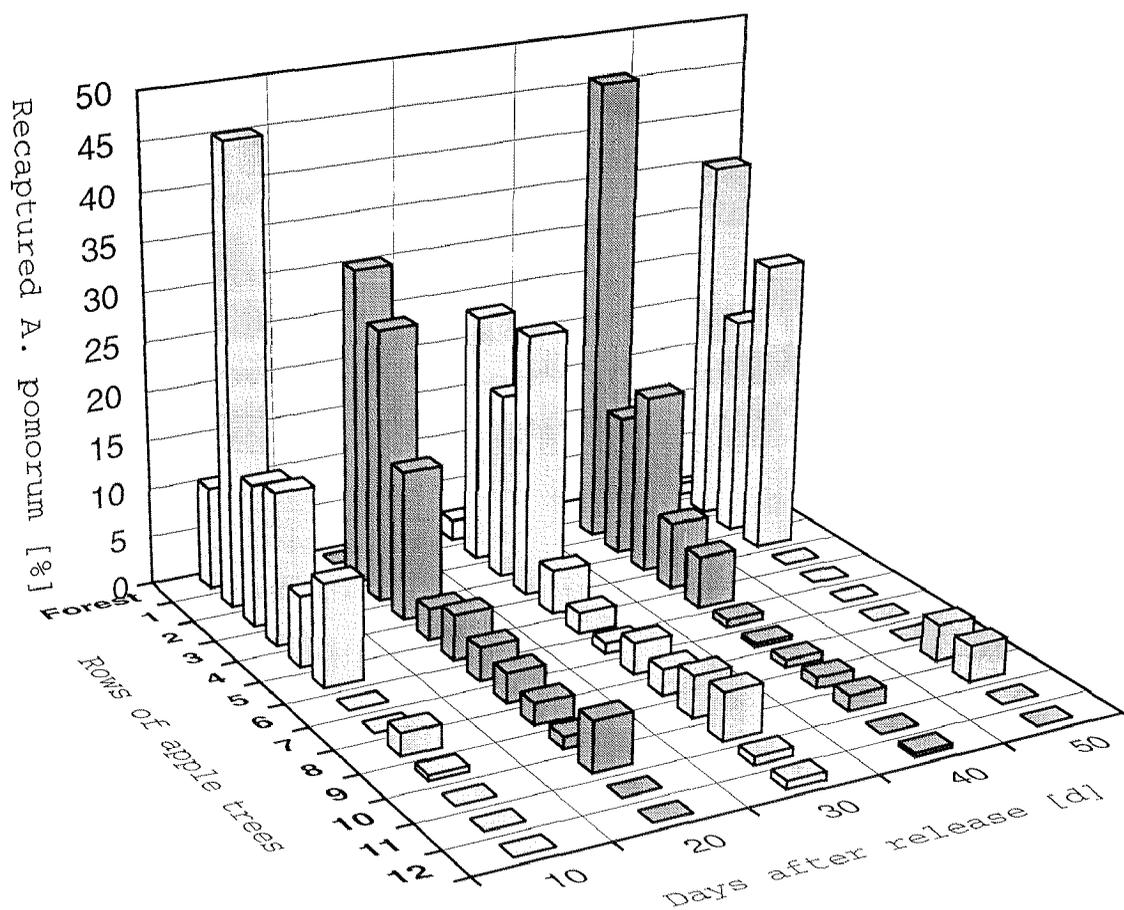


Fig. 5. Spatial and temporal pattern of colonisation of orchard A by *A. pomorum* in spring 1996 and 1997.

Dispersal dynamics in relation to host phenology: The colonisation period of *A. pomorum* in the orchard lasted 4 and 5 weeks in 1996 and 1997 respectively. In 1996 orchard colonisation started two weeks later due to cold weather conditions and the peak recapture period was delayed accordingly (see Fig. 1a, 1b). The time of the first recapture of weevils occurred between the start of bud-swelling (A) and buds with a slightly silvery greenish tip (B) in 1995 (Hirs, B. & Dorn, S., unpubl.), 1996 and 1997. The period when maximal numbers of weevils per tree were recaptured coincided with the mouse-ear growth stage of the apple buds and the half inch green tipped buds (C-C3, Fleckinger, 1948). This early period also corresponded to the highest dispersal speed of the population (7.3 ± 2 m per day with a maximum of 13 ± 3.7 m). After the pink bud growth stage and just before bloom, the dispersal speed decreased markedly to 2.4m daily, and thereafter most weevils remained relatively inactive. The dispersal speed of the weevils was affected by climatic factors (Chapt. 5).

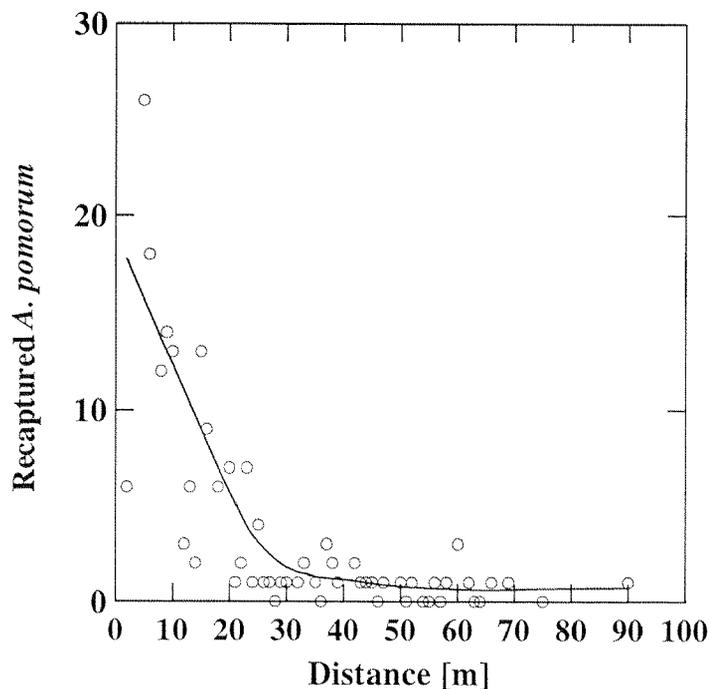


Fig. 6. Relationship between recaptures (y) of *A. pomorum* and distance (x) from the release point (Cauchy distribution fitted to the data obtained during the 30 days after colonisation in orchards A and B in spring 1996 and 1997, $y = 663 / (3.1415 * 12 * (1 + (x/12)^2))$, $R^2 = 0.67$).

4.5 Discussion

The release-recapture experiments have demonstrated that the early or late occurrence of spring dispersal and the resultant orchard colonisation by overwintered weevils is strongly related to temperature variations, regardless of habitat characteristics. Compared to the meteorological data for recent years, the weather conditions of 1996 appeared unusual. For example mean and maximum temperatures in March and April were 1.5 and 3 °C lower in 1996 than in 1997. Accordingly, the initial dispersal and colonisation of orchards by overwintered weevils in 1996 were 2 weeks later than in 1997.

Overwintered weevils showed a consistent pattern in which weevils dispersed from the adjacent forest border to the apple orchard in early spring. This pattern was independent of variation in climatic conditions from year to year and structural differences between orchards, *e.g.*, the angle of tree rows relative to the adjacent forest. A similar pattern of orientated migration from adjacent woods to apple orchards in spring occurs in another curculionid, the plum curculio, *Conotrachelus nenuphar*

(Herbst) (Lafleur & Hill, 1987). Orientation of spring migration was the reverse of the autumn movement of the weevil (Lafleur & Hill, 1987). *A. pomorum* and *C. nenuphar* share many biological and ecological characteristics, and the earth's magnetic field may be of significance in guiding spring dispersal in both species (see Lafleur & Hill, 1987). In *A. pomorum*, however, it is probable that chemical cues emanating from apple trees also play a role in initiating and directing the spring colonisation of orchards by weevils which overwintered in nearby forests. Currently sex or aggregation pheromones are not known in this species, but both male and female weevils are able to detect volatiles from apple leaves in antennae (Kalinova *et al.*, 1996). In experiments, the largest number of *A. pomorum* weevils from apple trees were captured at the mouse-ear growth stage of blossom buds (C-C3). This might be partially due to the high attractiveness of this bud stage to the weevils which are searching for food and oviposition sites (Miles, 1923; Rilishkene & Zayanchkauskas, 1985).

Although possible factors and mechanism for spring dispersal in *A. pomorum* remain to be investigated, the adaptiveness of this behaviour is apparent. In modern European orchards with dwarf apple trees *A. pomorum* must emigrate to seek suitable aestivation and/or hibernation sites elsewhere, mainly in forests and other non-managed habitats in the vicinity of orchards (Korchagin, 1978; Vyangelyauskaite, 1992). Furthermore, early in the season overwintered *A. pomorum* require a particular host plant, mainly apple trees, at a specific stage of bud development for maturation feeding and oviposition (Ctvrtecka & Zdárek, 1992; see Chapt. 7). Therefore, the orientated dispersal from hibernation sites to apple orchards is critical for the success of *A. pomorum*. Differences between the dispersal behaviour of female and male weevils are difficult to investigate in the field. However, laboratory experiments have demonstrated that females show a higher flight proclivity than males from the beginning to the end of February, whereas in March and April this difference was not apparent (Fig.A.6.7 & A.6.8).

The distance covered during the spring dispersal of recaptured overwintered *A. pomorum* is rather short. The majority of the released weevils did not move more than 20 m during the whole colonisation period, though a small proportion covered greater distances of up to 90 m. This dispersal distance is comparable to that recorded for *C. nenuphar*, in which the mean distance travelled by the female and male weevils was about 35 m (Lafleur & Hill, 1987), but is shorter than those reported for other curculionid weevils, such as *Cylas formicarius elegantulus* (Summers) (Miyatake *et al.*, 1995), *Anthonomus grandis* Boheman (Guerra, 1988) and *Hypera postica* (Gyllenhal)

(Meyer, 1982). The relatively small dispersal capacity observed in *A. pomorum* may reflect their low flight proclivity under the climatic conditions prevailing during the early spring season (see Fig. 1 and Duan *et al.*, 1996).

When *A. pomorum* weevils arrive at an apple tree with suitable buds, they tend to remain there. Therefore, any subsequent within-orchard movement of *A. pomorum* may be very limited and mainly occurs along the apple tree rows. The direction relative to the release point and to surrounding forests had no apparent influence on this movement pattern. Flight activity of immigrated weevils was seldom observed, and therefore, the sedentary behaviour of these invading weevils resulted in heavy infestation of the trees along the borders of orchards, especially, on those adjoining forested areas (Fig.A.4.4 & A.4.5). This result explains the edge effect of infestation by *A. pomorum* which has been reported previously (Tret'yakov, 1984; Brown *et al.*, 1993).

In summary, the reproductive success of *A. pomorum* and the resultant level of infestation strongly depend on the spring colonisation of orchards by overwintered weevils, especially, in modern cultivation systems. If the weevils were to disperse evenly over large distances at a low density, they would contribute to the thinning process of flowers, which might even be desirable. However, the results of our field experiments demonstrate that the characteristic dispersal behaviour of *A. pomorum* often leads to a high density at the borders of orchard. This can cause a considerable loss of yield in localised zones of the orchard. Therefore the findings of this study are not only important in gaining a better understanding of the spring colonisation of orchards by overwintered weevils, but also have direct relevance to the development of an effective management strategy against this pest. In this respect, two points are obvious from these findings. Firstly, sampling and scouting a few tree rows along the orchard borders adjoining forest areas should provide reliable information on the spring occurrence of the weevils in orchards. Secondly, the direction of pest management measures at these tree rows in a modern dwarf apple could be expected to limit the damage, but probably not to such a high degree as described for the plum curculio (Chouinard *et al.*, 1992). Furthermore, empirical data on spring dispersal and its relationship with the prevailing climatic conditions (Chapt. 5) will form a basis for predicting spring colonisation of orchards by overwintered weevils and the timing of intervention, with non-disruptive techniques can be optimised (Chapt. 5.4).

5. INFLUENCES OF CLIMATIC FACTORS ON THE SPRING DISPERSAL BEHAVIOUR OF *ANTHONOMUS POMORUM* *

5.1 Abstract

Climatic influences on the spring dispersal and orchard colonisation of overwintered apple blossom weevils, *Anthonomus pomorum* (L.), were monitored with field captures and repeated release-recapture experiments. The data obtained were used to produce a predictive model for adult immigration into the orchard to describe and forecast the temporal dynamics of the population. Temperature was found to be the driving force for the initiation of dispersal in early spring. Colonisation of orchards by immigrating weevils started at 161 ± 27 cumulative Celsius degree-days (DD), calculated from 1 January at temperatures above 0°C, and at 10 ± 1 DD calculated from 1 March at temperatures above 6°C. This colonising dispersal usually started when the mean daily threshold temperature reached a level of 7 to 9°C, which occurs mostly in the second week of March. The threshold temperature was estimated with regression analysis and found to be 5°C. Temperature was also a key factor for dispersal dynamics. The daily dispersal speed of individual weevils was positively correlated with the mean and maximum daily temperatures, as well as with the mean temperature at the weevils' activity peak, *i.e.* between 6:00 p.m. and 10:00 p.m. Furthermore, field cage observations showed that temperature also influenced the crepuscular activities of weevils on apple trees, such as crawling, feeding, mating and oviposition. Surprisingly, rain and wind did not influence dispersal significantly. Air humidity had a measurable effect; it was negatively correlated with dispersal speed and showed an optimal range for crawling, feeding, and mating activities. The implications of these findings for pest monitoring and management are discussed.

* Finalised for publication as: Toepfer, St., Gu, H., Dorn, S. Climatic Data-Based Analysis of Spring Dispersal in Apple Blossom Weevil (Coleoptera: Curculionidae).

5.2 Introduction

The apple blossom weevil, *Anthonomus pomorum* (L.) is a widespread univoltine herbivore in apple orchards in Europe. The weevil overwinters in the adult stage within and outside apple orchards. In early spring, the overwintered weevils seek apple trees for maturation feeding and oviposition on blossom buds (Ctvrtecka and Zdàrek 1992, Brown *et al.* 1993). Thus, spring dispersal is a crucial population process in the colonisation of orchards. Although the influence of temperature on emergence and colonisation has been discussed previously (Kaiser 1943, Grison and Chevalier 1963 and Korchagin 1978), quantitative field data was never presented. Moreover, most of the information available originates from isolated observations rather than from comprehensive, systematic studies.

The objective of this study was to quantify the effect of climatic variables on the temporal dynamics of early spring dispersal and on the activity of the weevils on apple trees. Multiple capture data and climatic data were collected to develop a predictive model, based on degree-days and threshold temperatures, to estimate when adult weevils would start their immigration into the orchard. In addition, the climatic influences on the crepuscular activities of the weevils on apple trees were studied to validate previous laboratory results (Duan *et al.* 1996).

5.3 Materials and methods

Insects. The weevils used in release-recapture experiments and in field cage observations were collected in the spring-summer of previous years in northern Switzerland. They were kept in plastic boxes until adult emergence and were fed with fresh apple leaves until the onset of hibernation. Then they were overwintered outdoors under semi-natural conditions in plastic boxes together with several leaves and corrugated cardboard. In early spring, the overwintered weevils were marked with enamel lacquer for release. The use of different colour codes at five positions on the elytra and pronotum enabled us to administer 1200 combinations of individual markings on the captured weevils. For the field cage experiments the weevils were distinguished by sex using the number of abdominal segments as a distinguishing criteria (Duan *et al.* 1999) and were marked in February.

Climatic data. Weather stations (CR 10, Campbell Scientific LTD, UK) were installed in the orchards and in observation cages to monitor the following parameters: mean daily, maximum and minimum temperature (°C), temperature between 6:00 p.m. and

10:00 p.m., *i.e.* during the peak activity of this species (Duan *et al.* 1996), mean daily and relative evening air humidity (% r.h.), mean wind speed (m / s) and direction (degree), mean daily light intensity and mean light intensity during four hours around sunset (W / m^2), and daily rainfall (mm). Recordings were made every 15 minutes at a height of 1.50 m near an apple tree.

Timing and speed of dispersal. To investigate the timing of dispersal and the beginning of colonisation, weevils were collected in early spring in 3 orchards in northern Switzerland (47 °N, 8 °E), referred to as A, B and C. Capturing in orchard A was carried out in 1996, 1997 and 1999, in orchard B in 1997, 1998 and 1999, and in orchard C in 1995. Orchard A, located in Zürich-Hoengg at an elevation of 509 m, is 1 hectare. The rows of dwarf apple trees (2.5 m high) were 3.5 m apart. This orchard is bordered along the east side by an old mixed forest, along the south and north sides by residential buildings and along the west side by a road. Orchard B, located in Niederwil AG at an elevation of 440 m, is 0.9 hectare. It consisted of two parts: an area of dwarf apple trees and an area of old high-stem apple trees (4m high, 4 m between rows). This orchard is bordered along the north side by a mixed forest (ca. 20 m high), along the south and west side by apple trees and along the east side by fallow land. Orchard C, located in Baar ZG at an elevation of 460 m, is 1 hectare. It consisted of dwarf apple trees of different ages and heights, 3.5 m apart. This orchard is bordered along the east side by a mixed forest, along the north by a road and high stem apple trees, along the north-west by buildings and the rest by fallow land.

Weevils were captured by limb-jarring, usually in dry, sunny afternoons (Lafleur and Hill 1987, Chapt. 4.3) from a few days before the termination of diapause until the end of spring colonisation. Each tree was struck three times with a wooden stick and the weevils collected from white sheets laid out below the trees (2 x 20 m). Totally, 14 ± 5 captures were made, depending on the experimental case. In orchard A, 850 weevils were captured on average from the end of February to May in 1996, 1997 and 1999. In orchard B, 2850 weevils were caught on average between the end of February and April in 1997, 1998 and 1999. In orchard C, 1150 weevils were captured totally from the end of February to April in 1995 (Hirs, B. and S. Dorn, unpublished data). Based on the number of captures the timing of dispersal was characterised according to Parajulee (1996). Firstly, the start of dispersal was defined by the first peak in capture rate lasting two or three successive days (Tab.1A). Secondly, the full start of the colonisation process was defined by the highest capture rates and the speed of dispersal during a few successive days (Tab.1B). Thirdly, the date on which

single weevils were first observed to reach apple trees was determined. This was usually a few days before the start of dispersal. These three parameters were analysed in relation to the current daily mean, maximum and minimum temperatures, and thereby threshold temperatures were calculated (see Tab.A.5.1)

Furthermore, the cumulative Celsius degree-days (DD) were calculated from 1 January, 1 February and 1 March to the start of dispersal at temperatures above 6°C, 5°C or 0°C (Tab.A.5.1). The 6°C was defined by a threshold for the termination of hibernation after Korchagin (1978), Ctvrticka and Zdàrek (1992) and the lowest temperature for the start of dispersal in this study. The 5°C threshold was defined by the estimation from regression analysis between daily temperature and dispersal speed. The temperature of 0°C was defined by observations of vital activities of *A. pomorum* in field cages. The mean daily temperature was the average of recordings every 15 min during 24 hours. The DD (>0°C) and (>6°C) were found to fit the dispersal data best, and they were presented in results (Tab.1).

Correlation between daily dispersal speed and different climatic factors in apple orchards were analysed with release-recapture experiments carried out in orchard A in 1996 and 1997 (Chapt. 4.3). About 4000 marked weevils were released in 18 March 1996 and about 1700 on 11 March 1997. In each case, two open plastic release boxes were set up at a height of 1 m on a portable apple tree near the orchard border adjacent to a forest. After release, weevils were recaptured every two to three days by limb-jarring until mid-May. The recaptured weevils were individually marked, indicating capture location, distance to the release point and date, and released again at the respective capture sites immediately. Weevils from the native population were marked and included in the experiment. Dispersal speed was calculated in meters per insect and day for 281 recaptured individuals in 1996 and for 262 in 1997. Regression analysis and the Generalised Linear Model, ANOVA and t-tests of regression coefficients were performed to determine the respective effect of these factors on dispersal speed.

Spring behaviour on apple trees. Four observation cages (1.5x1.5x2.2 m) were set up in the field each with one dwarf apple tree inside (var. Boskoop, rootstock M26) in Zürich in 1998. 40 overwintered females and 25 males were released on the trunk of each apple tree. This was done prior to the first overwintered weevils being detected in the orchards. From 11 February to 9 April, which covered the whole period of spring colonisation, the weevils were observed during periods of 15 min from 2 h before to 2 h after sunset every day. Every 15 min, five to seven new weevils were located, totally

3500 during the whole experiment. Ethogrammes were constructed for the following behavioural activities: feeding, mating, oviposition, crawling, flying, and non-activities, *i.e.* resting and hiding. Seven microhabitats were defined namely blossom buds, foliage, twigs and branches, main trunks, ground, gauze of the cage and refuges such as corrugated cardboard or bark. Red light was used to locate weevils in the dark.

Data were analysed using two pools summarising the observations 2 hours before and 2 hours after sunset. The relative proportion of each behaviour [%] and the relative proportion of behaviours observed on each substrate [%] were considered for 50 weevils. First the data were analysed in relation to climatic conditions during observation time, *i.e.* in the evening (see section *Climatic data*), to obtain insight into the physiological constraints of the weevil. Second the data were analysed in relation to the daily averages of climatic factors to get more generalised results. ANOVA and regression analysis were used to determine the influence of climatic factors on the weevil's behaviour, using the data transformed by $\lg(x+1)$. Differences between the behaviour of males and females were analysed with a Mann-Whitney-U-signed-rank-test.

5.4 Results

Timing of dispersal. The minimum daily threshold temperatures allowing the start of dispersal of apple blossom weevils into orchards were found to be 6°C, 8±1°C at a mean ($n=6$, Tab.1A). However, the weevils could perform some vital activities even at 0°C (Fig.4). Thus, both temperatures were used as thresholds for alternative calculation of cumulated day-degrees (Fig.1.). The dispersal into the three orchards started, when day degrees above 0°C, calculated from 1 January, reached 125 to 184 Celsius DD, with a mean of 161 DD (s.d.±27). Other good fitting temperature sums were 117±16 DD_{1 February} (>0°C), 16±7 DD_{1 February} (>6°C) and 10±1 DD_{1 March} (>6°C). The model based on the regression analysis between daily temperature and dispersal speed predicts a daily threshold temperature of 5°C, presuming a dispersal speed of 5m per insect and day (polynomial regression: $y=-0.04x^2+1.19x$, $R^2= 0.25$, $P<0.001$; linear regression: $y=2.8+0.4x$, $R^2= 0.5$, $P<0.001$, $n=58$).

The observed start of mass colonisation into the three orchards took place when a mean day-degree above 0°C was up to 210±26 DD, calculated from 1 January and 166±19 DD, calculated from 1 February (Tab.1B). The mean daily threshold temperature for mass colonisation was 9 ±1°C. The colonisation process was interrupted when the mean daily temperature fell below 3.7°C.

Typically few weevils were already captured 13 days before the population dispersal started, meaning 25 days before the mass colonisation of weevils started (s.d. ± 11 days, $n=5$, Tab.A.5.1D). In northern Switzerland, the dispersal of the apple blossom weevil into orchards started, on average, on 12 March in 1995 to 1999, with a standard deviation of 1 week ($n=7$, Tab.1A, see also Tab.A.5.1). The full start of mass colonisation into orchards was observed between 9 March and 7 April (Tab.1B).

Tab.1. Observed beginning of colonisation of three apple orchards in northern Switzerland by the apple blossom weevil in relation to ambient temperature from 1995 to 1999. Cumulative day-degree (DD) are calculated from 1 January, 1 February and 1 March. The first peak of captures (A) and the start of mass colonisation of the population (B) were recorded.

A Start of dispersal into orchard										
	Date	Threshold daily temperature			DD _{1 January}		DD _{1 February}		DD _{1 March}	
		Mean	Max.	Min.	>0 °C	>6°C	>0 °C	>6°C	>0 °C	>6°C
		Earliest	4 March	6	12	-2	125	10	93	10
Latest	23 March	10	18	5	184	25	130	24	88	10
Mean	12 March	8	15	3	161	17	117	16	64	10
s.d.	7	1	2	3	27	7	16	7	20	1
Locations	7	6	7	7	4	4	4	4	5	4

B Full start of colonisation & Highest speed of dispersal										
	Date	Threshold daily temperature			DD _{1 January}		DD _{1 February}		DD _{1 March}	
		Mean	Max.	Min.	>0 °C	>6°C	>0 °C	>6°C	>0 °C	>6°C
		Earliest	9 March	8	3	0	181	16	139	15
Latest	7 April	11	21	11	242	37	179	36	147	36
Mean	24 March	9	15	4	210	24	166	23	112	21
s.d.	8	1	6	3	26	10	19	9	26	11
Locations	7	7	7	7	4	4	4	4	6	6

Dispersal speed. The mean dispersal speed of individual weevils in orchard A was 6.8 m per day (s.d. ± 7 m, $n=755$) in early spring from March to the end of April in 1996 and 1997 (Fig.A.5.8). These weevils were most active in terms of distance travelled per day within the first 40 days after the start of dispersal (Tab. 2).

Tab.2. Mean dispersal speed of the weevil population in the early spring of 1996 and 1997 in orchard A.

Days after start of dispersal	10	20	30	40	50
Speed [m per insect and d]	6.1	5.4	7.3	5.8	2.4
s.d.	3.7	2.1	1.9	1.3	2.0
<i>n</i>	172	112	243	157	25

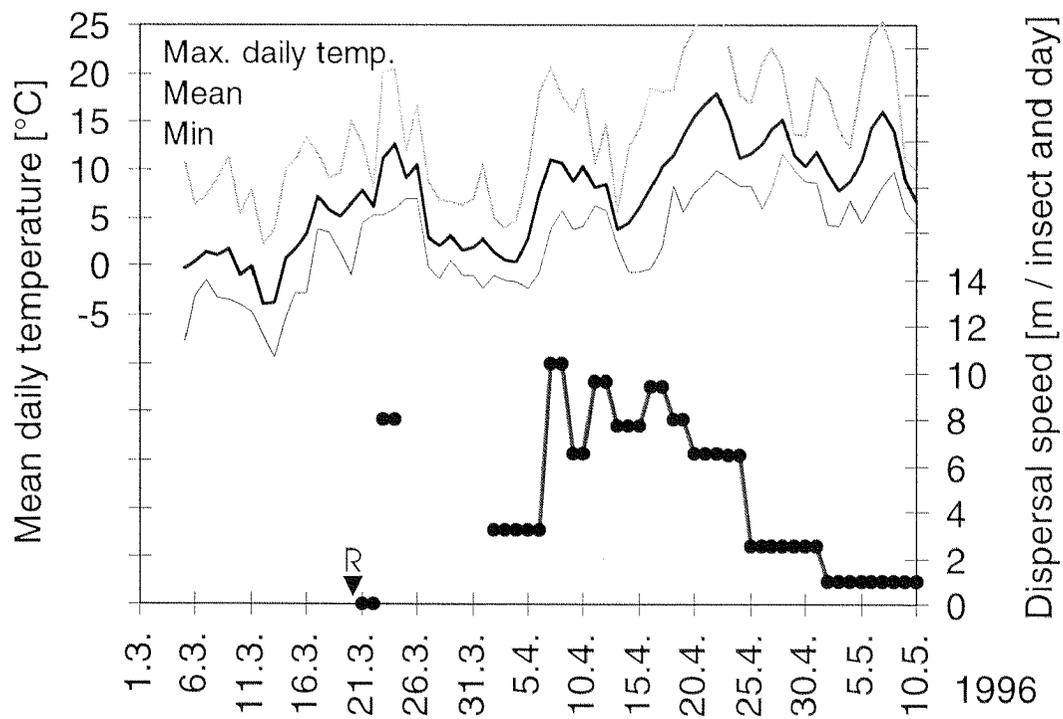


Fig.1. Mean speed of spring dispersal of marked apple blossom weevils released on 18 March 1996 (R), and ambient temperatures ($n=403$ recaptures, orchard A)

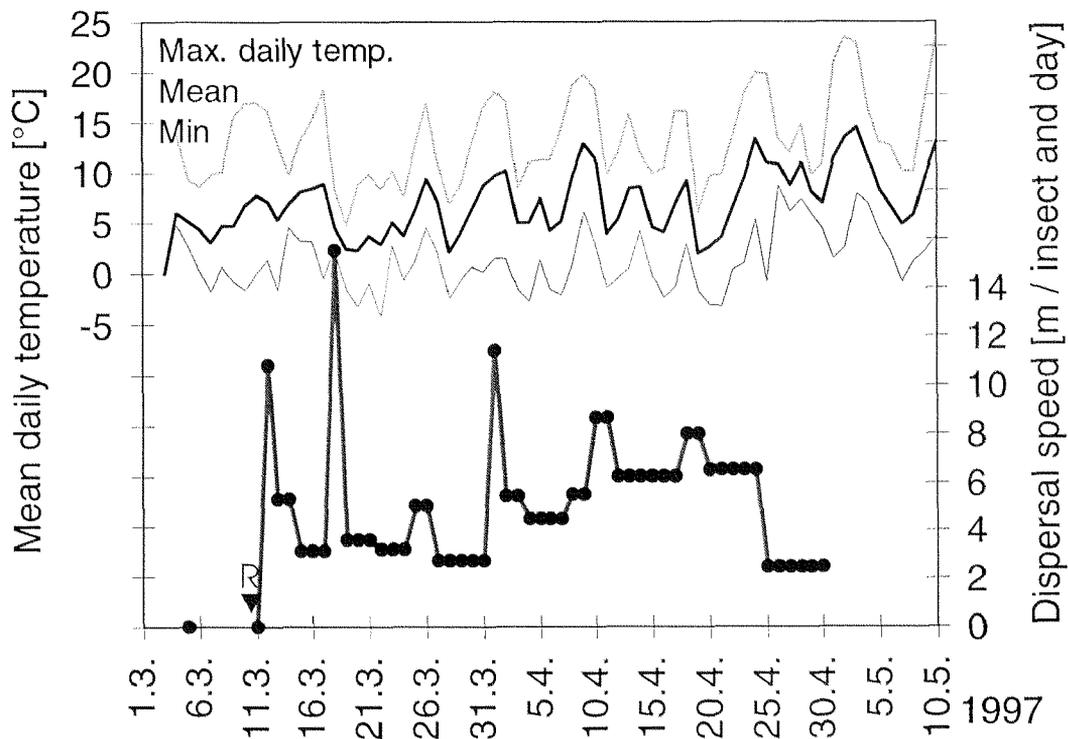


Fig.2. Mean speed of spring dispersal of marked apple blossom weevils, released on 11 March 1997 (R), and ambient temperatures ($n=368$ recaptures, orchard A)

The dispersal speed of the weevil was related to changes in climatic conditions (Figs.1 and 2). Series of single factor regression analysis (Tab.3, Fig.A.5.2 to A.5.6) showed significant influences of the maximum daily temperature ($y=1.7+0.3x$), the minimum daily temperature ($y=5.2+0.3x$), the air humidity, the mean temperature between 6:00 p.m. and 10:00 p.m. ($y=3.5+0.27x$) and the light intensity on dispersal speed. This order was confirmed by the multiple regression of the Generalised Linear Model, showing also a significant influence of all these factors (ANOVA; DF=3,18; $F= 3.7$; $P<0.05$, Tab.A.5.2). The mean daily temperature and the maximum or minimum temperature between 6.00 p.m. and 10.00 p.m. had the same influence and described the same relation as the maximum daily temperature did, which is shown by the tolerance value of this model. Relative air humidity influenced the dispersal speed negatively, with a decrease in dispersal speed to <5 m per day when air humidity was $>85\%$ ($y=10.1-0.06x$, Tab.3). Despite this influence no effect of daily rainfall could be detected. This was also the case for wind speed (Tab.3). The wind direction had no influence on the dispersal direction of the weevils either ($R^2= 0.2$ in 1996 and $R^2= 0.32$ in 1997, $P>0.05$, $n=29$).

Tab.3. Series of single factor regression analysis for the influence of climatic conditions on the dispersal speed of the apple blossom weevil in spring 1996 and 1997, and in pooled data of both years, ($n= 22$ in 1996, 37 in 1997, $R^2 =$ squared Pearson correlation coefficient (-1 to 1), in orchard A).

Climatic factor	Regression & P (ANOVA)					
	1996		1997		1996 & 1997	
	R^2		R^2		R^2	
Mean temp. per d	0.56	*	0.32	*	0.50	**
Max. temp. per d	0.56	*	0.41	*	0.51	**
Min. temp. per d	0.36		0.22		0.34	*
Mean temp. 6-10 p.m.	0.54	*	0.20		0.42	**
Max. temp. 6-10 p.m.	0.56	*	0.30		0.50	**
Min. temp. 6-10 p.m.	0.51	*	0.10		0.34	*
Air humidity	0.47	*	0.41	*	0.30	*
Light intensity	0.51	*	0.5	*	0.43	**
Mean wind speed	0.90		0.09		0.04	
Rainfall	0.17		0.29		0.12	

* P (ANOVA) <0.05, ** P <0.005

Tab.4. Series of single factor regression analysis for the influence of environmental factors on the crepuscular behaviour of the apple blossom weevil in spring 1998 (evening = two hours after sunset, $n=50$, $R^2 =$ squared Pearson correlation coefficient (-1 to 1), in orchard A).

Environmental factor	Regression & P (ANOVA)									
	Crawling		Feeding		Mating		Resting		Activity	
	R^2		R^2	R^2		R^2		R^2		R^2
Evening temperature	0.6	*	0.5		0.6	*	0.8	*	0.6	*
Mean temp. per d	0.6	*	0.5	*	0.8	*	0.8	*	0.6	*
Rel. evening humidity	0.9		0.7		0.9		0.9		0.8	
Mean rel. air humidity per d	0.7		0.8	*	0.7		0.6		0.8	*
Rainfall per d	0.6	*	0.3		0.2		0.3		0.5	*
Evening rainfall	0.2		0.1		0.5	*	0.4	*	0.2	*
Bud stage	0.2		0.05		0.6	*	0.5	*	0.2	*
Mean light intensity per d	0.4	*	0.2		0.5	*	0.5	*	0.4	*
Evening light intensity	0.3		0.3		0.3		0.4		0.4	

* P (ANOVA) <0.05

Spring behaviour on apple trees. The profiles of crepuscular behaviours of the weevil in relation to temperature are illustrated in Figs.3 & 4 (see also Fig.A.5.9. to A.5.11). The total activity of weevils, *i.e.* crawling, feeding, mating and oviposition, increased significantly with rising evening temperatures ($y=3.7x+11$, Tab.4) and rising mean daily temperatures ($y=4.3x+11$, Fig.3). The percentage of resting and hiding weevils decreased significantly as evening or mean daily temperatures increased (Fig.5). At evening temperatures above 12°C, most weevils were active (85%). At evening temperatures between 0°C and 12°C, 25 to 30% of the weevils were still active. In particular crawling on apple twigs was possible at all recorded evening and mean daily temperatures, *i.e.* between -1 and 18°C. According to the linear regression ($y=1.4x+13$), the minimal daily temperature for crawling was around minus 9°C. Observations showed, though, that the weevils already stopped moving at temperatures below 1.5°C when the relative air humidity rose above 95%. The highest increase in activity was found at a mean daily temperature of 8 to 11 °C (Fig.3). Flying was observed only two times when mean temperature was over 14°C in the evening and over 12°C during the day (Fig.A.5.7).

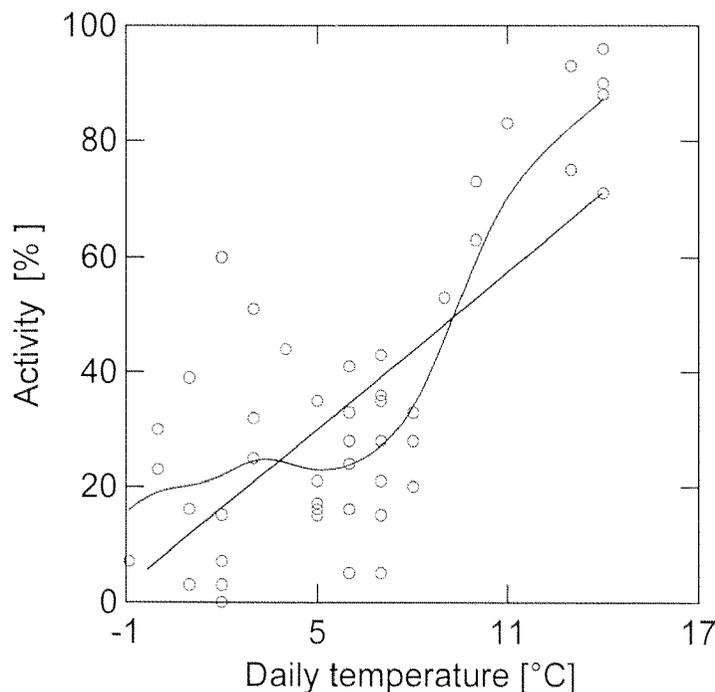


Fig. 3. Regression of activity level of the apple blossom weevils in the field cages on mean daily temperature (regression DWLS-model with 0.5 tension and linear regression $y=4.3x+11$)

Feeding behaviour was not significantly influenced by evening temperatures, but by mean daily temperatures (Tab.4). The threshold daily temperature for starting massive feeding was 9°C, but occasionally feeding by females was observed even at daily temperatures below 0°C.

Most mating occurred when evening or mean daily temperatures reached 12°C, though mating behaviour could still be observed even under cold conditions, *i.e.* an evening temperature >5°C and a mean daily temperature around 0°C. Oviposition was observed when evening temperatures and mean daily temperatures were above and around 10°C, respectively.

Mean light intensity during the day and 4 hours around sunset had no significant influence on the weevils' behaviour, except for full sunshine during the day, which could lead to more intensive crawling behaviour and a higher total evening activity.

With a higher relative air humidity the total crepuscular activity of the weevil decreased (Fig.A.5.12 to A.5.15 & A.5.17). The relationship between total activity and evening relative humidity was not significant, whereas the relationship between total activity and mean daily relative humidity was significant (Tab.4). Daily relative humidity below 40% and over 80% was not suitable for crawling and feeding; no mating and oviposition occurred in this range of humidity ($P < 0.05$, Mann-Whitney-U-test). Feeding was not significantly correlated with air humidity in the evening, but with the mean daily air humidity (Tab.4).

Daily rainfall significantly suppressed crawling ($y = -1.1x + 24$) and total activity ($y = -2.5x + 43$). Differences in total activities between the period without rain and the period with more than 10 mm rain per day were significant (Mann-Whitney-U-test, $P < 0.05$, Fig.A.5.16).

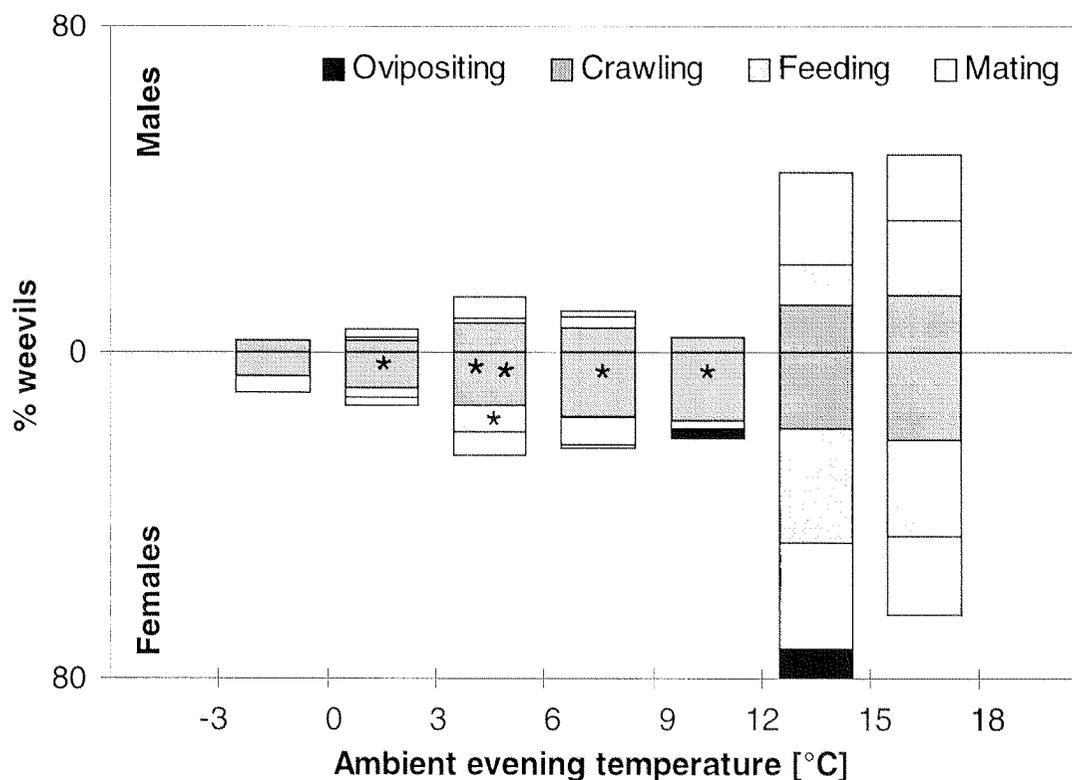


Fig. 4. Behavioural pattern of overwintered male and female apple blossom weevils in relation to ambient temperature in the field 2 hours after sunset in spring ($n=25$, Mann-Whitney-signed-rank-test between males and females, $*P<0.05$, $**P<0.005$)

Regarding total activity females were more active than males (t-test, $P<0.005$). Below 15°C , females were more than twice as active in crawling as males during the first 4 weeks after termination of hibernation (t-test, $P<0.05$). Females started to feed about 2 weeks earlier than males (Mann-Whitney-U-test, $P<0.05$). Females fed for more than 5 weeks before they started to oviposit. Differences in mating activity were not significant (t-test, $P=0.15$).

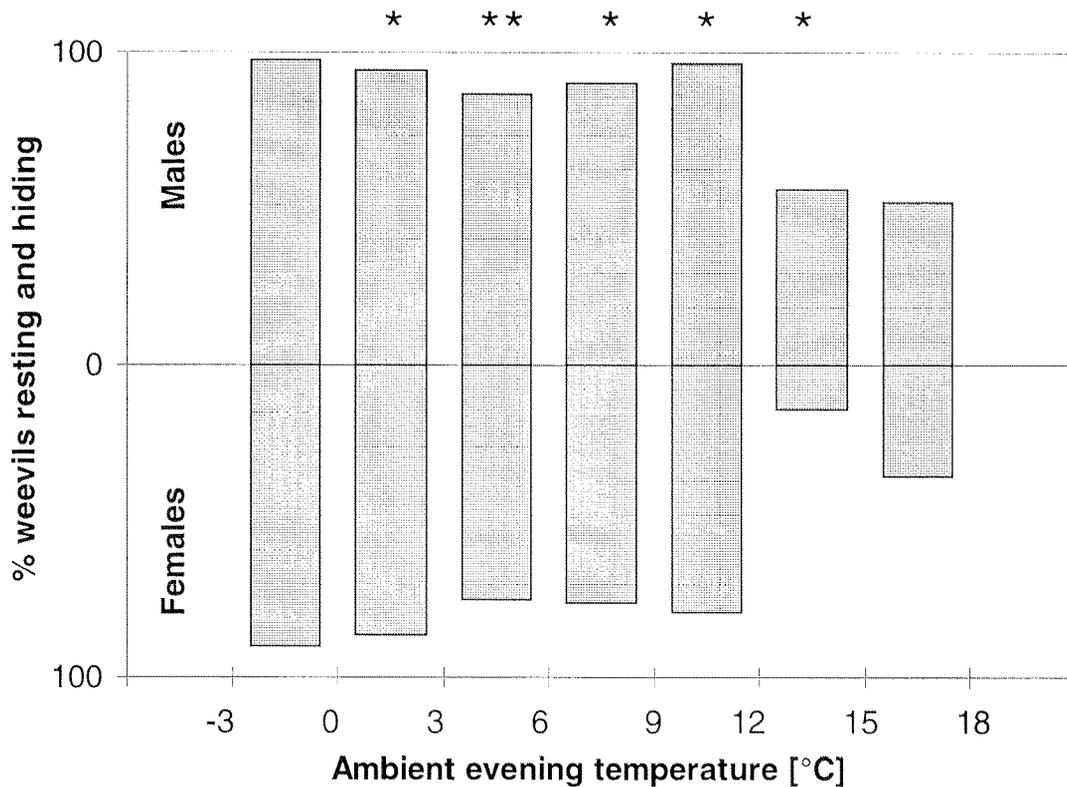


Fig.5. Resting and hiding behaviour of overwintered male and female apple blossom weevils in relation to ambient temperature in the field 2 hours after sunset in spring ($n=25$, Mann-Whitney-signed-rank-test between males and females, * $P<0.05$, ** $P<0.005$)

5.5 Discussion

Temperature can be considered to be the key climatic factor influencing the spring colonisation of apple orchards by overwintered apple blossom weevils. It determined the timing and speed of dispersal and the behavioural pattern of male and female weevils on apple trees. Analysis of field capture data reveals that early or late occurrence of spring dispersal and the resulting orchard colonisation by overwintered weevils are strongly related to changes in temperature, regardless of habitat characteristics. In northern Switzerland, the dispersal of weevil populations into orchards usually starts at a threshold daily temperature of 7 to 9°C (see also Kaiser 1943; Dicker 1946). This occurs usually in the second week of March in this region. However, earlier dispersal occurred in some years starting at 6°C, which is supported by the regression analysis. In Romania and Russia (Isac 1970; Korchagin 1978) temperatures of 6.5°C or 6°C were taken as a threshold temperature for the emergence of the apple blossom weevil from hibernation sites. In northern Switzerland, the full start of mass colonisation was usually at temperatures from 8 to 11°C. Our field data suggest that 161 ± 27 DD_{1 January} (>0°C) and 10 ± 1 DD_{1 March} (>6°C)

can most accurately be used to predict the start of dispersal, whereas 210 ± 26 DD₁ January ($>0^\circ\text{C}$) and 166 ± 19 DD₁ February ($>0^\circ\text{C}$) characterise the full start of mass colonisation best. Recently the degree-day model was found to be a suitable tool for monitoring adults of two other overwintered curculionid species as well, namely the boll weevil, *Anthonomus grandis* (Parajulee *et al.* 1996) and the strawberry bud weevil, *A. signatus* (Bostanian *et al.* 1999).

Analysis of release-recapture experimental data showed that variation in the speed of spring dispersal in the apple blossom weevil is significantly correlated with changes in temperature. A similar response to varied temperatures was reported for the dispersal of *A. grandis* (Parajulee 1996) and for the yucca weevil, *Scyphophorus yuccae* (Huxman *et al.* 1997). In the apple blossom weevil, the speed of spring dispersal could be predicted based on its linear relationships with maximum daily temperature, mean daily temperature or the temperature between 6:00 p.m. and 10:00 p.m.

Besides the climatic influences on the dispersal dynamics, behavioural activities of the weevils on apple trees are also clearly correlated with temperature. This validates previous findings from laboratory experiments (Duan *et al.* 1996). It is interesting that a few members of the weevil population in the field are adapted to colder temperatures than that from the laboratory results (Duan *et al.* 1996). Especially the ability to crawl, feed and even mate at temperatures around 0°C was astonishing and is supported by the measured low super cooling point of -11°C for postdiapausing weevils (Kostal and Simek 1996). However, for oviposition an evening temperature of around 10°C and a mean daily temperature of 10 to 12°C seem thresholds (see also Grison and Chevalier 1963; Tret'yakov 1984). Apple blossom weevils carried out all vital activities in the field when mean daily temperatures were between 8 and 11°C . Thus a mass colonisation of apple trees should only be possible at these temperatures, which is in agreement with the result of the dispersal studies in the field (see above). Flight activity is not frequent in the apple blossom weevil, as in many other curculionids. Occasional flying was observed at evening temperatures above 14°C and daily temperatures above 12°C , which is in accordance with the observations of Speyer (1939) and Trojtzky (1928). In the laboratory Isac (1970) and Duan *et al.* (1996) found 12°C to be a threshold temperature and 20°C the optimum temperature for taking off. In the field, Korchagin (1978) observed a few flying weevils even at evening temperatures of 10°C . The weather conditions allowing flight in early spring are a critical limitation for immigration into the orchard of weevils overwintering outside (Duan *et al.*, 1996).

Among other climatic factors, daily light intensity also affected the weevil's dispersal speed and crepuscular behaviour on apple trees significantly. Full sunshine caused the highest activities. This finding is surprising as this species is largely crepuscular and nocturnal, with its activity peak around sunset (Duan *et al.*, 1996). This effect is probably due to the strong association between temperature and sunlight, with a warming up of the main trunk in sunlight (F. Waeckers, personal communication). The dispersal speed is negatively correlated with air humidity, which is supported by the observations of weevils on apple trees in field cages. Although rainfall significantly influenced behavioural activities of the weevil, it exerted no detectable effect on the daily dispersal speed, despite the fact that persistent rainfall suppresses movement (Isac 1970). Similarly, wind can influence insect dispersal (Johnson 1969), but a significant influence of wind was not shown in our case. This might be due to their low flight frequency, or to the fact that the apple blossom weevil do not fly at all in strong wind (Duan *et al.* 1998).

Resting, crawling, mating and feeding activities were apparently similar between males and females regarding their response to ambient climatic conditions. The earlier start and generally higher activity of females, *i.e.* in feeding and crawling, reflects their need for a maturation feeding to find a suitable oviposition site. For most female insects dietary proteins are essential for development. Feeding promotes egg maturation and stimulates endocrine activity (Gillot 1980). Female weevils need suitable food such as sprouting apple leaves or buds (Ctvrtecka and Zdàrek 1992). An influence of feeding on the fertility of males is rarely observed (Wigglesworth 1955). Ctvrtecka and Zdàrek (1992) assume that spermatogenesis of the apple blossom weevil is already completed before the males go into hibernation.

The apple blossom weevil is a univoltine, early-season herbivore of apple trees. Population growth relies on a synchronisation of spring emergence of the overwintered weevils and the bud development of the host trees since the female weevils need to feed on and oviposit in apple buds (Ctvrtecka and Zdàrek, 1992). The evolved dependence of the weevil's spring activity on environmental temperature facilitates such a synchronisation. To broaden the data basis along the geographic latitudes I suggest that the temperature thresholds and the cumulative degree-days presented here should be validated at further locations.

6. SELECTION OF HIBERNATION SITES BY *ANTHONOMUS POMORUM*: PREFERENCES AND ECOLOGICAL CONSEQUENCES *

6.1 Abstract

The *Anthonomus pomorum* (L.) has a long period of aestivo-hibernation in the adult stage lasting from summer to early spring of the following year. Potential hibernation sites within an apple orchard consist of high-stem, rough-bark trees or dwarf, smooth-bark trees. Field release-recapture experiments in two consecutive years showed that 64 and 47 % of the weevils remained in the vicinity of the release sites in an area of rough-bark trees and smooth-bark trees, respectively. The dispersing weevils moved over an average distance of 5.5 m in the smooth-bark tree area, as compared to 3.8 m in the rough-bark tree area. The prevalent direction of dispersal was along tree rows in both areas. Some weevils displayed, after release in mid-July, a directional dispersal to the adjacent forests. Others, released in the smooth-bark tree area, dispersed towards the area of rough-bark apple trees. Experiments simulating various hibernation sites demonstrated that the litter of dry leaves was the most preferred overwintering shelter, yielding a relatively high survival rate. Branches with rough bark ranked second, while branches with smooth bark, grass and pure soil were not favourable for overwintering. Flight proclivity in newly emerged weevils of summer generation was significantly higher in June/July than in August/September. This corresponds to the dispersal behaviour in the field. The timing of spring colonisation of apple trees was similar for weevils overwintering within the orchard and for those immigrating from outside. These results suggest that modern dwarf apple orchards offer unfavourable conditions for overwintering, but that the relatively small proportion of weevils successfully reaching the adjacent forests find optimal hibernation sites there.

* Based on the publication manuscript: Toepfer, St., Gu, H., Dorn, S. 2000. Selection of hibernation sites by *Anthonomus pomorum*: Preferences and ecological consequences. *Entomologia Experimentalis et Applicata* (in press).

6.2 Introduction

The apple blossom weevil, *Anthonomus pomorum* (L.), is a univoltine herbivore pest in European apple orchards. This pest has recently re-gained importance due to a reduction in the use of broad-spectrum insecticides. Adults of this species are characterised by a long period of quiescence (or aestivo-hibernation after Masaki, 1980), lasting from early summer to early spring (Kostal & Simek, 1996), and by a short period of spring activity in synchronisation with the development of apple flower buds. Thus, selection of hibernation sites is critical for surviving the prolonged unfavourable conditions and facilitating spring colonisation of orchards.

When daily temperatures reach 6 °C, the weevils leave their dormancy sites, colonise apple trees and feed on buds for sexual maturation (Ctvrtecka & Zdarek, 1992). After fertilisation, female weevils oviposit into blossom buds. This leads to sterile and capped flowers, and causes economic damage. The newly emerged adults feed on the apple leaves for about 6 weeks and then search for an aestivo-hibernation site (Miles, 1923).

In apple orchards with high-stem trees, weevils were described to spend the period of dormancy under the rough bark of the trunk and in the litter of fallen leaves below (Trojtzky, 1928). In modern dwarf apple orchards, no rough-bark trees and little ground litter are available. The pre-diapaused weevils must thus search for aestivo-hibernation sites outside the orchards, such as nearby forests (Brown *et al.*, 1993). The availability and accessibility of these habitats is generally regarded as a crucial factor for the abundance and dynamics of the pest population (Szentkiralyi & Kozar, 1991). With respect to the selection of hibernation sites, knowledge is lacking concerning the timing and the pattern of pre-diapause dispersal as well as on the orientation to the hibernation sites. The behavioural adaptations of pre-diapaused weevils to commercial orchard systems are still poorly understood. Yet these issues are of great significance for understanding the population dynamics of *A. pomorum* and for proper pest management.

The present study focuses on aestivo-hibernation site selection by pre-diapaused weevils and on the ecological consequences; that is, on the survival of the overwintering weevils and on the re-colonisation of orchards in the following spring. Specifically, it addresses the following issues: (1) Is the pattern of dispersal for aestivo-hibernation by pre-diapaused *A. pomorum* in high-stem apple orchards different from that in dwarf apple orchards? (2) Does the selection of hibernation sites influence spring colonisation of orchards? (3) Do changes in flight proclivity correspond to

searching time for aestivo-hibernation sites? (4) Which hibernation substrate facilitates the survival of overwintering *A. pomorum*?

6.3 Materials and methods

Field studies on dispersal for aestivation and/or hibernation. Release-recapture experiments were carried out in an apple orchard whose tree rows ran perpendicular to an adjacent mixed forest (*Fagus silvatica*, *Picea abies*, *Fraxinus excelsior*, etc.). The orchard was 0.9 ha in size and situated at an elevation of 440 m in Niederwil AG (47 °N, 8 °E) in northern Switzerland (Fig.A.2). The orchard consisted of two parts: an area of dwarf trees with smooth bark and one of high-stem trees (4m in height) with rough bark. This orchard included eleven varieties of *Malus domestica*: Alkmene, Retina, Idared, Florina, Liberty, Priam, Jonathan, Vista Bella, Spartan, Summerred and Roter Marlet. It was bordered to the north by the mixed forest with ca. 20m tall trees, to the south and west by apple trees and to the east by fallow land (Fig.1a,b). Organic pest and disease control treatments were only carried out at the end of the trial period, and the subsequent effect on the behaviour of *A. pomorum* was thus not observed.

Several thousands of capped brown blossoms bearing *A. pomorum* pupae were collected in the spring and summer. They were kept in plastic field boxes for emergence. Adults were fed fresh apple leaves. Before releasing the weevils were marked with enamel lacquer. An individual marking with colour codes at five positions on the elytra and pronotum, enabled us to follow the dispersal of recaptured weevils from the location and date of their release.

Marked weevils were released at two different points within the orchard in autumn 1996 and in summer 1997. One point was in the area of modern dwarf trees with smooth bark and the other in the area of high-stem trees with rough bark, (□ in Fig.1a,b). One thousand weevils were released at each point on September 1, 1996, while 900 and 1000 weevils were released, respectively, on July 17, 1997. The early release in the second year was based on recapture experience from the first year. Two plastic release boxes with pieces of corrugated cardboard were attached to apple trees at a height of 1m at each point (Fig.1). The weevils were maintained in boxes for acclimatisation for at least two days prior to release under warm, dry weather conditions.

Five days after release, weevils were recaptured weekly until November. Recapture was resumed in the spring seasons (*i.e.*, from March 4 to April 1997 and from mid-February to April 1998, see Tab.A.4 & A.5). The method of limb-jarring (Lafleur *et al.*, 1987) was used to capture weevils from trees in the orchard and in the

mixed forest. Each small tree or the branches of big trees were hit three times with a wooden stick and the weevils that fall off were collected in a white sheet (2 x 20 m) placed underneath. This was usually done in the afternoon on dry, sunny days. The captured weevils were marked and released again at the same spot. In addition, 120 shelter traps, consisting of 5 cm long multiple layers of corrugated cardboard, were attached to the trunk of every third tree at a height of 1.5 m in both the orchard and the forest. In mid-November these traps were collected and the weevils recorded as to their location and the distance from the release point. A climate station (CR 10, Campbell Scientific LTD, UK) was installed within the orchard to monitor various weather parameters.

In the analysis data obtained from the two orchard areas were treated separately. For each recaptured weevil, the distance between the recapture and the corresponding release point and the dispersal direction were recorded along with the recapture and release dates. The dispersal direction of each weevil from the corresponding release point was used to calculate the co-ordinates of the vector of displacement $\left\{ \begin{bmatrix} x \\ y \end{bmatrix} \right\}$, ($x_i = \cos \phi_i$; $y_i = \sin \phi_i$). These co-ordinates for different recaptured weevils were averaged in intervals of 15° $\left\{ \begin{bmatrix} X \\ Y \end{bmatrix} \right\}$, of an interval, ($X = 1/n^*(\cos \phi_1 + \dots + \cos \phi_n$; $Y = 1/n^*(\sin \phi_1 + \dots + \sin \phi_n)$). The resultant vectors of dispersal (R), *i.e.* the product of mean vector lengths ($r = \sqrt{X^2 + Y^2}$) at the chosen intervals of 15° and the number of weevils (n) moving in this direction, were calculated and are illustrated in Fig.2.,3.& 4. Mean vector lengths close to 1 indicates the highest level of concentration. To test significance of mean vector's length (r), a Rayleigh-Test was used (Batschelet, 1981) (see Tab.1.). This statistic describes whether the population from which the sample was drawn differs significantly from randomness or whether there is statistical evidence of one-sidedness or directness. Because of the two-directional dispersal pattern, the two average angles of the bimodal dispersal axis, ϕ_1 and ϕ_2 , were calculated. Finally, the mean average angle of dispersal of the dispersing population (ϕ_{all}) was calculated with the main average vector $\{\phi_{all} = \arctan (Y_{all}/X_{all})$ if $X_{all} > 0$ or $= 180^\circ + \arctan (Y_{all}/X_{all})$ if $X_{all} < 0\}$. Since the calculated main dispersal patterns were consistent between recaptures in the autumn and in the spring of each year, the data from the two seasons were pooled in further analyses. The confidence ellipse (Hotelling's ellipse) was calculated as a mathematical description of population centres with a probability of $Q = 95\%$ (Batschelet, 1981). The Hotelling's one sample test was applied to determine differences between the possible centre of population

and the corresponding release point. The Watson-Williams test was performed to determine differences between mean angles of dispersal in different years (Zar, 1984).

To analyse the timing of orchard colonisation by the weevils in spring, data from captures of the native population that immigrated from the outside were also included.

Laboratory studies on flight proclivity. To gain insight into the timing of the search for aestivo-hibernation sites by pre-diapaused weevils, their flight proclivity was tested monthly from June to September. The tendency of newly emerged *A. pomorum* to take off was evaluated as a measure of flight proclivity according to Duan *et al.* (1996). Take-offs were observed in the afternoons on flight stands in a climatic chamber with a light intensity of 4,000 lux and 23°C. Each flight stand consisted of a small cross-shaped piece of acetate glued to the top of an upright glass stirring rod (ϕ 3 mm, 150 mm high). These stands were set up in a cup that was sprayed on inside with Teflon and filled with water to prevent the weevil from walking away (Duan *et al.*, 1998). The weevils were placed in the climatic chamber at least 12 h before the trials. For the bioassay, a weevil of known sex was gently introduced onto a flight stand. The number of weevils taking off and the time from release to take-off were recorded. The trial ended when the weevil flew off the stand or when 30 min had elapsed (Duan *et al.*, 1998). 44 male and 44 female weevils were tested in each month.

Furthermore, nutritional effects on flight proclivity of *A. pomorum* were evaluated. Weevils were either fed for 10 or 20 days with apple leaves or starved over 10 or 20 days. The effects of sex and feeding status on flight proclivity was analysed using ANOVA in a generalised linear model.

Simulation experiments on hibernation substrate selection. The selection of hibernation substrates by *A. pomorum* was examined in multiple choice tests. Various substrates were collected from apple orchards and adjacent forests. They included apple tree branches with rough bark and with smooth bark, leaf litter, grass and pure soil. Both the habitat in a high-stem apple orchard and that in a dwarf apple orchard were simulated with these substrates. To simulate the habitat in a modern dwarf apple tree orchard, all these substrates except rough bark were used. Each of the different substrates was randomised in a 0.15m thick block within a plastic box (0.3 m x 0.6 m x 0.5 m). Six boxes (replicates) were set up, each with 30 weevils. The number of weevils in a box was maintained so that possible intraspecific interactions could be minimised (Duan *et al.*, 1996). The weevils were given two weeks to select substrates freely under standardised conditions (70%r.h., L8:D16, 15°C). Subsequently, the

climatic conditions prevailing in the field during September and October (temperature ranging from 0 to 10°C) were simulated to allow the weevils to enter diapause. At the end of November, the number of weevils in each substrate was counted after chilling for 14 days at a temperature of 2.5°C. The effect of substrate on the distribution of weevils within boxes was analysed with ANOVA. Preferences for different substrates were compared using Fisher's LSD test.

Dual choice tests were undertaken to examine the relative preference of dry and moist leaf litter as a substrate for overwintering. The trial was also carried out in plastic boxes containing approximately 1,000 gr. of litter. The wet leaf litter was maintained by spraying with water twice a week (ca. 8 ml) and the dry litter by spraying every second week. A Wilcoxon-signed-rank test was performed to analyse differences in the number of weevils overwintering in wet and dry leaf litters.

To test the effect of substrate selection on winter survival, further simulation experiments were carried out. Six weevils were placed into small plastic tubes (ϕ 0.05m) within perforated boxes ($n=7$). These boxes were filled with smooth bark, rough bark, dry leaf litter, wet leaf litter, leaves over soil, grass over soil, or pure soil. Seven replicates were set up for each substrate. Each box was placed in the corresponding substrate environment of an orchard in October. The survival of weevils was checked to mid-February. A Kruskal-Wallis multiple comparison was applied to test differences in overwintering mortality between hibernation substrates.

6.4 Results

Recapture profiles. About 1400 marked weevils (*i.e.*, 70%) left the release boxes in autumn of the first year (1996) and 1650 (*i.e.*, 87%) in late summer of the second year (1997). They moved to the trees nearby or further into the orchard to seek for aestivo-hibernation sites. The rest of the weevils remained in the boxes till they died.

The total recapture rate was $28.5 \pm 17\%$ (mean \pm s.d.), *i.e.* $16.5 \pm 4\%$ from limb-jarring collections and $12 \pm 10\%$ from shelter trap collections (Tab.A.4.2). 530 marked individuals were recaptured once and 17 individuals twice from September to November of the first year and during the early period of spring dispersal in the second year. 110 marked individuals were recaptured once and 2 individuals twice from mid-July to October in the second year and during the early period of spring dispersal in the third year. The release of weevils in the summer of the second year rendered a lower rate of recapture. Many weevils probably dispersed over a longer distance or even left the orchard. The recapture of weevils with limb-jarring is negatively effected by cold, wet weather (Chapt. 4), which often occurred in autumn. The recapture with cardboard

shelter traps was only successful in the first experiment, with a release in late autumn, when weevils are more inclined to search for hibernation sites. Both methods did not work well in the mixed forest, and consequently the data was limited for this habitat. In addition to the marked captures, 748 weevils from the native population were caught in the first recapture period and 1071 during the second period.

Dispersal for aestivation and/or hibernation. In both years of the investigation, most weevils remained in the vicinity of the release points (*i.e.*, within 4 m): $47 \pm 9\%$ of the weevils in the area with the smooth-bark dwarf apple trees stayed near the release point in the two studied autumns, whereas $64 \pm 16\%$ in the area with the high-stem rough-bark trees. These percentages were not significantly different ($P > 0.05$, Mann-Whitney-U test, Tab.1).

Tab.1. Proportion and distances of dispersing *Anthonomus pomorum* more than 4 m from 2 release points in apple orchard B in autumn 1996 and summer and autumn 1997. 377 recaptures (82 in 1997) from release in area with smooth bark apple trees and 167 (27) from release in area with rough bark trees. M.-Whitney-U test at * $P < 0.05$, ** $P < 0.005$.

Areas of apple orchard B	Dispersing weevils [%]			Dispersal distances [m/weevil]		
	1996	1997	1996&97	1996	1997	1996&97
Smooth bark trees	47	60	53.5 ± 9	3.2 ± 0.3	7.8 ± 0.9	5.5 ± 3.2
Rough bark trees	25	48	36.6 ± 16	1.8 ± 0.3	5.8 ± 0.5	3.8 ± 2.8
$P < 0.05$			n.s.	*	*	**

Pre-diapausing dispersal occurred primarily along apple tree rows in each of the two areas. But dispersing weevils in the area with smooth-bark trees moved over a longer distances, than those in the area with rough-bark trees, *i.e.* 5.5 m in the smooth-bark tree area and 3.8 m in the rough-bark tree area. A few weevils travelled up to 54 m. Figure 1 shows the dispersal pattern of the populations released in each orchard area in each year (Fig.1a. September 1996, Fig.1b. July 1997). The dispersal in the orchard area with smooth-bark trees is drawn in solid lines, and the dispersal in the area with older rough-bark trees in dashed lines. The Hotelling's confidence ellipses indicate the calculated centre of the population with a statistical probability of 95%. The ellipses are found to situate around the release points in both areas of each year. Due to the relatively limited dispersal range in either situation only a small part of the experimental orchard was covered by the released weevils, *i.e.* 0.26-0.28 ha in the smooth-bark area and 0.1-0.3 ha in the rough-bark tree area.

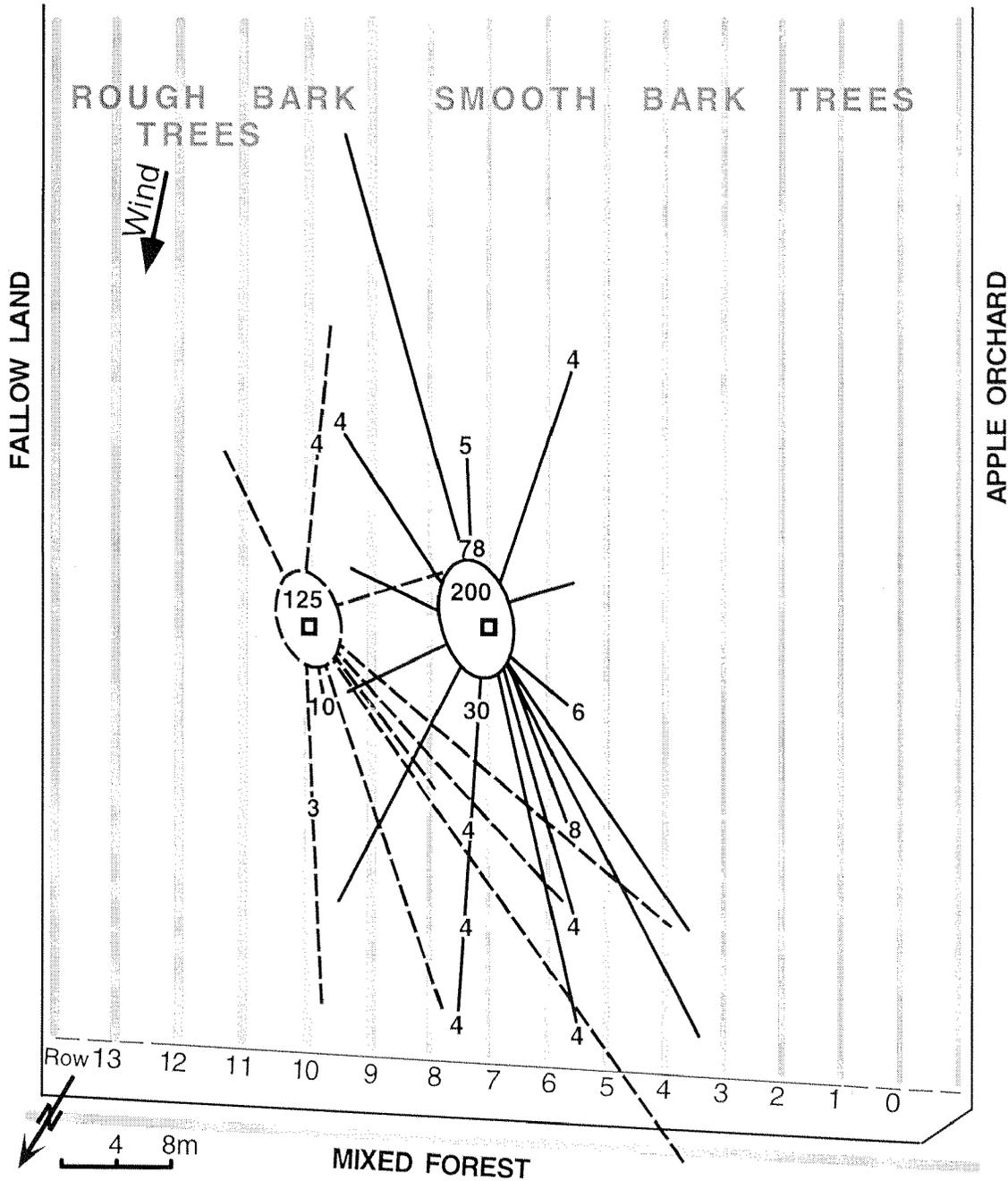


Fig. 1a. Recaptures of marked *Anthonomus pomorum* released in September 1996 at two sites (□): in the area of smooth bark apple trees (solid lines) and in the area of older rough bark trees (dashed lines). Lines indicate vectors and numbers of dispersing weevils found in sectors within the orchard, at its edge, and in the adjacent forest. Hotelling's confidence ellipses for unknown population centres are presented with a coefficient $Q=95\%$.

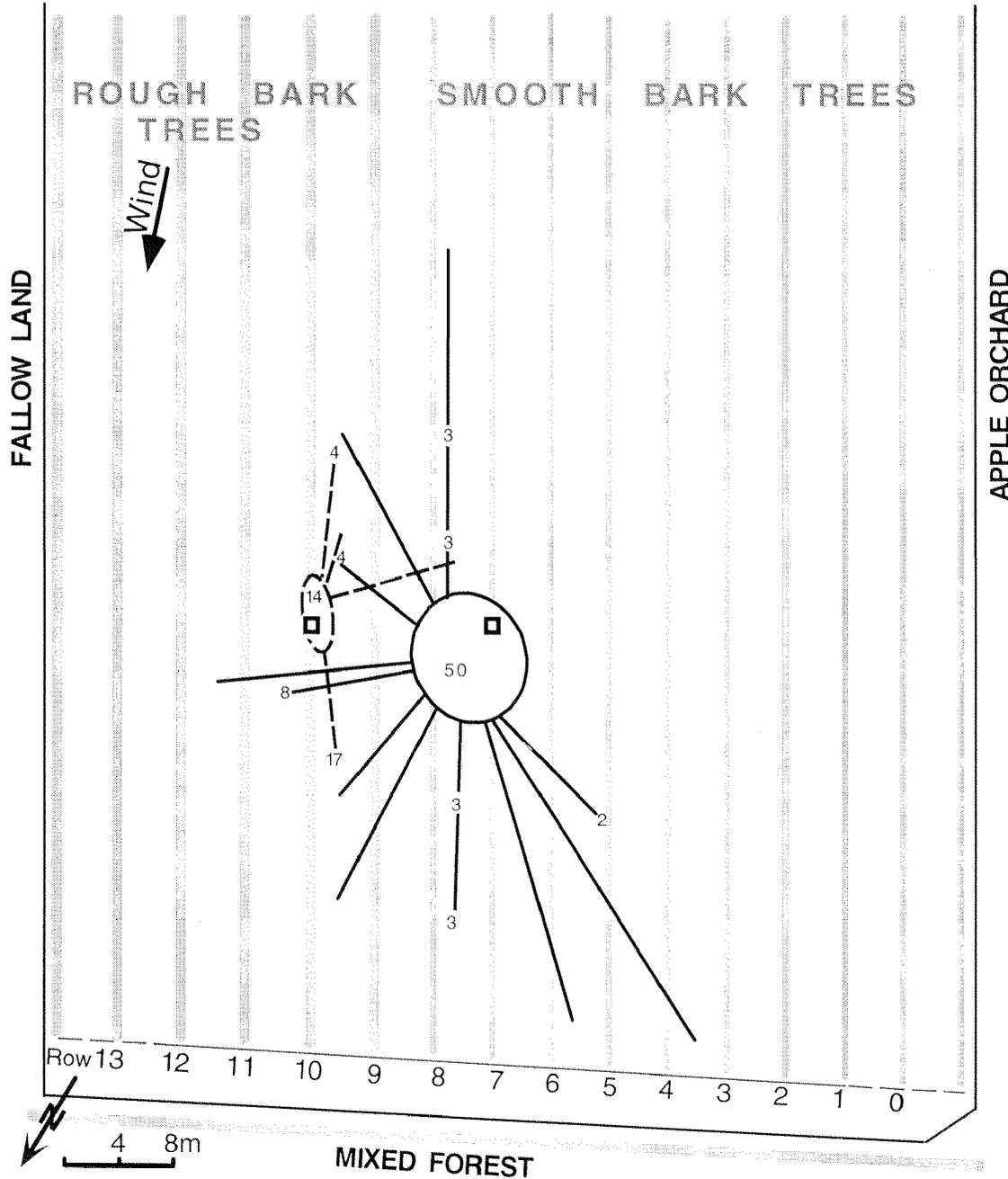


Fig.1b. Recaptures of marked *Anthonomus pomorum* released in Mid July 1997 at two sites (□): in the area of smooth bark apple trees (solid lines) and in the area of older rough bark trees (dashed lines). Lines indicate vectors and numbers of dispersing weevils found in sectors within the orchard, and its edge, and in the adjacent forest. Hotelling's confidence ellipses for unknown population centres are presented with a coefficient $Q=95\%$.

The direction of dispersal of the weevils were represented by resultant vectors (Fig.A.6.1,2,3,4). These vectors correspond to the above observation that the dispersing weevils moved primarily along tree rows in both orchard areas. Mean angles of the mean axis show the typical bimodal dispersal pattern in both directions

along tree rows in all cases. In the area of smooth-bark trees mean angles of the mean axis (φ_1, φ_2) were $323 \pm 21^\circ / 143 \pm 21^\circ$ in the first year and $325 \pm 28^\circ / 145 \pm 28^\circ$ in the second year (Fig.A.6.1 & A.6.3). In the area of rough-bark trees mean angles were $312 \pm 25^\circ / 132 \pm 25^\circ$ and $322 \pm 25^\circ / 142 \pm 25^\circ$ (Fig.A.6.2 & A.6.4). No statistical differences between the bimodal angles of both orchard areas were found in either year ($P > 0.05$, Watson-Williams test). The r-value in the first year indicates a high level of concentration of dispersing weevils in the smooth-bark tree area with $r_{\text{all}} = 0.74$ of the average main angle $\varphi_{\text{all}} = 286 \pm 41^\circ$. A medium level of concentration was shown in the rough-bark tree area with $r_{\text{all}} = 0.61$ ($286 \pm 41^\circ$). The r-value in the second year indicates a lower concentration of dispersing weevils than in the first year and a lower degree of movement along tree rows, with $r_{\text{all}} = 0.62$ in the smooth-bark tree area ($284 \pm 50^\circ$) and $r_{\text{all}} = 0.54$ in the rough-bark tree area ($290 \pm 55^\circ$). In the first year only small deviations could be recognised; for example, a few *A. pomorum* in the area of smooth-bark trees were found to move towards the rough-bark trees. A small part of the population in the areas of rough-bark trees showed an opposite pattern with a movement west and north-west to the area of dwarf apple trees. Analyses of the first year's data did not show a significant orientation to any of the studied areas. Moreover, the ellipses of population centres in the area of rough-bark trees (dashed lines) and in the area of smooth-bark trees (solid lines) were comparable in the first year (Fig.1a). In the second year (autumn 1997 and spring 1998) the analyses of vectors and the Hotelling's confidence ellipses showed an additional direction of movement towards the mixed forest by a small proportion of weevils (*i.e.*, north and north-west). A preference was shown for the direction of the adjacent forest by the weevil populations in both types of orchard areas. Weevils in the smooth-bark tree area also showed an orientation towards the area of high-stem apple trees. Furthermore, the Hotelling's confidence ellipse in the area with smooth-bark trees was wider in the second year than in the first year. Finally, in the area with smooth-bark trees the population centre of the ellipse deviated significantly from the corresponding release site in the second year ($P < 0.05$, Hotelling's one sample test), with a very small confidence ellipse of the population.

On the other hand, spring colonisation by weevils overwintering within the orchard was not earlier than by weevils overwintering outside the orchard ($P > 0.05$, Two-sample t test). Also the timing of colonisation by weevils overwintering in the area of dwarf smooth-bark apple trees did not differ from that by the weevils overwintering in the area of old rough-bark trees ($P > 0.05$, Two-sample t test).

Flight proclivity of prediapause weevils. Newly emerged weevils showed a significantly higher tendency to take off in summer (June and July) than in autumn (August and September) ($P < 0.05$, Kruskal-Wallis multiple comparison, Fig.2). Furthermore, the time lapse until 60% of the tested weevils flew off was only one third as long in June or July as in August and September ($P < 0.05$, Kruskal-Wallis multiple comparison). In June and July, differences between males and females were not significant in tendency to take off. In September, however, males showed a significantly lower tendency to take off than females ($P < 0.005$, M.-Whitney U test, Fig.2). They also needed a significantly longer latent time before taking off ($P < 0.05$, M.-Whitney U test). The tendency of the newly emerged weevils to take off in June or July was generally influenced by their nutritional status (ANOVA GLM of a two way nested experimental design; $F=53.6$; $DF=1$; $P < 0.001$) as well as by the duration of feeding or starving (ANOVA GLM; $F=110$; $DF=2$; $P < 0.001$). Moreover, flight proclivity was reduced after starving for 20 days (Fig.3).

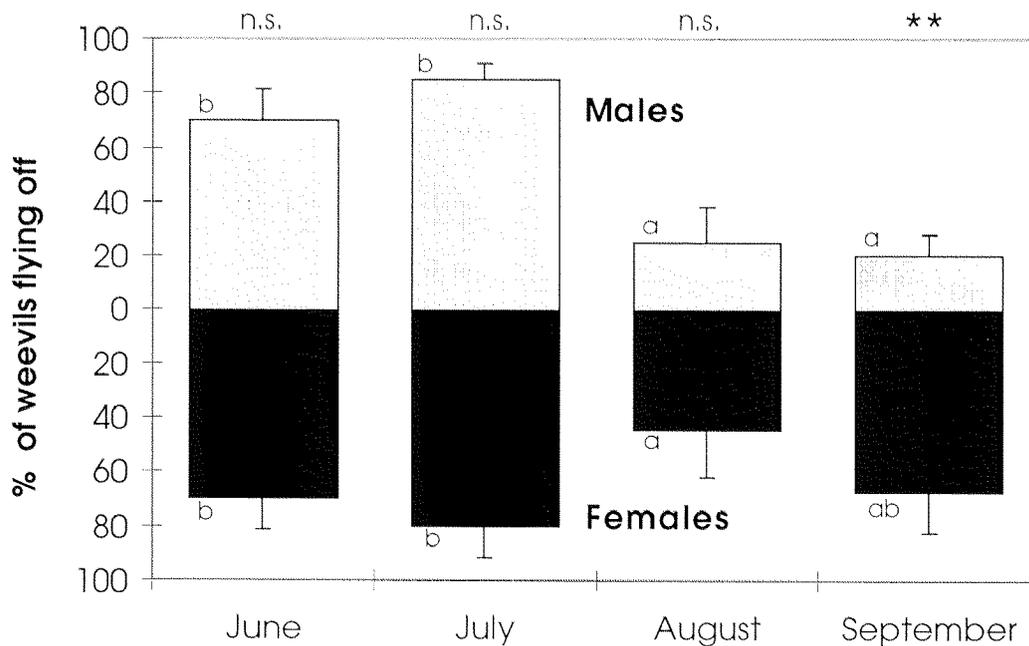


Fig.2. Seasonal flight proclivity of *Anthonomus pomorum* measured as the percentage of weevils taking off in afternoon between 3 and 5 p.m. Tests with $n=4 \times 11$ male and female weevils. Kruskal-Wallis multiple comparison between months (letters on bars) and Mann-Whitney-U test between males and females (letters on top) at $*P < 0.05$, $**P < 0.005$.

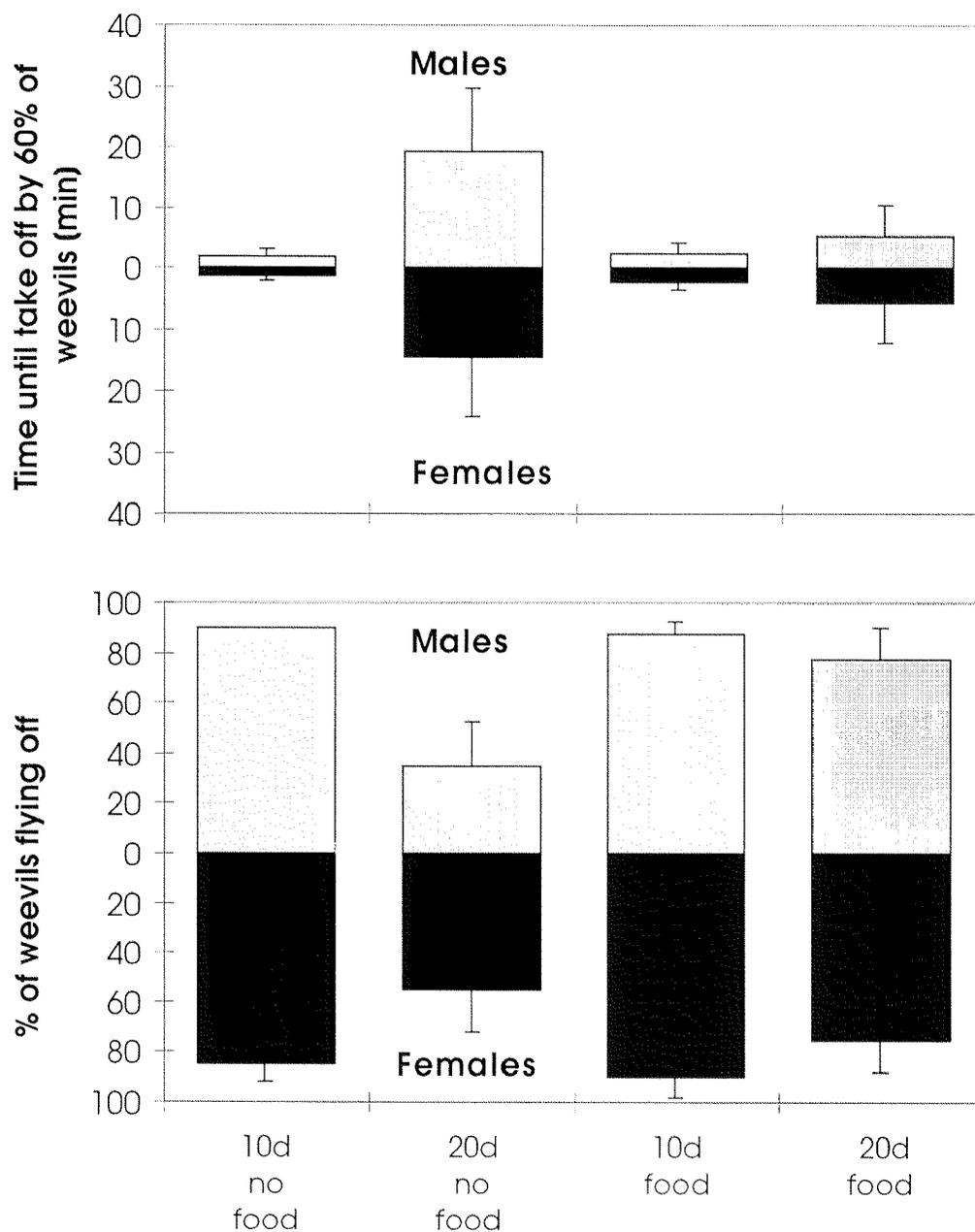


Fig.3. Effects of nutritional status on flight proclivity and on the latent time to take off in *Anthonomus pomorum* (n=4x11males and females, 3 to 5 p.m.). ANOVA GLM, $P < 0.001$ in both cases.

Simulation experiments on hibernation substrate selection. About 70-80% of the released weevils were recovered in the hibernation boxes. The influence of hibernation substrates on the distribution of weevils within these trial boxes was significant (ANOVA: $F=36.1$; $DF=4,15$; $P < 0.005$). *A. pomorum* preferred leaf litter as an overwintering shelter over all other substrates, *i.e.* rough and smooth bark, grass and pure soil ($P < 0.05$, Fisher's LSD test, Fig.4, Tab.A.6.1). Rough bark was used less often for hibernation than leaf litter but more often than other substrates ($P < 0.05$,

Fisher's LSD test). A very low number of *A. pomorum* overwintered in grass, pure soil and smooth bark of apple branches (Fig.4). Comparable results were obtained from a second multiple choice test on hibernation in grass, smooth bark, leaf litter or soil, which simulated the situation in modern dwarf apple tree orchards (ANOVA; $F=24.3$; $DF=3,20$; $P<0.005$, Tab.A.6.5, Tab.A.6.2). Again, the leaf litter was the most preferred hibernation substrate ($P<0.001$, Fisher's LSD test). The dual choice test between dry and wet leaf litters demonstrated that weevils preferred dry over wet leaf litter ($P<0.05$, Wilcoxon-Signed-Rank test, Fig.A.6.6).

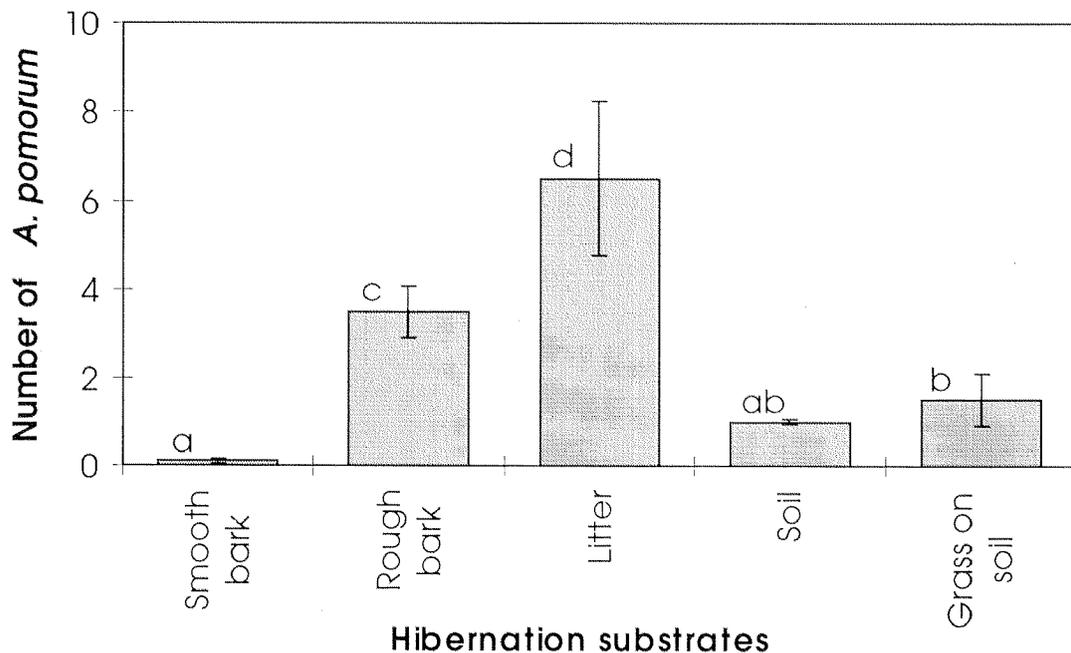


Fig.4. Choice of hibernation substrate by *Anthonomus pomorum*. Laboratory simulation of orchards with rough bark trees and of adjacent forest. Multiple choice tests for 30 weevils in each of 6 replicates. Multiple comparison at $P<0.05$, Fisher's LSD test.

Winter mortality of weevils overwintering in different substrates is shown in Fig.5. Substrates rendering a lower mortality were dry leaf litter and both kinds of bark. Significantly lower survival rates were found in relatively moist substrates, *i.e.* in soil, leaves on soil and wet leaf litter. The mortality of weevils in grass may be of limited reliability due to a large standard deviation resulting from two missing replicates. Under the simulated condition, a mean winter mortality for all hibernation substrates was found to be $73\pm 12\%$ (mean \pm s.d). In a different experiment (data not reported) over three winters the mortality of weevils overwintering in a mixture of natural substrates on the ground of observation cages was about 26%.

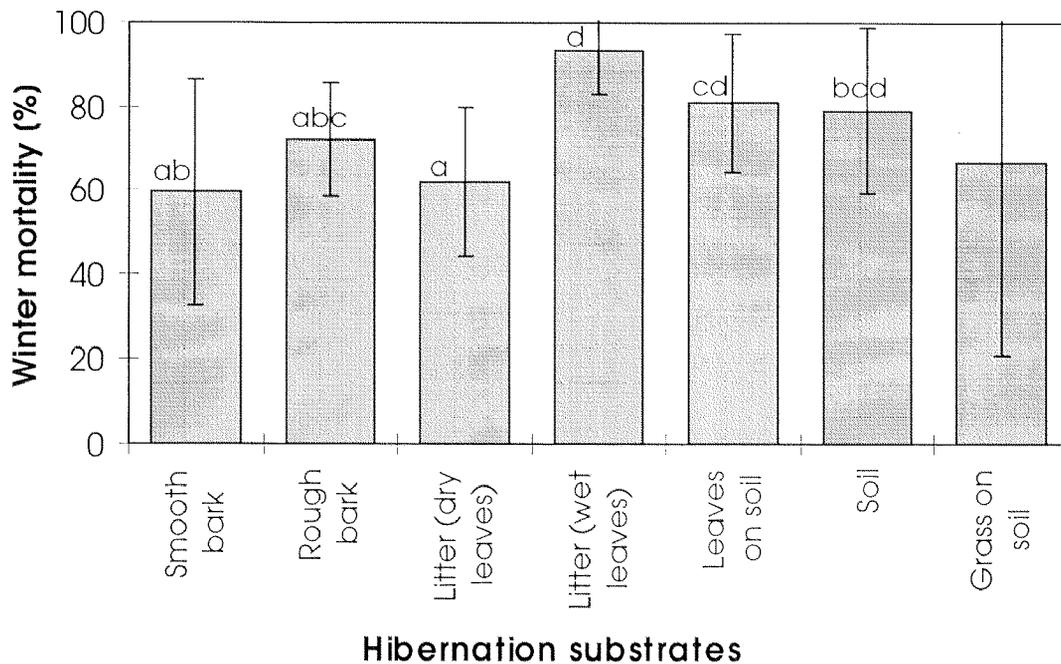


Fig.5. Mortality of overwintering *Anthonomus pomorum* in different substrates under field conditions in 1996/97 and 1997/98 (7 replicates with 6 weevils (grass n=5). Kruskal Wallis multiple comparison test at $P < 0.05$).

6.5 Discussion

A large proportion of the weevils released in both high-stem and dwarf apple orchard areas remained in the vicinity of the release points or displayed a bi-directional dispersal within a limited distance, mostly along the apple tree rows. In the two orchard areas, however, there were apparent differences in the pattern of dispersal of pre-diapaused *A. pomorum*, especially when released in July. Firstly, the weevils released in the area of dwarf, smooth-bark apple trees dispersed over longer distances, which resulted in a larger dispersal radius as compared with those released in the area of high-stem, rough-bark apple trees. Secondly, some weevils displayed after release in the area of smooth-bark trees a directional dispersal to the adjacent forests and towards the orchard area with rough-bark trees. The lower occurrence of this behaviour of orientation in weevils released in the high-stem apple orchard area implies that these weevils are able to find suitable aestivo-hibernation shelters under the rough bark of tree stems and/or leaf litter on the ground.

The dispersal of *A. pomorum* towards suitable hibernation sites is similar to the behaviour observed in other curculionid species, such as *Conotrachelus nenuphar* (Herbst) (Lafleur *et al.*, 1987) and *Anthonomus grandis* Boheman (Bottrell, 1972). The mechanism underlying this directional dispersal for selection of hibernation sites in

these curculionids, however, remains unclear. For example, olfactory cues from microhabitats may play a role in search of hibernation sites. This has been demonstrated for *C. nenuphar*, although the weevils do not show a consistent response to such cues (Lafleur *et al.*, 1987).

Generally, the weevils released in autumn (September) were less dispersive, as compared to those released in summer (July). Field observations of Masee (1925) also showed that the highest dispersal activity of *A. pomorum* occurs in July and that this activity decreases in autumn. Our laboratory tests showed that both male and female weevils display a greater flight proclivity in June and July than in August and September (see also Fig.A.6.7 & A.6.8). Since most *A. pomorum* weevils are believed to start diapause in late summer or early autumn (Speyer, 1939), the reduction in flight proclivity and dispersal capacity in autumn may be due to the initiation of diapause. Our field and laboratory results are consistent with the previously published opinion that the search for an aestivation shelter is connected with the search for a hibernation site and that this activity takes place primarily in summer (Miles, 1923; Rilishkene, 1985).

Despite a relatively good tolerance of diapaused weevils to low winter temperatures (Kostal & Simek, 1996), suitable shelters are indispensable for the weevils to avoid desiccation and/or freezing during the aestivo-hibernation period. As in *C. nenuphar* (Whitcomb, 1954) and *A. grandis* (Graham, 1978), the litter of dry leaves on the ground is the most important microhabitat for overwintering in *A. pomorum* (Korchagin, 1978, Tret'yakov, 1991). However, some weevils could also be found under the bark of different tree species, such as *Malus sp.*, *Pyrus sp.*, *Cerasus sp.* (Speyer, 1939), *Ulmus sp.* and *Quercus sp.* (Tret'yakov, 1984) and at the occultation place of apple trees (Wiesmann, 1928, B. Hirs & S. Dorn, unpub. data). Leaf litter is the substrate most continuously available on the ground in old, high-stem apple orchards (Miles, 1923). The ecological significance of this preferential selection is shown by the relatively low mortality of the weevils overwintering in the dry leaf litter. Generally, the higher preference for a particular hibernation substrate corresponds to a lower overwintering mortality of the weevils in the substrate. Furthermore, overwintering mortality is related to a high level of moisture in a given substrate. This is in contrast to the finding that desiccation is a cause of high mortality in *A. pomorum* during aestivation (Kostal & Simek, 1996). During hibernation, therefore, freezing rather than desiccation may be an important factor causing death. Indeed, *A. pomorum* cannot survive after being frozen, although it has a super-cooling point of as low as -20 °C during diapause (Kostal & Simek, 1996).

The overwintering mortality obtained from our simulation experiments is very high. This is probably due to the fact that the experiment was carried out under semi-natural conditions with no exposure to snow. Snow can reduce mortality significantly (Tret'yakov, 1984). Under field conditions in a mixture of natural substrates, a mortality of 26% in overwintering *A. pomorum* was observed, which is much lower than the average mortality in our simulation experiments. This field mortality is comparable to the estimate of 13.1% from four orchards in Russia between 1979 and 1982 (Tret'yakov, 1984). The figure is also similar to the winter mortality of 23-59% in *C. nenuphar* (Smith & Flessel, 1968). Nevertheless, this moderate mortality occurs only when the weevils find and overwinter in a suitable substrate, such as dry leaf litter.

Consequently, the hypothesis could be confirmed that an apple orchard with old, high-stem trees offer a better site for hibernation than a modern dwarf apple orchard, because of an abundance of leaf litter and rough bark. Although a large proportion of the population does overwinter within the dwarf apple orchard, this proportion is subject to high mortality due to a lack of suitable shelter. Thus, the weevil population may be under a selective pressure to emigrate to adjacent forest where litter and even rough bark is readily available (Korchagin, 1978; Tret'yakov, 1984; Brown *et al.*, 1993; Duan *et al.*, 1996). Many modern dwarf apple orchards in Switzerland and other central European countries lie close to mixed forests or woodlands. It could be confirmed that overwintering weevils in adjacent forests are a major source for the yearly colonisation of these orchards in spring (Chapt. 4.).

7. PHENOLOGICAL RELATIONSHIP BETWEEN APPLE BUD DEVELOPMENT AND SPRING ACTIVITY IN *ANTHONOMUS POMORUM* *

7.1. Abstract

Postdiapaused *Anthonomus pomorum* (L.) (Coleoptera: Curculionidae) colonises apple orchards in early spring for feeding and reproduction. To investigate the timing of dispersal in relation to bud growth stages we applied multiple-capture experiments in three orchards in northern Switzerland between 1995 and 1999. The start of spring dispersal by *A. pomorum* was not related to a single bud growth stage within orchards. This period covered bud stages ranging from the little silver greenish tip B(51) to the mouse ear stage C3(54). Immigrating weevils developed fully mature gonads within 24 ± 3 days after start of colonisation of orchards, usually when the mouse ear buds and tight cluster of green buds, C3(54) or D(56), appeared. Weevils which overwintered within orchards matured their gonads up to ten days earlier. On the other hand, the bud growth stage had a significant influence on behavioural activities of *A. pomorum* on apple trees. Females fed on all stages, starting already on the closed bud stage A(00), and most intensively on the little silver greenish tip stage B(51) and the pink bud stage E(57). Males started to feed on later bud growth stages, with a remarkable increase only on the pink bud stage E(57). Oviposition was observed during growth stages D(56) and E(57). When different bud growth stages were available, *A. pomorum* preferred the most advanced stages for feeding and oviposition. As for the variety *A. pomorum* did not show any consistent preference under laboratory conditions when given the choice between Golden Delicious, Jonagold, Idared, Gala, Maigold, and Gloster 69. The implication of these findings for pest management is discussed.

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7.2 Introduction

The apple blossom weevil, *Anthonomus pomorum* (L.) (Coleoptera: Curculionidae) has recently resumed pest status in biologically and IP-managed apple, *Malus domestica* Borkh., orchards in Switzerland (Wildbolz, 1992). This poses new challenges to the systems currently in use, as ecology and behaviour of this weevil are poorly understood (Blommers, 1994). In dwarf apple orchards, *A. pomorum* is forced to emigrate for hibernation sites in summer or autumn and need to re-colonise apple trees for feeding and oviposition in spring. Following fertilisation, females oviposit in the blossom buds in which larval feeding causes sterile and capped flowers. Spring dispersal and/or other behaviours may be influenced by the phenology of apple trees since the phenological synchronisation of weevils' activity and bud development is critical for the population success and is a major limitation of the host range and abundance of herbivores (Holliday, 1977). Indeed, many insects, such as beetles and aphids (Kearsley, 1989) and Lepidoptera (Stamp *et al.*, 1990), show sensitivity to the phenology of their woody hosts.

This study was conducted to clarify the relationship between the phenology of apple trees and the spring activity of *A. pomorum*. We postulated that a stage preference of *A. pomorum* will cause an increased population abundance in the area of certain apple varieties and consequently an increased risk for economic damage. Three approaches were adopted: 1) field multiple captures of weevils to observe the temporal pattern of colonising dispersal and female gonad development in relation to apple bud growth stages, 2) field-cage observations of various crepuscular behaviours, 3) climate-chamber experiments on feeding and/or oviposition preferences of *A. pomorum* for different bud growth stages and for different apple varieties.

7.3 Materials and methods

Insects. See also Chapt. 5.3. The weevils for observations in field cages and for laboratory experiments were collected as pupae in the summer of previous years in northern Switzerland. After emergence they were kept in plastic boxes and fed with fresh apple leaves until hibernation. Then they were overwintered under semi-natural conditions (Chapt. 5.3). In early spring, the post-diapaused weevils were distinguished by sexes and marked for identification. These weevils were acclimatised to the

conditions within climate chambers or observation field cages for at least two days before the beginning of experiments.

Phenology of spring colonisation. The timing of spring dispersal and the beginning of the colonisation process were investigated, by means of capturing weevils in three orchards, referred to as 1,2,3 in northern Switzerland (47 °N, 8 °E). Orchard 1 was investigated in 1996, 1997 and 1999, orchard 2 in 1997, 1998 and 1999 and orchard 3 in 1995. The dwarf apple tree orchard 1, 1 ha large, was located in Zürich at an elevation of 509 m (Chapt. 4.3). Rows consisted of 2.5 m high apple trees with five different varieties: Primerouge, Gravensteiner, RubINETTE, Arlet and Gala. Orchard 2, 0.9 ha large, was located in Niederwil AG at an elevation of 440 m. It consisted of two parts: one area of dwarf apple trees and other area of old high-stem apple trees. This orchard contained 11 varieties: Alkmene, Retina, Idared, Florina, Liberty, Priam, Jonathan, Vista Bella, Spartan, Summerred and Roter Marlet. Orchard 3, 1 ha large, was located in Baar ZG at an elevation of 460 m. The rows consisted of dwarf apple trees of different age and height with 14 different varieties: Golden Delicious, Jonathan, Idared, Elstar, Maigold, Cox Orange, Jonagold, Spartan, Glockenapfel, Roter Marlet, Alkmene, Gravensteiner, Boskoop and Gloster. The weevils were captured by limb-jarring (Lafleur & Hill, 1987; Chapt. 4.3). Each whole tree was struck three times with a wooden stick and the weevils were collected from white sheets laid out below the trees (2 x 20 m). The capture was carried out from 3 to 7 days before termination of hibernation, *i.e.* usually in February, until the end of the colonisation period, which lasts 5 or 6 weeks. Totally 14 (s.d. ± 5) captures were made in each experimental case. At the same time the bud growth stages were recorded on ten arbitrarily chosen trees of each variety in the orchards (scale after Fleckinger, 1948 and BBCH numbers after Anonymous, 1992, Tab.A.7.1). Afterwards the temporal pattern of dispersal were characterised in relation to the current bud growth stages.

Phenology of gonad maturation. To determine the gonad status of *A. pomorum* in the field we captured weevils every 5th day in early spring of 1995 to 1997. Weevils were captured with the limb-jarring method in orchard 1,2,3, but only in the sectors which were not used in other experiments. Afterwards all weevils were removed from the sector. Fifteen of the captured weevils were dissected to determine gonad development under a binocular microscope. Gonad development was characterised with the scale from A to H after Cvrtecka and Zdárek (1992)(Tab.A.7.2). Ovarioles are undifferentiated and entirely transparent in gonad stage A. The pre-vitellogenesis

starts in stage *B* with 2 to 3 small but indistinct proximal oocytes. More than four pre-vitellogenetical oocytes and growing eggs without nutriment are found in gonad stage *C*. The number and volume of eggs increase with the visible epithelium of follicle in stage *D*. The vitellogenesis with production of dotter starts at stage *E*. First terminated egg of full size is visible from stage *F* on. The vitellogenesis is terminated in stage *G* where a few eggs already descended to calyx. Stage *H* means that the weevils had eggs in calyx of gonads or in the oviduct and were ready to oviposit.

Furthermore weevils were collected and dissected after emergence from hibernation out of three leaf litter boxes in the field.

Behavioural activities in relation to apple bud growth stages. In the field the crepuscular behaviour of *A. pomorum* on apple trees was observed in relation to the current bud growth stages in spring 1998. Four observation cages (1.5 x 1.5 x 2.2 m) were set up each with one dwarf apple tree inside (cv. Boskoop, rootstock M 26) in Zürich. Forty overwintered females and 25 males were released on the trunk of each apple tree. This was done before the first post-diapaused weevils were detected in the orchards. From February 11 to April 9, which covered the whole period of spring colonisation, the weevils were observed continuously for 15 min, from 2 h before to 2 h after sunset every day. During the period of 15 min, five to seven new weevils were located. Distinct behavioural activities were recorded, *i.e.* feeding, mating, oviposition, crawling, flying, and non-activities, *i.e.* resting and hiding. Seven microhabitats were differentiated namely, blossom buds, foliage, twigs and branches, main trunks, ground, gauze of the cage and refuges such as corrugated cardboard, bark, etc. The relative proportion of each behaviour [%] and the relative proportion of behaviours observed on each microhabitat [%] were calculated for 50 randomly chosen weevils. ANOVA and regression analyses were performed to determine the influence of bud growth stages on the weevil's crepuscular behaviour based on the data transformed by $\lg(x+1)$. Behavioural differences between males and females were tested with a Mann-Whitney-U-signed-rank-test.

Feeding and ovipositional preferences for bud growth stages. Multiple choice tests were conducted among different growth stages of apple blossom buds in climate chambers. Bud stages of the variety Boskoop were the retarded closed bud A(00), the bud with little silver greenish tip B(51), buds with half inch green tip C(53), the mouse ear stage C3(54), the tight cluster of green bud D(56), the pink bud E(57) and the balloon stage E2(59). The growth stage F(61) is the start of blooming. The

experiments were undertaken in 15 glass petri-dishes (\varnothing 250 mm, 30 mm high, covered with gauze) in a climate chamber (Maintova, L:D 12:12, L 17 °C, D 12 °C, 80 % r.h., 3500 lux). Wet corrugated paper was placed inside. The multiple choice test was applied with 5 buds per growth stage on 5 cm long apple branches. Branches were put into small glass tubes with water. One pair of unmated weevils was introduced into each dish. Feeding holes on buds and young leaves around buds were measured as feeding damage in five-day intervals. After 10 days the branches were renewed for a second or third ten-day trial. Oviposition was investigated as well. After experiments female weevils were dissected to determine their gonad status after Ctvrtecka and Zdàrek (1992). The total feeding damage per pair of *A. pomorum* was analysed in relation to the bud growth stages with ANOVA based on the data transformed by $\lg(x+1)$ and with Fisher's LSD tests.

Feeding response to apple varieties. To test the influence of apple varieties on weevils' feeding response triple choice tests were applied of four different combinations of six varieties, *i.e.* Golden Delicious, Jonagold, Idared, Gala, Maigold and Gloster 69, in climate chambers (Tab.2). The branches of these varieties were grown into the same bud stage, the mouse ear stage C3(54). The trial set up and the analyses of data were the same as described above for the multiple choice tests.

7.4 Results

Phenology of spring colonisation. The spring occurrence of weevils at the apple trees was not timed with the occurrence of a specific bud growth stage in the field (Tab.1). The weevils started to emerge from the overwintering substrate, *i.e.* of leaf litter, when the apple buds were still closed (growth stage A(00), Tab.1). Even four weeks after the first weevil was found, newly emerged weevils still occurred on the leaf litter. The bud stages during this period developed from A(00) to D(56), sometimes to E(57). Between 1995 and 1999 the dispersal of weevils into the orchards started when apple buds had a little silver greenish tip B(51) up to buds in the mouse ear stage C3(54), (Tab.1). When most weevils arrived in the orchard the buds were found to have a half inch open tip C(53) up to tight clusters of green buds D(56).

Tab.1. Start of colonisation of apple orchards by *Anthonomus pomorum* in relation to bud stages within orchards. Orchard 1 to 3 in northern Switzerland. Full start of colonisation means the highest dispersal speed and the highest capture rates. (1995 after Hirs, B. and Dorn, S., unpubl.)

Place	Year	First captured weevils		Start of dispersal		Full start of colonisation	
		Date	Bud growth stage	Date	Bud growth stage	Date	Bud growth stage
3	1995	21.2.	B	11.3.	B-C	24.3.	C.C3
1	1996	20.3.	A	23.3.	A-B	7.4.	C-D
1	1997			4.3.	C	15.3.	C3
2	1997			4.3.	B	14.3.	B-C
2	1998	17.2.	A	17.3.	C-C3	28.3.	C3-D
1	1999	2.3.	A	14.3.	B-C	25.3.	C-C3
2	1999	10.3.	A	14.3.	B-C	25.3.	C-C3

Phenology of gonad maturation. Weevils, which just emerged from ground leaf litter, were found to have always slightly developed gonads of stages *A* to *B*, maximum *D* independently of the date of emergence (Fig.A.7.1). Most of the immigrating female weevils had slightly developed gonads of stages *B* to *F*, some *G* during the first 10 days after the start of dispersal (Fig.1). These weevils had no eggs in the calyx or oviduct and thus were not ready for oviposition. At this time very few individuals were found with fully matured gonads, which was at a bud growth stage of half inch green tip, C(53). Usually weevils with fully mature gonads (*H*) occurred 24 ± 3 days after the start of dispersal into orchards, *i.e.* from the time of mouse ear buds to tight cluster of green buds, C3(54) to D(56). Colonising weevils, which had overwintered within the orchards, matured their gonads up to ten days earlier, which coincided with the bud growth stages C(53) to C3(54). About 50 % of the colonising females which overwintered outside were ready to oviposit between April 1 and April 15 in northern Switzerland in the year 1995 to 1997. During this period the apple buds were mostly at the tight cluster of green bud stage D(56), sometimes at the mouse ear stage C3(54) or until the pink bud stage E(57).

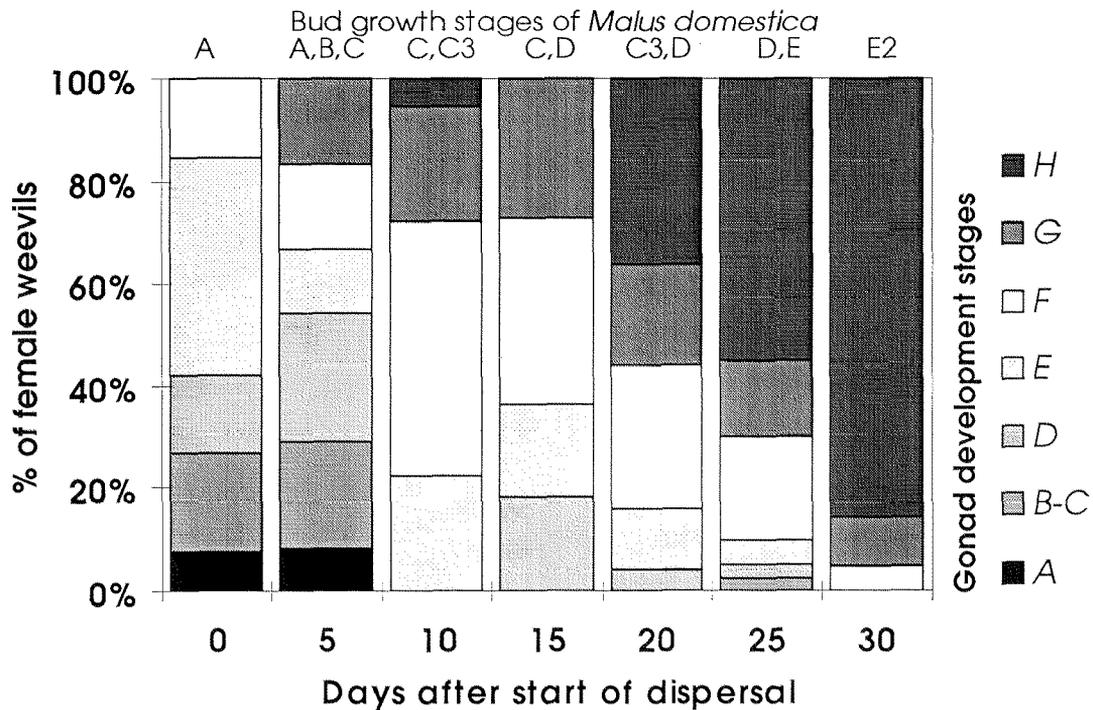


Fig. 1. Mean gonad development of *Anthonomus pomorum*, immigrated into apple orchards in spring 1995,96 & 97 in northern Switzerland, what was around the March 12., s.d. ± 7 days. 15 individuals per capture date were checked and their most developed ovarioles were recorded. Gonad of stage A= ovarioles non-differentiated, E= starting vitellogenesis, F= first eggs of full size visible, H= ready to oviposite, after Cvrtecka and Zdarèk (1992).

Behavioural activities in relation to apple growth stages. The bud growth stage had a significant influence on the mating (ANOVA; DF= 5,44; F= 11.2; $P < 0.01$) and resting behaviour (DF= 5,44; F= 8.6; $P < 0.01$) of *A. pomorum* on apple trees in spring. The dependence of total activity on bud growth stages, i.e. the sum of observations of crawling, mating and feeding, was not significant (ANOVA, DF= 5,44; F= 2.3; $P = 0.059$, Fig.A.7.3). During the period of stages A(00) to C3(54), that is from the closed bud to the mouse ear stage, only 25% of weevils were active (Fig.2). Relatively high activity was shown at bud growth stages D(56) and E(57), the tight cluster of green bud or pink buds ($P < 0.05$, Mann-Whitney-U-test). Female *A. pomorum* were more active than males, especially in the early spring season ($P < 0.05$ for all bud growth stage periods, Mann-Whitney-U-test, Fig.2, Tab.A.7.3). Crawling behaviour was more commonly observed for females than for males at bud growth stages A(00), C3(54) and D(56) ($P < 0.05$). Only at pink buds E(57), males and females showed a rather similar pattern in their behaviours. Females fed much more on young buds of the stages A(00), B(51) and C3(54) than did males ($P < 0.05$, t-test). Buds with little

silver greenish tip B(51) were the most important feeding material for females in early spring. A frequent feeding activity was observed on pink buds E(57) for both males and females ($P > 0.05$, t-test). Feeding on other natural resources of the apple tree than buds was not observed. Mating behaviour occurred at stage B(51), but mostly at stage D(56), *i.e.* the tight cluster of green bud. Oviposition was observed at stages D(56) and E(57).

Feeding and ovipositional preferences for bud growth stages. In multiple choices in laboratory the distribution of *A. pomorum* on buds was significantly influenced by the growth stage of the offered buds. This influence was shown during the period from the 5th to 15th day after termination of hibernation (ANOVA; DF= 4,45; F= 13.6; P= 0.00) as well as during the period from the 15th to 25th day (ANOVA; DF= 4,45; F= 29.6, P= 0.00). *A. pomorum* responded to the most developed growth stages, *i.e.* the stage E(57) of pink bud or balloon stage, more than to stages A(00), B(51), C3(54) and D(56) (Fig.3). This response was consistent among the elapsing time period of 10, 15, 20 or 25 days after termination of hibernation (Tab.A.7.4). Stages D(56) and C3(54), *i.e.* the tight cluster of green bud and the mouse ear stage, ranked the second and third in the order of preferences. Except during the period from the 5th to 15th day after termination of hibernation stages D(56) and C3(54) were equally used for feeding, but significantly more than A(00) or B(51) and significantly less than E(57) (Fisher's LSD test, $P < 0.05$, Tab.A.7.5). In laboratory one pair of weevils produced totally 258 ± 72 feeding holes during 20 days with 115 ± 58 in the first 10 days and 143 ± 54 in the second 10 days ($n = 15$). Totally only 18 eggs were laid by five of the tested weevils. No eggs were laid into closed buds A(00), whereas 11 % were laid into buds with silver greenish tip B(51), 22 % into buds of the mouse ear stage C3(54), 44 % into tight cluster of green buds D(56) and 22 % into pink buds E(57).

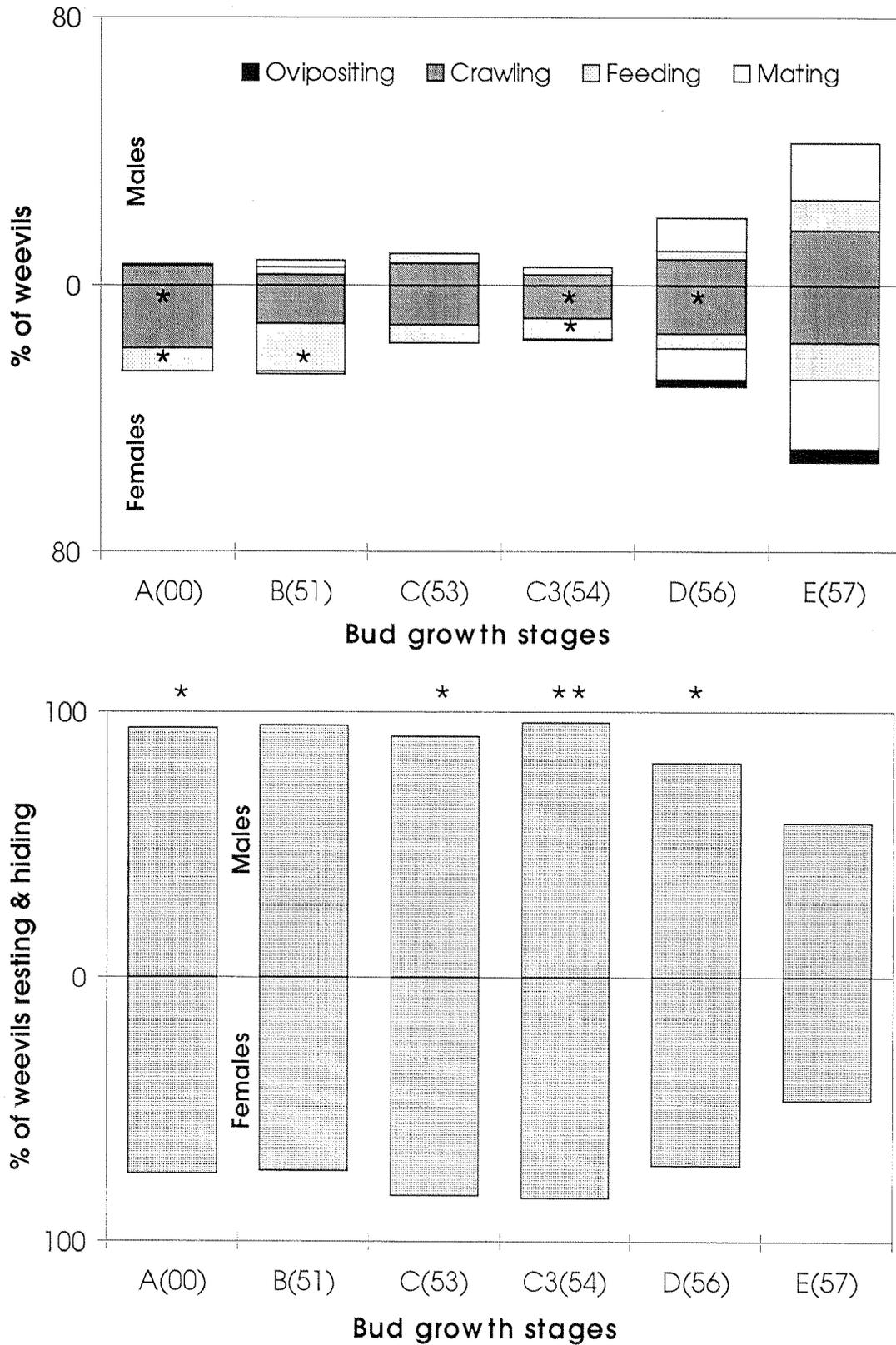


Fig.2. Crepuscular behavioural patterns of male and female *Anthonomus pomorum* two hours after sunset on the apple tree and blossom bud stages (n=25, Mann-Whitney-U-signed-rank-test at *P<0.05, bud stages after Fleckinger, 1948)

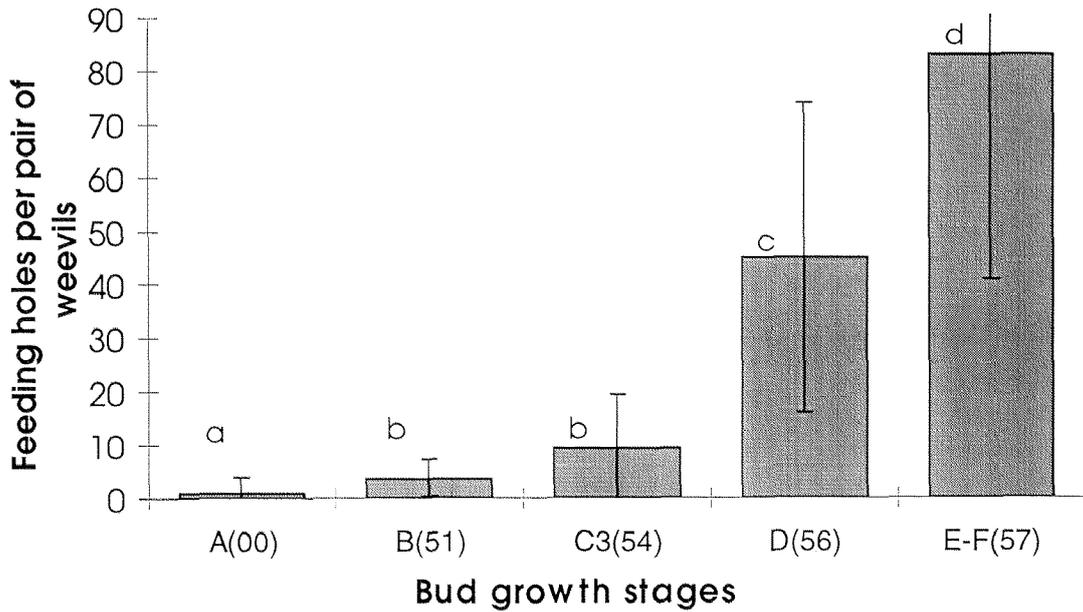


Fig.3. Average feeding damage by postdiapaused pairs of *Anthonomus pomorum* on buds of different stages during 15 to 25 days after termination of hibernation. Weevils were fed during 10 days before the experiment. Feeding damage was measured as feeding holes in buds, LD 12:12, L 17 °C, D 12 °C, 80 % r.h., n= 15, Fisher's LSD test at *P<0.05.

Tab.2. Feeding damage by *Anthonomus pomorum* on buds of different varieties of the same growth stage, C3(54), in triple choice tests. Test between each 3 varieties with n= 12 pairs of weevils; ANOVA and multiple comparison by Fisher's LSD test at *P<0.05. Damage is expressed as feeding holes on 5 buds per variety, at exposure time of 10 d, LD 12:12, 80 % r.h., L 17 °C, D 12 °C. Apple varieties tested: Golden Delicious, Jonagold, Idared, Gala, Maigold, Gloster 69.

	Choice 1			Choice 2			Choice 3			Choice 4		
Feeding damage	Gold. Del.	Ida- red	Jona- gold	Gold. Del.	Ida- red	Gala	Mai- gold	Glo- ster	Gala	Mai- gold	Glo- ster	Jona- gold
Mean	32.0	34.0	13.0	30.3	33.5	24.3	45.8	23.4	20.8	10.0	27.0	12.0
± s.d.	20.0	20.0	4.0	18.8	18.4	22.2	18.9	12.2	13.4	3.0	20.0	14.0
Fisher's LSD	a	a	a	a	a	a	b	a	a	ab	a	abc

Feeding response to apple varieties of the same growth stage. In laboratory a consistent preference for the varieties Golden Delicious, Jonagold, Idared, Gala, Maigold and Gloster 69 of the same bud stage were not observed in four triple choice

tests (Tab.2, see also Tab.A.7.6). Significant differences between feeding damages on the offered varieties occurred only in a single triple choice test. For example, a significant preference for Maigold or Gloster 69 over others was shown once (Tab.2).

7.5 Discussion

Our observations showed that *A. pomorum* preferably fed on buds of growth stage D(56) or E(57), though the earlier growth stages A(00) to C3(54) were also used for feeding especially by females. The percentage of bud damage caused by feeding is unknown. The bud with little silver greenish tip B(51) seems to be particularly important for feeding of females in early spring, since the overwintering buds may contain a high amount of starch and carbohydrates such as glucose and maltose (Friedrich *et al.*, 1986). On the other hand female weevils mature their gonads much faster when feeding on bud growth stages C3(54), D(56) or E(57) than on an earlier growth stage B(51) (Hirs, B. and Dorn, S., unpubl.). Weevils which fed on bud stage C3(54) were able to mature their gonads completely within 20 days in laboratory. Ten days feeding or no feeding resulted in less developed gonads (Fig.A.7.2). Cvrtecka and Zdàrek (1992) reported the necessity of suitable food such as sprouting apple buds for a fast gonad maturation of *A. pomorum*. This explains our results of the multiple choice experiments in laboratory. They showed that *A. pomorum* significantly preferred the development-accelerated buds for feeding among buds of growth stage A(00) to F(61). This result supports that *A. pomorum* tend to use the most development-accelerated trees in the field (Wiesmann, 1928). The lack of feeding by males on growth stage A(00), *i.e.* the closed bud, in the field, is probably explainable because maturation feeding is unnecessary in this sex (Wiesmann, 1928).

In field cages and in dwarf apple tree orchards oviposition was observed during stage D(56) or E(57) (see also Duan, *et al.*, 1996). Most weevils had fully matured gonads in this period. In areas where *A. pomorum* overwinters within the orchard probably an earlier date of oviposition would be observed because of an accelerated gonad maturation by these weevils. The field experiments are in good coincidence with the multiple choice tests in laboratory which showed that *A. pomorum* laid eggs into buds of growth stages B(51) to E(57), but preferably into stages C3(54), D(56) or E(57).

Interestingly, the tested varieties irrespective of their bud growth stages caused no significant differences in the behaviour of weevils in our study. Kalinova *et al.*

(1996) found a host-cultivar preference with field collections and records of infestation patterns; however, the growth stage differed between trees and varieties. It is still not clarified if *A. pomorum* can distinguish between bud growth stages or varieties by olfactation under field conditions, though the volatile emission from apple buds can differ between growth stages and between varieties (Kalinova *et al.*, 1996). Moreover the number of buds per tree is an important factor influencing the weevils' choice (Zdàrek, pers. comm.). Finally the use of buds seems to be influenced by the interdependency of the time regarding the completion of gonad maturation, the oviposition period and the start of blooming. Thus most damage occurs when the bud development is prolonged in the spring (Korchagin, 1978). Our field experiments showed that the growth stage of available buds differ from year to year when weevils arrive on the trees. Indeed, the timing and speed of bud growing is dependent on temperature in December and January (Friedrich *et al.*, 1986). Not only sums of temperature, but also the sequence of cold and warm days during overwintering influences the start of bud growing. However, this complex of temperature influence on apple buds can not adequately explain the influence of temperature on *A. pomorum* (Ctvrtecka and Zdarek, 1992, Kostal *et al.*, 1996). Moreover different varieties have different genetically fixed temperature ranges for starting blooming (Friedrich *et al.*, 1986) and could show up to one week difference in their development of buds (Kellerhals *et al.*, 1997). Therefore, the different threshold values for apple bud development and for *A. pomorum* colonisation render the tree development stage an unsuitable tool for forecasting the population dynamics of *A. pomorum*, although a spraying against the pest is yet recommended at the early dates of bud growth stages B(51) to C3(54) (Rizzolli and Paoli, 1995, Hoehn *et al.*, 1999). A prediction of dispersal dynamics by ambient temperature is more recommendable (Chapt. 5.4).

In conclusion, *A. pomorum* weevils are well adapted to, but not totally synchronised with the development of buds in the field. We suggest that the stage preference of *A. pomorum* would cause increased population abundance in areas with certain accelerated growing apple varieties with a high number of buds and a long blooming period. These areas might be subjected to an increased risk for economic damage. Some development-accelerated varieties, such as Gravensteiner and Summerred (Kellerhals *et al.* 1997), might be particularly vulnerable to infestation by *A. pomorum* (Tab.A.7.7).

8. GENERAL DISCUSSION

Knowledge on dispersal behaviours and ecology of insect pests is decisive in two ways: in a basic scientific way to understand key mechanisms behind dispersal processes, and in an application oriented way to allow design of more sustainable strategies for pest management. The spatial aspects of herbivores gain importance when modern selective pest management tools are employed (Dorn, 1999). From an agricultural prospective the spring dispersal of a pest insect and the prediction of the colonisation process are of particular interest (Stinner *et al.*, 1986, Weber and Ferro, 1994). This work focused on the dispersal of the apple herbivore *A. pomorum* between apple orchards and its hibernation sites with a special emphasis on adjacent forests.

Dispersal, movement, or migration? The movement of *A. pomorum* in spring or in summer/autumn, collectively or alone, leads to a change of spatial co-ordinates or local density. In Entomology, this behaviour is called migration (Taylor, 1986). However, it is still unknown whether *A. pomorum* responds to “vegetative” stimuli (trivial movement) such as host plants and hibernation substrates, or whether the movement is a true migration (*sensu* Southwood, 1977). Therefore, on population level, I considered the process always dispersal, which is produced by individual movements. Dispersal is a more general term than migration used in ecology for one-way movements. It is applied to insects and other animals such as mammals and birds to describe movements including changes of habitats. On individual level, I named the process simply movement instead of migration because the latter term is often used as the orientated two-way movement with an obligate return to the starting place. Such patterns do not apply to *A. pomorum*. By the entomological definition, the described behaviour of *A. pomorum* could be defined as “migration of the second kind”, since this is “the one-way movement made by a living organism between its own birthplace and those of its offspring” (Taylor, 1986). Prospects of return are increased, but not defined. Thus, the terminology chosen in my study, confined to “dispersal” and “movement”, helps to keep things clear and to avoid confusion.

Orientation in dispersal. A dispersal navigation as in birds is unlikely to exist in *A. pomorum* and in most other insects (Price, 1984). It is possibly the host foraging behaviour that results in dispersal activities in spring. Dispersal is adaptive (Price, 1984), and usually insects are able to react to shifting environments very fast (Dingle, 1986). Apple orchards exist for over 1000 years in middle Europe and modern dwarf apple trees exist for at least 30 years (Kellerhals *et al.*, 1997). This time span seems to be sufficient for *A. pomorum* to adapt to environmental cues for orientation. Furthermore, Dethier (1947) hypothesised that not one attractant alone services to guide an insect to its proper host-plant; the desired end being achieved only by a complex array of stimuli, such as chemicals, light, temperature, humidity and silhouettes, acting in harmony. In our case, *A. pomorum* needs to locate apple trees in spring and hibernation sites in summer or autumn. The cues behind the long range foraging behaviour of *A. pomorum*, *i.e.* before landing, and the sequence of decisions were never investigated before, nor for most other Coleoptera species (Miller and Miller, 1986). For *A. pomorum*, probably both olfactory and visual cues are involved in the orientation of the weevils' dispersal as preliminary studies indicated. First, among numerous colours offered, dark or brown colours were clearly preferred under laboratory conditions (J.J. Duan, and S. Dorn, unpubl.). Second, chemical cues, *i.e.* volatiles from apple twigs, were shown to play a certain role for short range foraging of *A. pomorum*, *i.e.* after landing (D. Schaerer, unpubl.). A similar phenomenon was found for *Conotrachelus nenuphar* in North-eastern America (Leskey *et al.*, 1998). Third, our study demonstrates that *A. pomorum* is able to distinguish between apple buds of different stages under laboratory conditions. The most developed apple buds were significantly more acceptable for feeding by weevils than the less developed ones. The mechanism underlying the preference is unknown yet.

Patterns of curculionid dispersal. Field experiments clearly demonstrated that *A. pomorum* can display directed dispersal. The orientation was particularly strong in spring with the colonisation of apple orchards from adjacent forest habitats. The pattern described coincides well with the few known examples of dispersal of weevils from the family of Curculionidae. Spring dispersal distances of *A. pomorum* amounted to 5 to 25 m. This distance is similar to that of the North-eastern American apple pest *Conotrachelus nenuphar*, the plum curculio (Lafleur and Hill, 1987), but much shorter than that found for *Anthonomus grandis*, the cotton boll weevil (Guerra, 1988; McKibben *et al.*, 1988). The dispersal of insects is strongly density-dependent (Price, 1984), but since the number of released weevils in this study was relatively low, it is

unlikely that it promoted dispersal. Similarly, the influence of intraspecific competition can be considered negligible.

Spring dispersal orientated in the direction of apple orchards suggests reverse dispersal in autumn. This was shown in *C. nenuphar* (Lafleur *et al.*, 1987). In contrast *A. pomorum* performed only a limited dispersal activity in summer or autumn, when weevils search for aestivation and hibernation sites simultaneously. Most weevils of the newly emerged generation stayed in the vicinity of release sites within the orchards, moving more or less randomly along the apple tree rows. Our quantitative data confirm a previous observation on random movements in colonisation of orchards in summer (Korchagin, 1978). Only a small proportion of the population dispersed over longer distances and was able to reach an adjacent forest or orchard areas with high stem trees. This finding indicates that most *A. pomorum* try to overwinter within orchards, although this low activity behaviour will result in a higher mortality for the species, when the availability of leaf litter or rough bark is too low, or when unpredictable harsh climate conditions occur. Thus, the dispersal of *A. pomorum* found in this study is a simple resource to resource movement (Stinner *et al.* 1986), resulting in a dynamic change of spatial co-ordinates. This process can be considered as an emigration from the birth-place to aestivo-hibernation sites in summer/autumn and as an immigration to the place of offspring production in spring.

Consequences of dispersal on population success. The specific patterns of *A. pomorum* dispersal in spring and in summer/autumn are probably behaviourally determined, which can be considered the product of natural selection. The selection operates on this dispersal behaviour to maximise the survival of the present generation during a transit and, after arrival, to protect the next generation by selecting a place for it to live (Taylor, 1986). It leads to a wider distribution of the weevils' population in orchards in autumn and to a more concentrated distribution on orchard borders in spring. *A. pomorum* did not colonise the whole orchard within one season when enough plant resources were available at orchard borders. This applies to a large proportion of the population. In contrast a small proportion of weevils' population always tended to colonise wider areas and to bear more costs for dispersal in the apple orchard or adjacent hibernation sites. New food resources can be exploited or new hibernation sites, *e.g.* outside orchards, can be found by dispersing individuals. Their chance of survival remains high even in harsh winters, and subsequent a re-colonisation of orchards in spring is possible. Theoretically, overwintering within the orchard is profitable for the weevils if enough leaf litter and rough bark trees are

available, and if early spring will be mild. On the other case, dispersal becomes a profitable activity.

The investigated organic or IP managed orchards in Switzerland were small, and some offered abundant leaf litter for hibernation under the apple trees. There was a low selection pressure for increased dispersal activity. In contrast, dispersal behaviour in autumn might be more pronounced in large and homogeneous orchards of 30 to 80 ha as they were often found in eastern Germany or Hungary (Freier *et al.*, 1989; Friedrich, 1993). These orchards of dwarf trees produce a very low quantity of leaf litter as compared to high-stem trees, and offer no rough bark. In such habitats *A. pomorum* is expected to be more strongly selected for emigration in response to the deteriorating conditions in autumn.

Mechanisms underlying implications of dispersal on timing of pest management techniques. This study clearly demonstrates that climatic conditions are the key promoting factors for spring dispersal and orchard colonisation by postdiapaused weevils. As the pest status of *A. pomorum* has been increasing (Wildbolz, 1992; Bloomers, 1994), interventions at the beginning of the spring season are required to control this herbivore. Apple growers have no satisfactory control method against the weevil so far. This study provides essential information for the development of new management strategies against *A. pomorum*.

Based on the presented results the timing of the dispersal pattern of *A. pomorum* can be predicted using a threshold temperature and a degree-day model. Sprays should be carried out after the start of dispersal, optionally at the peak of movement and colonisation, when most weevils have reached orchards but have not yet started oviposition. Similarly Bostanian *et al.* (1999) used adult behaviour to predict *Anthonomus signatus*, the strawberry bud weevil. In northern Switzerland the peak of mass colonisation of orchards occurred 8 to 12 days after the start of dispersal into orchards. Usually this occurred between the third and last week of March when mean daily temperature of 8 to 11°C lasted for two or three successive days (mean March 24 ±8days). The timing of intervention can also be predicted using the cumulative Celsius degree-days above 0°C: 210 ±26 DD calculated from January 1 or 166 ±19 DD from February 1. However, few weevils colonised orchards already up to 13 days before the start of the dispersal process. This is probably due to the intra-population variation (Price, 1984). Many insects in northern temperate regions show individual variations in diapause development (Istock, 1981). The fast developing weevils can produce more

progeny when the season is long whereas late emerging weevils have less chance of their destruction owing to the unpredictable onset of harsh spring conditions.

Usually weevils with fully mature gonads occurred 24 ± 3 days after the start of dispersal into orchards at the beginning of April. However, colonising weevils which had overwintered within the orchards near old trees matured their gonads up to 10 days earlier than weevils immigrating from outside. Probably these weevils saved energy and nutrients because of reduced dispersal activity especially in flight (Duan *et al.*, 1998). Despite a similar timing of dispersal for both the weevils that overwintered inside and outside the orchard, this difference in gonad development between the two groups might render the timing of intervention a complex matter. Fortunately enough modern commercial orchards are poor in good overwintering sites (Balachowsky, 1963; Merckens, 1977) and light infestation of *A. pomorum* only causes fruit thinning (Reijbroek, 1983; Blommers, 1994). Thus the above described forecasting model is likely to be successful for modern commercial orchards. For orchards with a very diverse structure of apple trees, the critical orchard areas with suitable overwintering sites might need an immediate intervention coinciding with the start of dispersal. Thus, a successful monitoring should consider the habitat structures appropriately.

The field experiments showed that the apple bud development and the dispersal dynamics are not totally synchronised. Therefore bud growth stage is thus not considered a suitable indication for the timing of dispersal of *A. pomorum*.

Outlook based on available data.

A. Timing of interventions:

I suggest that prediction of the colonisation process based on models with threshold temperatures and cumulative degree-days should be validated in further locations of different geographic latitudes throughout the distribution range of *A. pomorum* in Europe. The experimental data gained over several years and at two different locations in Switzerland provide a solid basis for such extrapolation.

B. Trap crop technique

I suggest to further investigate the potential contribution of specifically arranged and treated border rows of apple trees to an integrated *A. pomorum* management program. One or two border rows of one or more apple varieties with accelerated blooming and a vast number of flower buds should be planted adjacent to the forest border. In

modern dwarf apple orchards weevils immigrate from surrounding hibernation habitats and probably feed and lay eggs on the first colonised tree with buds. This cultural technique results in a concentration of weevils' population in border rows. It is expected to limit the damage but probably not to such a high degree as described for the plum curculio (Chouinard *et al.*, 1992), because the apple blossom weevil can overwinter both in the adjacent forest as well as within the orchard.

C. Monitoring of weevil immigration into the orchard

I suggest to further investigate the potential of a monitoring trap of the type of pyramid traps developed by Tedders and Wood (1995) for the pecan weevil, *Curculio caryae*. A comparable trap is applied for *Anthonomus grandis* in cotton fields based on findings by Rummel and Adkisson (1970). Visual cues mimicking the stem of an apple tree seem to be promising, and could possibly be complemented by olfactory stimuli. These suggestions are based on a pilot study which I helped to supervise (diploma thesis by D. Schaerer and semester thesis by L. Frey).

In conclusion, this project promoted our understanding of the dispersal behaviour and ecology of the apple blossom weevil. It also lays the fundamental for a temperature-based model to predict the timing of interventions. It further provides evidence for promising cultural techniques and monitoring tools. More research is needed to find satisfactory solutions to manage this old and new apple pest.

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APPENDIX

Fig.A.1. Studied apple orchard A in Hoengg, ZH, northern Switzerland.



Fig.A.2. Studied apple orchard B in Niederwil, AG, northern Switzerland

Tab.A.1. Summarised data from release-recapture experiment of *Anthonomus pomorum* in 11 rows of orchard A (Hoengg) in spring 1996. Release of 4200 weevils (escape of 3250 weevils from release box until 29.5.96), Recapture-rate 8.6%. Weevils were released after recaptures.

Spring 1996				Start of release		Rainy weather	Start of colonisation							
Bud stage		A	A	A	A	A	A	A	A-B	A-B				
Date		29.2.	6.3.	10.3.	14.3.	18.3.	20.3.	22.3.	24.3.	28.3.	30.3.			
Total captures 96		0	0	0	0	0	1	0	10	1	0			
Captured native pop.96		0	0	0	0	0	0	0	2	0	0			
Total recaptures 96		0	0	0	0	0	1	0	8	1	0			
Recaptured weevils :														
<i>released in spring '96</i>														
1st recapture		0	0	0	0	0	1	0	7	1	0			
2nd...recapture		0	0	0	0	0	0	0	1	0	0			
New weevils in orchard		0	0	0	0	0	1	0	9	1	0			
		Full start of colonisation			Rainy all out of weather rel. box									
		B	B-C	C	C-C3	C3	C3	C3-D	C3-D	D	D	E-E2	F	
		1.4.	6.4	8.4.	10.4.	12.4.	15.4.	17.4.	19.4.	22.4.	24.4.	1.5.	18.5.	29.2.-18.5.96
		2	5	25	23	46	22	60	78	87	50	22	7	439 100%
		1	0	1	3	6	1	8	5	3	4	2	0	36 8%
		1	5	24	20	40	21	52	73	84	46	20	7	403 92%
		1	5	23	17	32	16	32	41	63	23	11	7	280 69%
		0	0	1	3	8	5	20	32	21	23	9	0	123 31%
		2	5	24	20	38	17	40	46	66	27	13	7	316

Tab.A.2. Data from release-recapture experiment of *A. pomorum* in 11 rows of orchard A (Hoengg) in spring 1997. Release of 2000 weevils in spring (escape of 1700 from release boxes until 11.4.97), Recapture-rate of 15% of all marked weevils, 6% for weevils released in 1997. 110 recaptures more than once. Weevils were released after recapture, marking of 135 natives until 14.3.97.

Spring 1997	Start of colon.	Start of release	Full start of colon.		all out of re- lease box		
Bud stage	B	C	C	C3	C3-D	C3-D	D
Date	5.3.	11.3.	12.3.	14.3.	17.3.	18.3.	21.3
Total captures 97	45	56	58	65	56	70	25
Captured native pop. 97	29	40	37	29	21	12	2
Total recaptures 97	16	16	21	36	35	58	23
Recaptured weevils:							
<i>released in spring '97</i>							
1st recapture	0	0	8	6	12	18	6
2nd....recapture	0	0	0	2	0	6	2
<i>released in spring '96</i>							
1st recap. in spring 97	16	16	5	17	6	12	2
of these individ.marked in 96	6	2	4	3	2	2	0
2nd....recapture in 97	0	0	3	0	6	6	7
of these individ.marked in 96	0	0	1	0	1	1	0
Marked native pop. 97		0	5	11	11	16	6
New weevils in orchard	45	56	50	52	39	42	10

D	D	D-E	D-E	E	E	E-E2	E-E2	E2-3		
24.3.	26.3.	31.3.	1.4.	3.4.	7.4.	9.4.	11.4.	17.4.	5.3.-17.4.97	
10	48	24	38	19	6	11	15	4	550	100%
1	8	3	8	5	0	0	0	1	196	36%
9	40	21	30	14	6	11	15	3	354	64%
0	6	8	10	6	6	6	8	2	102	29%
2	12	0	6	2	0	4	6	0	42	12%
2	7	7	5	1	0	0	0	0	96	27%
0	1	2	2	0	0	0	0	0	24	7%
2	2	3	2	0	0	1	0	0	32	9%
0	0	0	0	0	0	1	0	0	4	1%
3	13	3	7	5	0	0	1	1	82	23%
3	21	18	23	12	6	6	8	3	394	

Tab.A.3. Data from capture-recapture experiment of *Anthonomus pomorum* in 11 rows of orchard A (Hoengg) in spring 1998 and 1999. No mass release of weevils. Recapture-rate of 7.3% of all marked weevils. In 1999 marking of 257 natives until 24.3.99 and release. In 1998 marking of 135 natives until 14.3.98 and release (1999 after L.Frey, unpubl.)

Spring 1999	First weevils				Start			Full start		
	in orchard				of colon.			of colon.		
	A	A	A	A	B-C	C	C-C3	C-C3		
Bud stage	3.3.	8.3.	10.3.	12.3.	16.3.	18.3.	24.3.	26.3.		
Date	3.3.	8.3.	10.3.	12.3.	16.3.	18.3.	24.3.	26.3.		
Total captures 99	4	0	9	21	151	55	111	242		
Captured native pop. 99	4	0	9	21	143	44	69	183		
Total recaptures 99	0	0	0	0	8	11	42	59		
Recaptured weevils:										
<i>released in spring 97</i>										
1st recapture	0	0	0	0	0	0	0	0		
2nd recapture	0	0	0	0	0	0	0	0		
<i>released in spring 96</i>										
1st recapture	0	0	0	0	0	0	0	0		
of these individ. marked in 96/97										
2nd recapture	0	0	0	0	0	0	0	0		
<i>marked native pop. 97/98</i>	0	0	0	0	0	0	0	0		
Marked native pop. 99		0	0	0	8	11	42	59		
New weevils in orchard	4	0	7	18	120	41	67	183		
<hr/>										
Rainy					Spring 1998					
weather										
C3	C3	D	D-E		D	D-E	E2-F			
30.3.	31.3.	8.4	10.4.	3.3.-10.4.99	31.3.	2.4.	22.4	31.3.-22.4.98		
303	247	139	215	1497	100%	130	28	2	160	100%
231	190	114	172	1180	79%	111	28	2	141	88%
72	57	25	43	317	21%	19	0	0	19	12%
0	0	0	0	0		16	0	0	16	84%
0	0	0	0	0		0	0	0	0	0%
0	0	0	0	0		3	0	0	3	16%
0	0	0	0	0		/2	0	0		
0	0	0	0	0		0	0	0	0	0%
0	0	0	0	0		0	0	0	0	0%
72	57	25	43	317	100%					
440										

Tab.A.4. Data from release-recapture experiment of *A. pomorum* in orchard B (Niederwil, AG) in autumn 1996 and spring 1997. Release of 2x800 weevils (escape of 2x650) at sites K1,K2 (blue, red marked) in autumn. Release of 1300 (escape 1200) at site R near forest in spring. Weevils were released after recapture.

Autumn 1996 and spring 1997	Release 1.9.96	from cardboards	Start of colon.	Start of Full start release of colon.				
Bud stage Date	9.-11.96	10.11.96	A 4.3.	B 10.3.	B-C 12.3	B-C 13.3	C3-D 18.3.	
Total captures	121	133	83	96	108	185	132	
Captured native pop.	1	21	80	92	96	138	76	
Total recaptures	120	112	3	4	12	47	56	
Recaptured weevils <i>released autumn '96</i>								
1st recapt. in aut.'96/sp.'97	107	102	2	4	12	16	19	
of these were blue	78	65	2	3	10	10	14	
red	29	37	0	1	2	6	5	
2nd...rec. in aut.'96/sp.'97	13	10	1	0	0	3	0	
of these were blue	10	9	1	0	0	2	0	
red	3	1	0	0	0	1	0	
<i>released in spring '97</i>								
1st recapt. in sp.'97			0	0	0	12	20	
2nd recapt. in sp.'97			0	0	0	0	2	
<i>marked native pop. '97</i>								
1st recapt. in sp.'97			0	0	0	16	11	
2nd recapt. in sp.'97			0	0	0	0	4	
 New weevils in orchard			82	96	108	166	115	
			Spring		Autumn			
D-D2 26.3	E 1.4.	E-E2 7.4.	E2-F 15.4.	E3-F 23.4.	4.3.-23.4.97		9.9.-1.11.96	
71	155	73	48	14	965	100%	254	100%
34	92	58	26	5	697	72%	22	9%
37	63	15	22	9	268	28%	232	91%
10	18	1	2	0	84	31%	209	90%
5	10	0	2	0	56		143	
5	8	1	0	0	28		66	
0	0	0	1	0	5	2%	23	10%
0	0	0	1	0	4		19	
0	0	0	0	0	1		4	
8	30	4	8	6	88	33%		
8	6	4	8	0	28	10%		
4	4	4	1	0	40	15%		
7	5	2	2	3	23	9%		
 52	140	63	36	11	869			

Tab.A.5. Data from release-recapture experiment of *Anthonomus pomorum* in orchard B (Niederwil, AG) in autumn 1997 and spring 1998. Release of 1000 weevils at K2 (red) and 900 at K1 (blue) on 17.7.97 (escape of 1700 until 13.8.97). Weevils were not released after recapture.

Autumn 1997 and spring 1998	Release		card boards		warm	cold	fog	warm			
	17.7.97										
Bud stage					A	A	A	A	A-B	A-B	
Date			13.8.	1.10.	20.11.	11.2.	16.2.	18.2.	19.2.	20.2.	25.2.
Total captures			11	3	8	0	0	1	0	0	0
Captured native pop.			0	1	6	0	0	1	0	0	0
Total recaptures			11	2	2	0	0	0	0	0	0
Recaptured weevils											
<i>released in autumn '96</i>											
1st rec. in aut.'97/sp.'98			0	0	0	0	0	0	0	0	0
of these were blue			0	0	0	0	0	0	0	0	0
red			0	0	0	0	0	0	0	0	0
2nd. rec. in aut.97/sp.'98			0	0	0	no values because of remove after recaptures in previous spring 1997					
<i>released in spring '97</i>											
1st rec. in aut.'97/sp.'98			0	0	0	0	0	0	0	0	0
2nd...rec. in aut.97/sp.'98			0	0	0	no values because of remove after recaptures in previous spring 1997					
<i>marked native pop. 97</i>											
1st rec. in aut.'97/sp.'98			0	0	0	0	0	0	0	0	0
2nd recapt. in aut.97/sp.'98			0	0	0						
<i>released in autumn '97</i>											
1st rec. in aut.'97/sp.'98			11	2	2	0	0	0	0	0	0
of these were blue			8	2	2	0	0	0	0	0	0
red			3	0	0	0	0	0	0	0	0
2nd...rec. in aut.97/sp.'98			0	0	0	no values because of remove after recapture in previous spring 1997					
New weevils in orchard											
cold	rain	warm	warm	Full start				cold	Spring		Autumn
	start of colon.			of colon.							
A-B	B	C	C	C-C3	C-C3	C3-D	D	D-E			
3.3.	7.3.	18.3.	20.3.	25.3.	26.3.	29.3.	30.3.	1.4.	11.2.-1.4.98	13.8.-20.11.97	
0	0	119	103	22	24	277	243	414	1203	100%	22 100%
0	0	92	87	19	21	252	220	372	1064	100%	7 100%
0	0	27	16	3	3	25	23	42	139	13%	15 214%
											0
											0
0	0	3	1	1	0	0	1	4	10		0
0	0	1	1	1	0	0	1	2	6		
0	0	2	0	0	0	0	0	2	4		
											0
0	0	6	8	0	0	6	2	4	26		0
0	0	1	0	0	0	0	1	1	3		0
0	0	17	7	2	3	19	19	33	100		15
0	0	13	5	1	1	14	14	25	73		12
0	0	4	2	1	2	5	5	8	27		3
0	0	119	103	22	24	277	243	414	1203		

Tab.A.6. Data from capture-recapture experiment of *Anthonomus pomorum* in orchard B (Niederwil, AG) in spring 1999. Marked weevils were not released after recapture. In the first six capture days all captured native weevils were marked and released, n=804. Then for four capture days native weevils were not marked, but released. At the three last captured days all native weevils were removed. (after Schaerer, D., unpubl.)

Spring 1999	windy cloudy	cloudy	sunny warm	sunny warm no wind	windy cold sunny	sunny	sunny fog
Bud stage	A	A	A	B-C	C	C-C3	C-C3
Date	3.1.	10.3.	12.3.	15.3.	17.3.	24.3.	25.3.
Total captures	0	6	32	305	229	386	623
Captured native pop. 99	0	6	29	301	218	342	573
Recaptures							
<i>yellow marked, (spring 99)</i>	0	0	3	4	11	44	50
<i>marked red/blue left (autumn 96)</i>	0	0	0	1	1	0	0
<i>marked white (spring 97)</i>	0	0	0	0	0	0	0
<i>marked red/blue right (summer 97)</i>	0	0	0	1	1	0	4
Proportion marked weevils/ Total captured weevils							8%

cloudy	cloudy	sunny	sunny windy D	sunny windy D	sunny windy D-E	Spring 3.1.-14.4.99
C3	C3	C3	D	D	D-E	
28.3.	29.3.	1.4.	6.4.	9.4.	14.4.	
478	584	1634	1305	552	256	6390
399	496	1455	1164	462	205	5650
79	88	179	141	90	51	740
0	0	0	0	0	0	2
0	0	1	0	0	0	1
0	0	2	2	0	0	10
17%	15%	11%	11%	16%	20%	

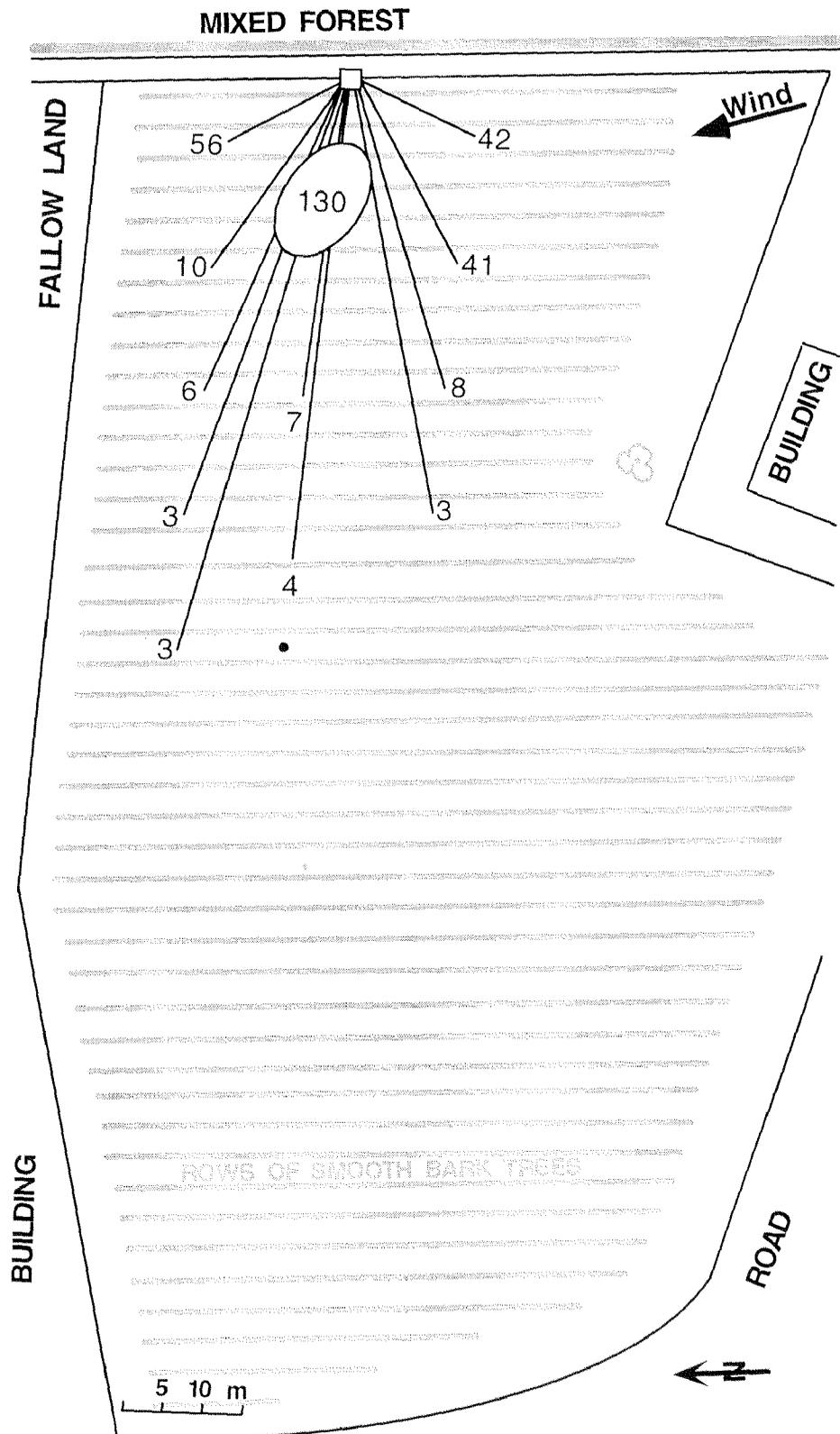


Fig.A.4.1. Orientation into the dwarf apple tree orchard A by recaptured and marked *A. pomorum*, released in spring 1996 at a release point \square near the adjacent forest. Lines indicate vectors and numbers of dispersing weevils found in sectors within the orchard, orchard edges and in forest sectors. Hotelling's confidence ellipse for unknown population centres is presented with $Q=95\%$. Recaptures with limb jarring, (IP-managed orchard A).

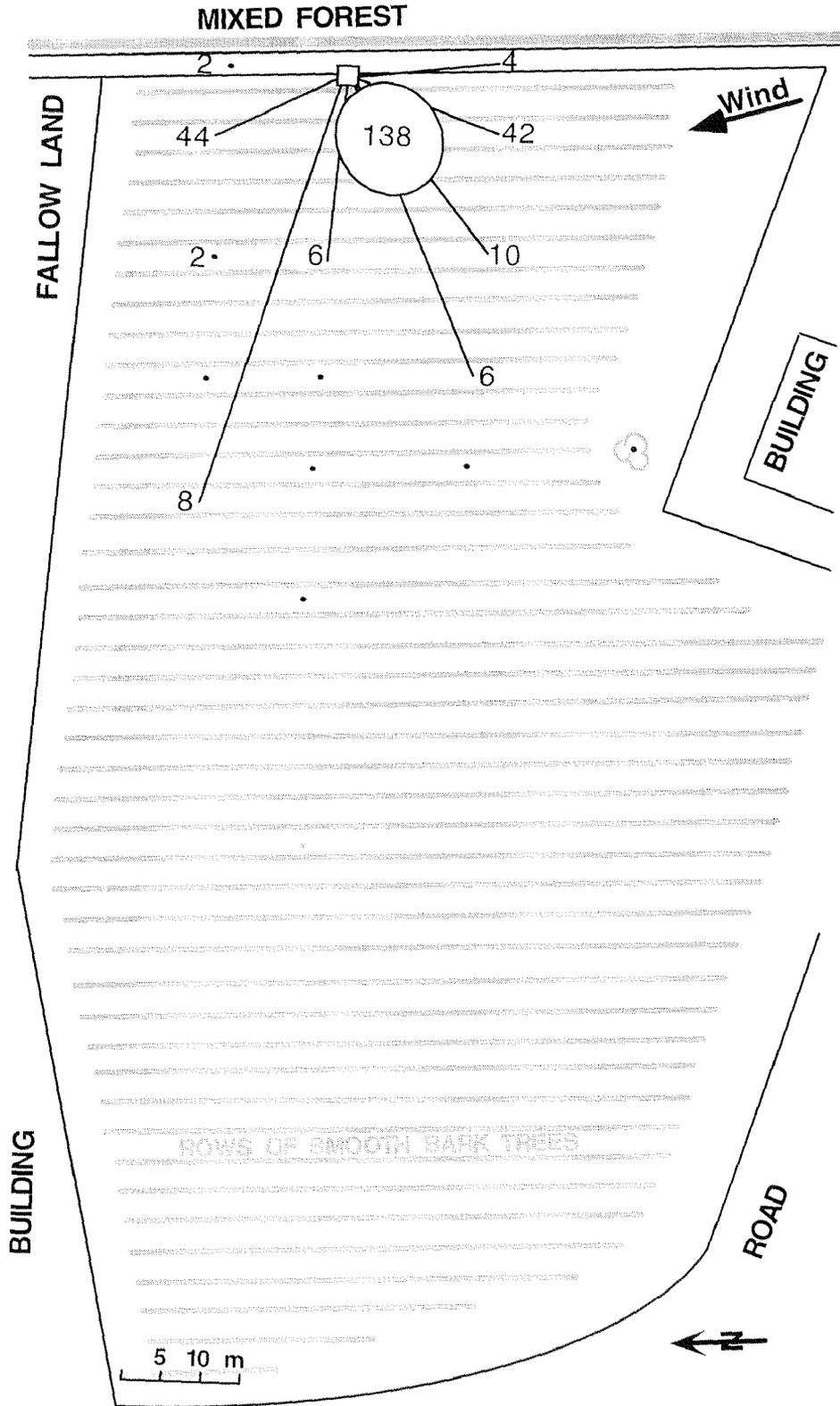


Fig.A.4.2. Orientation into the dwarf apple tree orchard A by recaptured and marked *A. pomorum*, released in spring 1997 at a release point □ near the adjacent forest. Lines indicate vectors and numbers of dispersing weevils found in sectors within the orchard, orchard edges and in forest sectors. Hotelling's confidence ellipse for unknown population centres is presented with $Q=95\%$. Recaptures with limb jarring, $n=368$, but 138 of them stayed near the release point. (IP-managed orchard A)

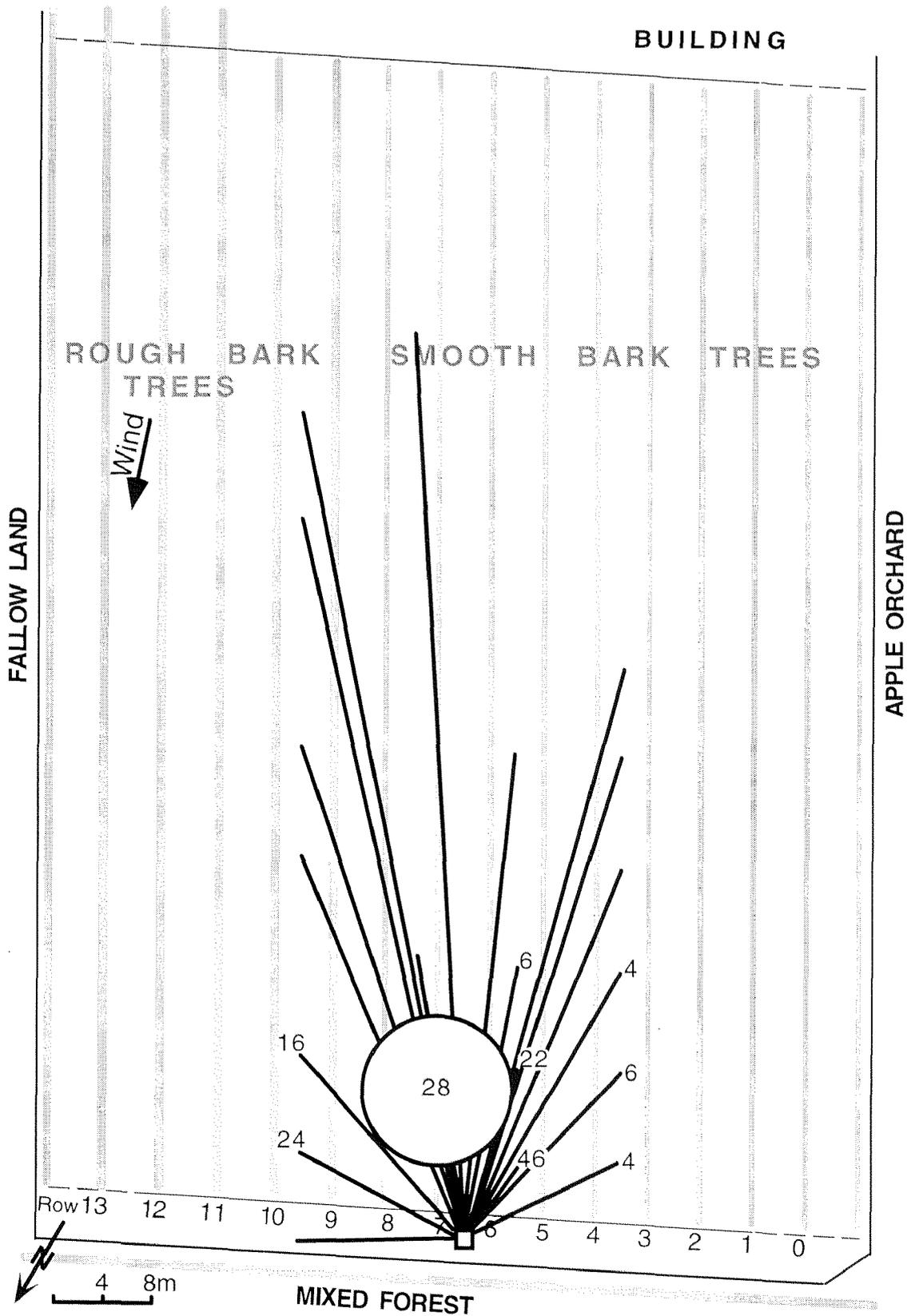


Fig.A.4.3. Orientation into the orchard B by recaptured and marked *A. pomorum*, released in spring 1997 near the adjacent forest □. Lines indicate vectors and numbers of dispersing weevils found within the orchard, orchard edges and in forest. Hotelling's confidence ellipse for unknown population centres is shown with $Q=95\%$. Recaptures with limb jarring, $n=240$, but 92 of them stayed near the release point. (organic-managed orchard B).

Tab.A.4.1. Mean vectors of dispersal in relation to days after release, based on recapture of marked *A. pomorum* in orchard A in spring 1996 and 1997. Orchard in 270° relative to release point; v = mean angle of displacement, s.d.= standard angular deviation, n = recapture number, r = length of main vector as a measure of concentration at $P<0.05$, Rayleigh-test.

Orchard A 1996							
Days	10	20	30	40	50	Σ	Mean
Date	20.-30.3.	31.3.-10.4.	11.-20.4.	21.-30.4.	1.-20.5.	20.3.-20.5.	wind direction
Characteristics of Mean vectors							direction
v [°]=	291	279	279	279	288	280	200
s.d. [°]=	70.6	33.4	35.3	38.0	32.4	34.8	27
n =	9	43	127	83	18	281	77
r =	0.2	0.8	0.8	0.8	0.8	0.8	0.9
P (of r)	>0.5	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Orchard A 1997							
Days	10	20	30	40	50	Σ	Mean
Date	10.-20.3.	21.-30.3.	31.3.-10.4.	11.-20.4.	21.-30.4.	10.3.-20.4.	wind direction
Characteristics of Mean vectors							direction
v [°]=	282	279	297	284		287	162
s.d. [°]=	51.5	47.0	57.6	49.6		51.2	41
n =	68	24	31	78		262	37
r =	0.6	0.7	0.5	0.6		0.6	0.7
P (of r)	<0.001	<0.001	<0.005	<0.001		<0.001	<0.01

Tab.A.4.2. Mean vectors of dispersal in relation to days after release, based on recapture of marked *A. pomorum* in orchard B in spring 1997; v = mean angle of displacement, s.d.= standard angular deviation, n = recapture number, r = length of main vector as a measure of concentration at $P<0.05$, Rayleigh-test.

Orchard B 1997						
Days	10	20	30	50	Σ	Mean
Date	10.-20.3.	21.-30.3.	31.3.-10.4.	21.-30.4.	10.3.-30.4.	wind direction
Characteristics of Mean vectors						direction
v [°]=	154	142	134	183	148	163
s.d. [°]=	39	37	43	47	41.4	41
n =	98	16	54	6	174	37
r =	0.8	0.8	0.7	0.7	0.7	0.7
P (of r)	<0.001	<0.05	<0.001		<0.001	<0.01

Tab.A.4.3. Average distances of dispersal by *A. pomorum* into the apple orchards in spring 1996 & 1997.

Orchards	A (Hoengg)	A (Hoengg)	B (Niederwil)	Average
Year	1996	1997	1997	
Mean distance	20.1 m	14.4 m	16 m	17 m
s.d.	12.1 m	12.5 m	13.3 m	12.8 m

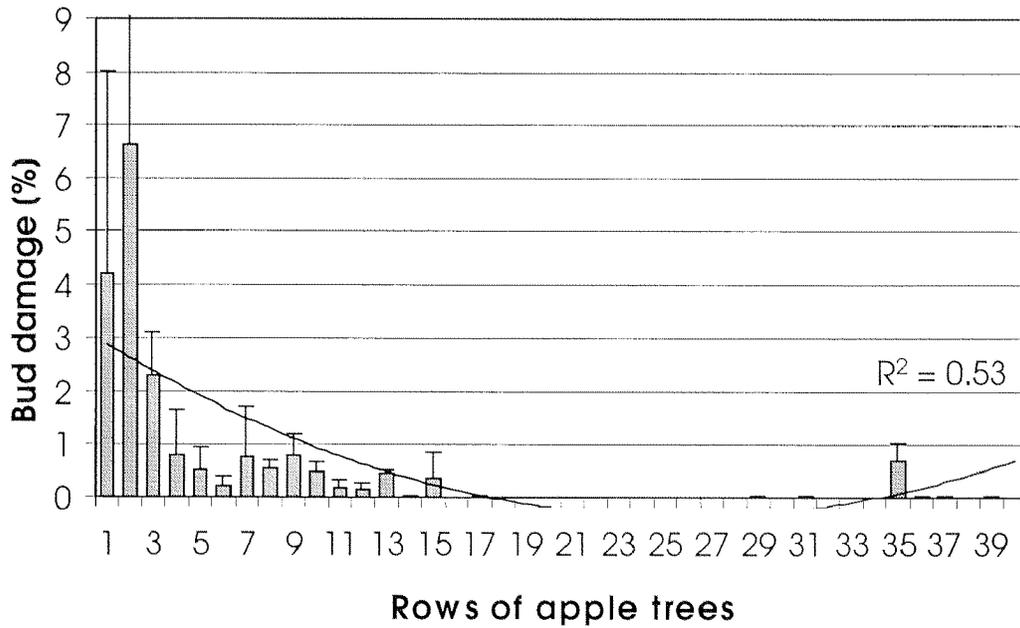


Fig.A.4.4. Percentage of damaged blossom buds (y) per row (x) by *A. pomorum* in apple orchard A in spring 1996 and 1997. Rows were parallel to forest's border, row 1 near forest.

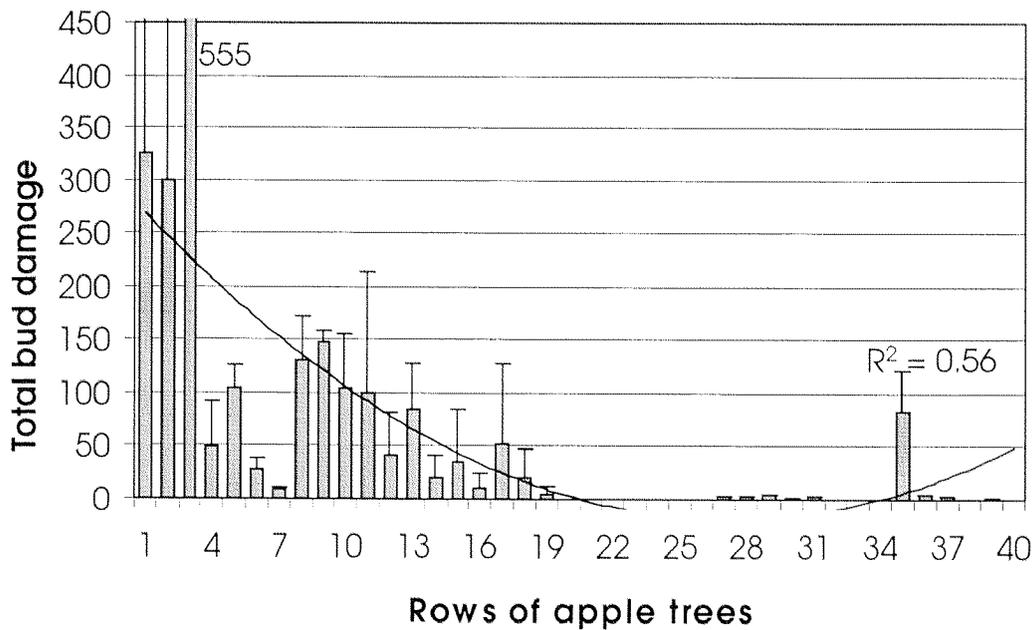


Fig.A.4.5. Total damage on blossom buds (y) per row (x) by *A. pomorum* in apple orchard A in spring 1996 and 1997. Rows were parallel to forest's border, row 1 near forest.

Tab.A.5.1. Begin of colonisation of apple orchards by *Anthonomus pomorum* in relation to ambient temperature [°C] in height of 1.5 m within orchards. Orchard A in Hoengg ZH, B in Niederwil AG, C in Baar ZG in northern Switzerland. (data 1994/95 after B. Hirs, unpubl.)

A Start of dispersal into orchard																					
Place	Year	Date	Day	Threshold daily temperature			DD 1.January				DD 1.February				DD 1.March						
				Mean	Max	Min	>0 °C	>5 °C	>6° C	n	>0 °C	>5 °C	n	>6° C	>0 °C	n	>5 °C	>6° C	n		
C	1994	7.3.	67																		
C	1995	11.3.	71	6.0	17.0	-1.5									{24}	10	{1}	{1}	{1}	{1}	
A	1996	23.3.	83	{11}	18.0	4.5									62	16	16	7	10	6	
A	1997	4.3.	64	8.5	14.0	5.0															
B	1997	4.3.	64	8.5	14.0	5.0	125	31	20	10	122	31	13	20	10	33	4	13	4	9	4
B	1998	17.3.	77	6.0	11.5	1.0	178	22	11	4	130	18	10	11	4	70	15	16	7	10	3
A	1999	14.3.	74	9.5	16.0	5.0	184	38	25	12	121	34	10	24	9	88	14	{33}	9	{24}	9
B	1999	14.3.	74	8.0	15.0	0.5	156	24	10	11	93	19	10	10	8	69	14	19	9	10	8
Min.		4.3.	64	6	12	-2	125	22	10	4	93	18	10	10	4	33	4	13	4	9	3
Max.		23.3.	83	10	18	5	184	38	25	12	130	34	13	24	10	88	16	19	9	10	9
Mean		12.3.	72	8	15	3	161	29	17	9	117	25	11	16	8	64	12	16	7	10	6
s.d.			7	1	2	3	27	7	7	4	16	8	2	7	3	20	4	2	2	1	3
n			7	6	7	7	4	4	4	4	4	4	4	4	4	5	6	4	5	4	5

B Full start of colonisation & highest speed of dispersal																					
Place	Year	Date	Day	Threshold daily temperature			DD 1.January				DD 1.February				DD 1.March						
				Mean	Max	Min	>0 °C	>5 °C	>6° C	n	>0 °C	>5 °C	n	>6° C	>0 °C	n	>5 °C	>6° C	n		
C	1994	9.3.	69																		
C	1995	24.3.	84	8.5	17.5	0.0										80	23	{11}	{5}	11	5
A	1996	7.4.	98	11.0	18.0	3.0										135	31	43	12	36	11
A	1997	15.3.	75	8.0	3.0	3.5															
B	1997	14.3.	74	8.2	12.0	5.5	181	40	24	14	178	40	22	24	14	89	14	22	10	14	8
B	1998	28.3.	88	10.3	21.0	11	215	28	17	6	167	26	13	17	6	107	23	24	10	16	5
A	1999	25.3.	85	10.5	16.0	5.0	242	54	37	16	179	50	15	36	13	147	25	49	14	36	13
B	1999	25.3.	85	8.5	14.5	3.0	201	33	16	14	139	28	14	15	11	115	25	27	13	15	11
Min.		9.3.	69	8	3	0	181	28	16	6	139	26	13	15	6	80	14	22	10	11	5
Max.		7.4.	98	11	21	11	242	54	37	16	179	50	22	36	14	147	31	49	14	36	13
Mean		24.3.	84	9	15	4	210	39	24	13	166	36	16	23	11	112	24	33	12	21	9
s.d.			8	1	6	3	26	11	10	4	19	11	4	9	4	26	6	12	2	11	3
n			7	7	7	7	4	4	4	4	4	4	4	4	4	6	6	5	5	6	6

C Interruption of dispersal						
Place	Year	Date	Day	Threshold daily		
				temperature		
				Mean	Max	Min
C	1994					
C	1995					
A	1996	30.3.	90	1.5	5.0	-2.0
A	1997	24.3.	84	3.7	7.5	-1.0
B	1997					
B	1998	25.3.	85	1.5	11.0	-7.0
A	1999	7.3.	67	2.0	6.5	-2.0
B	1999					
Max.				4	11	-1
Mean				2	8	-3
s.d.				1	3	3
n				4	4	4

D First captured weevils							
Place	Year	Date	Day	Threshold daily			Days before start
				temperature			
				Mean	Max	Min	
C	1994						
C	1995	21.2.	52	7	16	1	-52
A	1996	20.3.	80	7	14	-2	-80
A	1997						
B	1997						
B	1998	17.2.	48	5	9	-1	-48
A	1999	2.3.	62	9	14	5	-62
B	1999	10.3.	70	7	9	4	-70
Min.		17.2.	48	5	9	-2	-80
Max.		20.3.	80	9	16	5	-48
Mean		2.3.	62	7	12	1	-62
s.d.			13	1	3	3	13
n			5	5	5	5	5

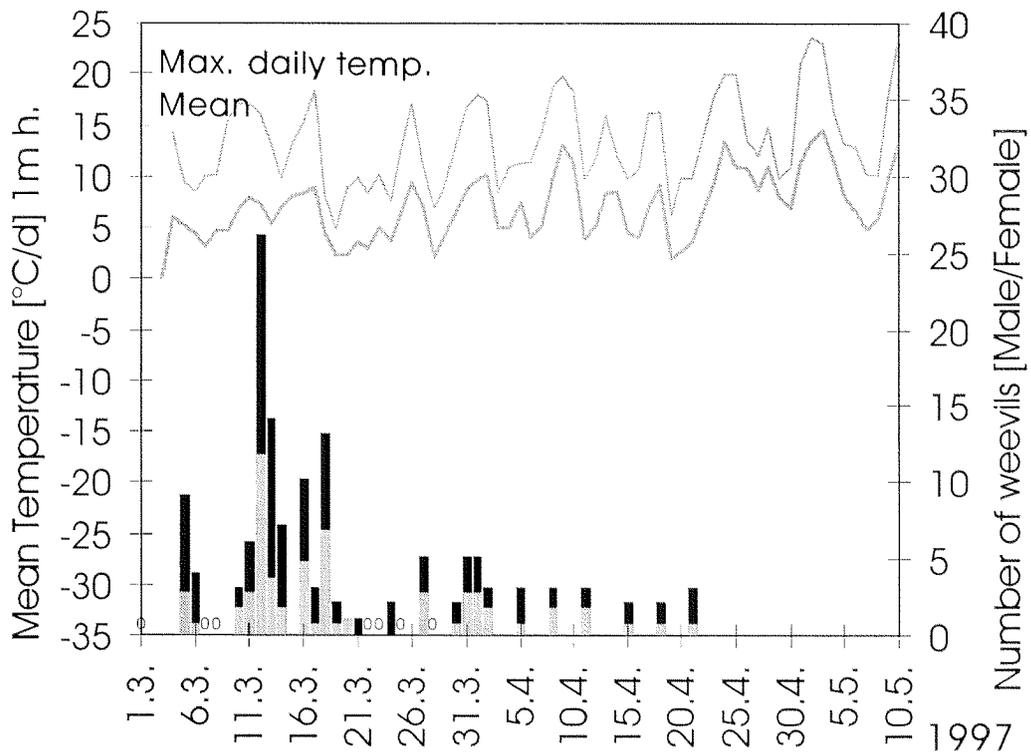


Fig.A.5.1. Emergence of hibernating *A. pomorum* (y_2) from leaf litter on ground in early spring 1997 and temperature conditions (y_1), Zuerich, CH. Grey bars are males, black are females.

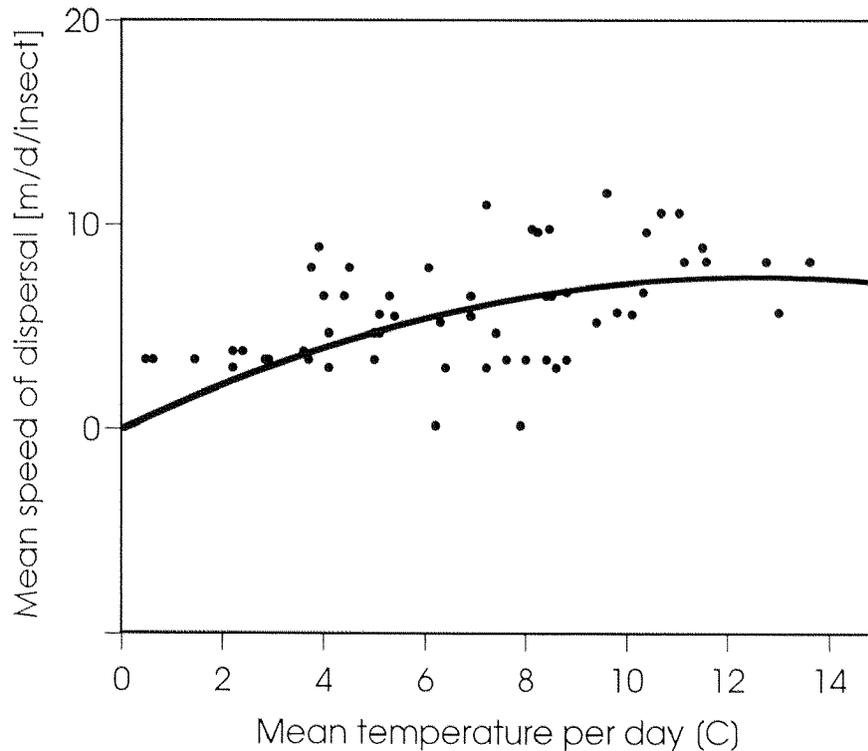


Fig.A.5.2. Relation of mean dispersal speed (y) of *Anthonomus pomorum* and mean daily air temperature (x) in spring 1996 & 1997 ($n=58$, polynomial regression, $y = -0.04x^2 + 1.18x$, $R^2 = 0.23$, $P = 0.00$)

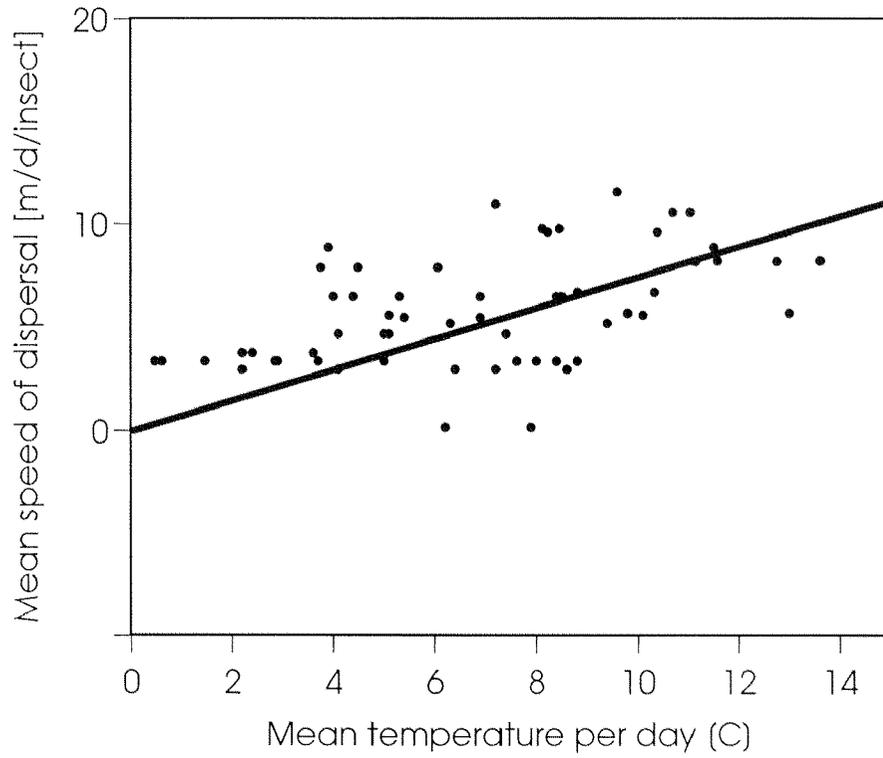


Fig.A.5.3. Relation of mean dispersal speed (y) of *Anthonomus pomorum* and mean daily air temperature (x) in spring 1996 & 1997 ($n=58$, $y= 2.8+0.4x$, $R^2 = 0.56$, $P= 0.00$)

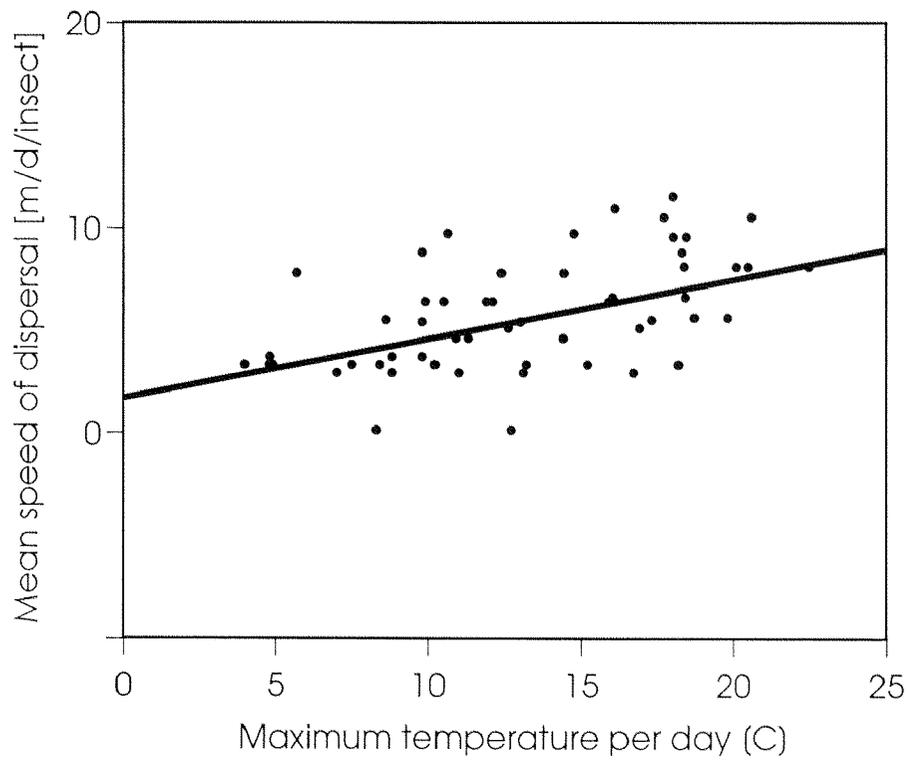


Fig.A.5.4. Relation of mean dispersal speed (y) of *Anthonomus pomorum* and maximum daily temperature (x) in spring 1996 & 1997 ($n=58$, $y= 1.7+0.3x$, $R^2 = 0.56$, $P= 0.00$)

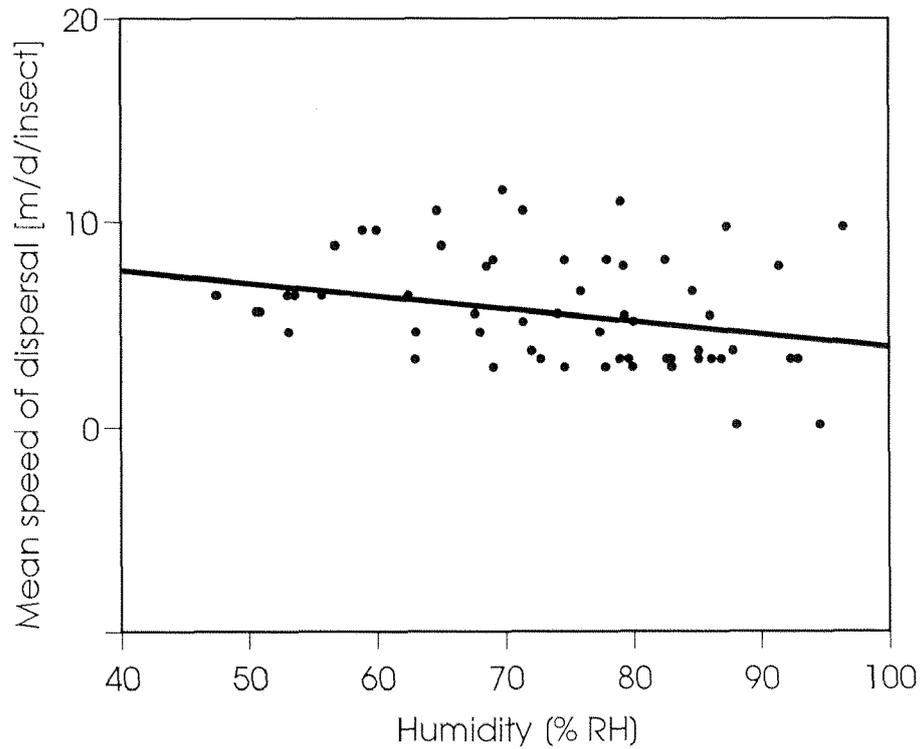


Fig.A.5.5. Relation of mean dispersal speed (y) of *Anthonomus pomorum* and daily air humidity (x) in spring 1996 & 1997 ($n=58$, $y= 10.1-0.06x$, $R^2 = 0.47$, $P= 0.024$)

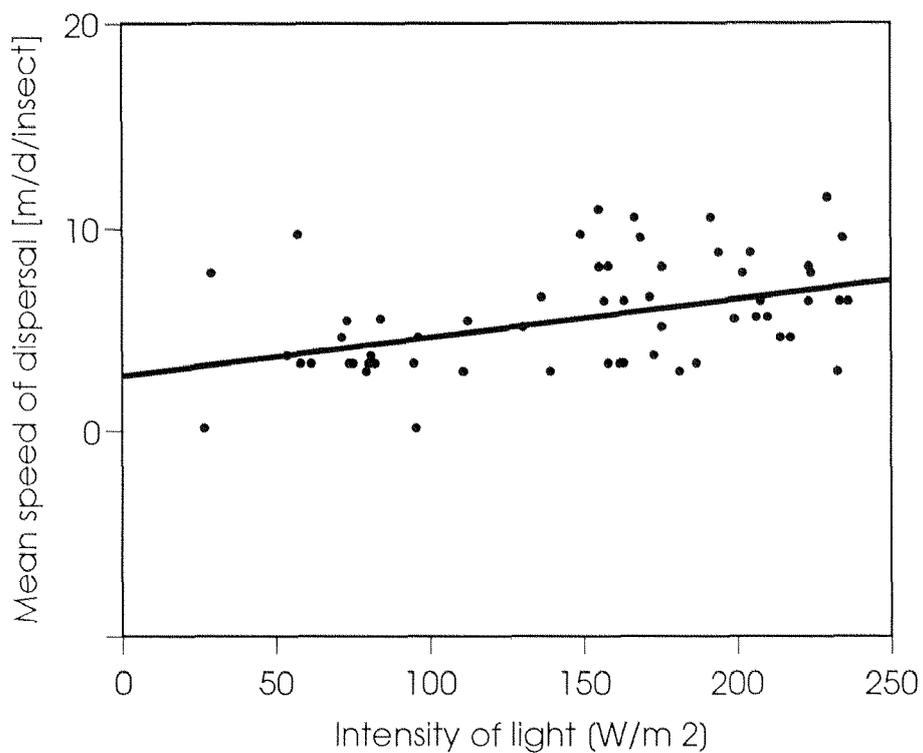


Fig.A.5.6. Relation of mean dispersal speed (y) of *Anthonomus pomorum* and intensity of daily light (x) in spring 1996 & 1997 ($n=58$, $y= 2.7+00.2x$, $R^2 = 0.51$, $P= 0.01$)

Tab.A.5.2. Multiple regression analysis of dispersal speed and correlated climatic factors (n= 22; multiple Pearson correlation coefficient = 0.62, squared multiple $R^2 = 0.38$, adjusted multiple $R = 0.278$, standard error of estimate = 0.746; a,b= Regression coefficients (a constant); T= t-test-value at $P < 0.05$; F= F-ratio of F-test)

VARIABLE	COEF	STD ERROR	STD COEF	TOLER	T	P(2 TAIL)
CONSTANT	7.18	10.19	0.00	0.00	0.705	0.490
Air humidity	-0.05	0.10	-0.17	0.309	0.526	0.605
Mean temp./d	0.33	0.18	0.40	0.707	1.828	0.084
Intensity of light	0.007	0.018	0.14	0.269	0.405	0.690

ANALYSIS OF VARIANCE					
SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	83.544	3	27.848	3.692	0.031
RESIDUAL	135.774	18	7.543		

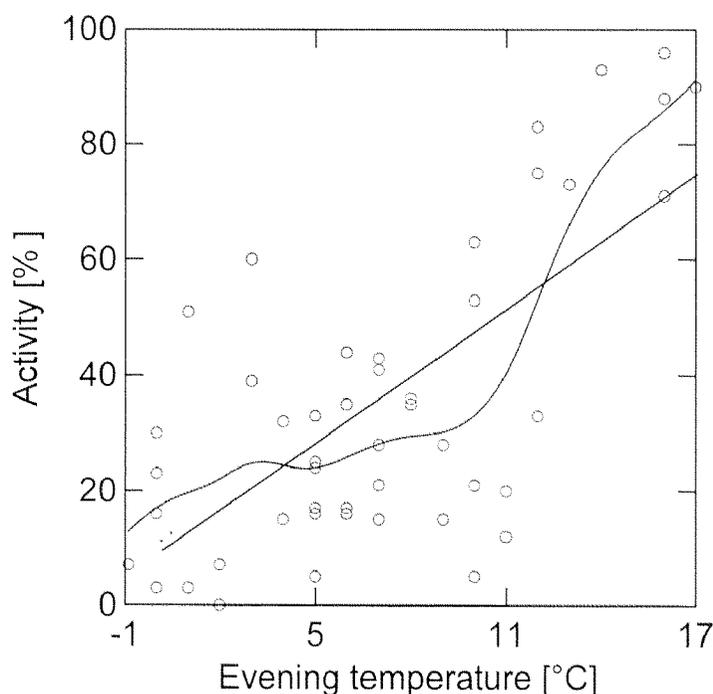


Fig.A.5.7. Regression lines of activity of *Anthonomus pomorum* (y) in relation to evening temperature (x) two hours after sunset (regression DWLS-model with 0.5 tension and linear regression $y = 3.7x + 11$)

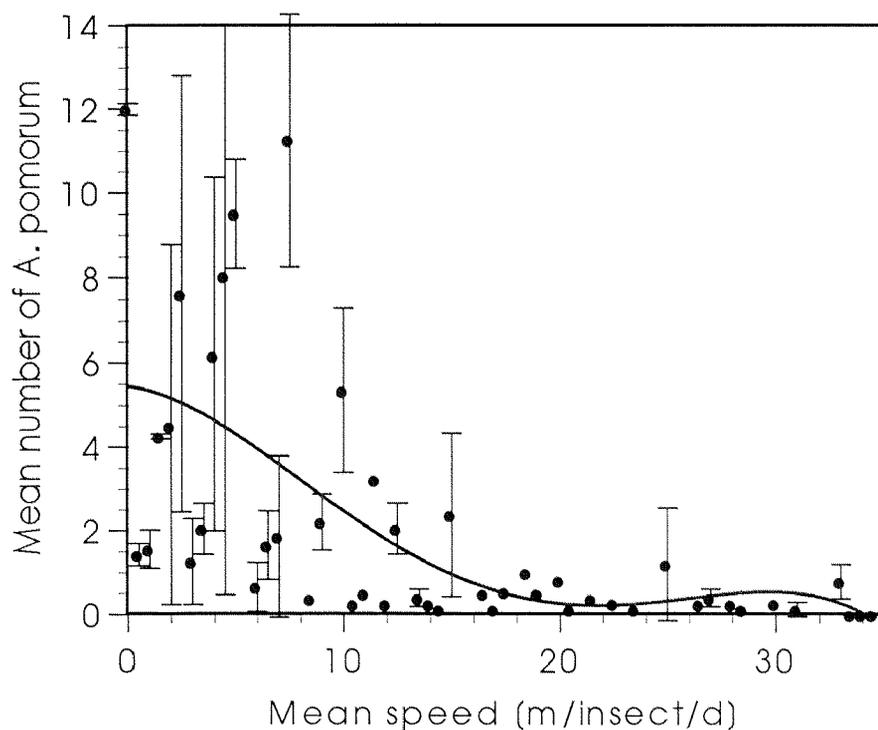


Fig.A.5.8. Mean speed (y) of dispersing *Anthonomus pomorum* (y) from release point near the adjacent forest in orchard A in spring 1996 and 1997. Polynomial regression $R^2=0.5$.

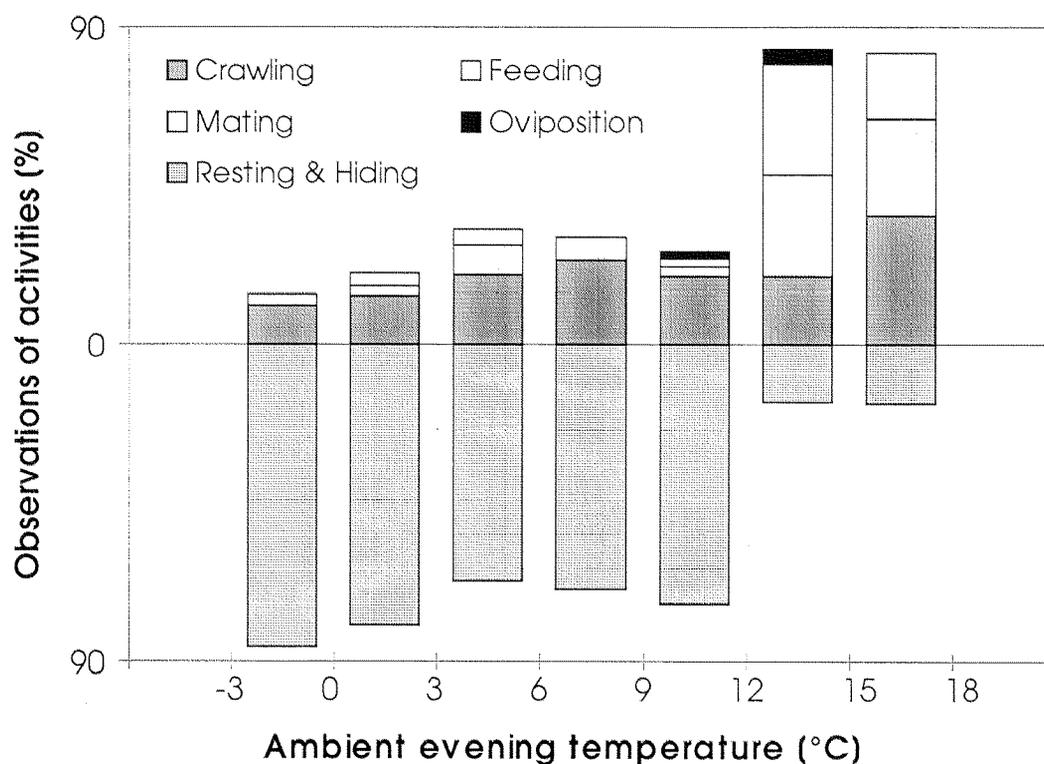


Fig.A.5.9. Behavioural patterns of overwintered *Anthonomus pomorum* (y) in relation to ambient evening temperature (x) under field conditions two hours after sunset in spring (n=25)

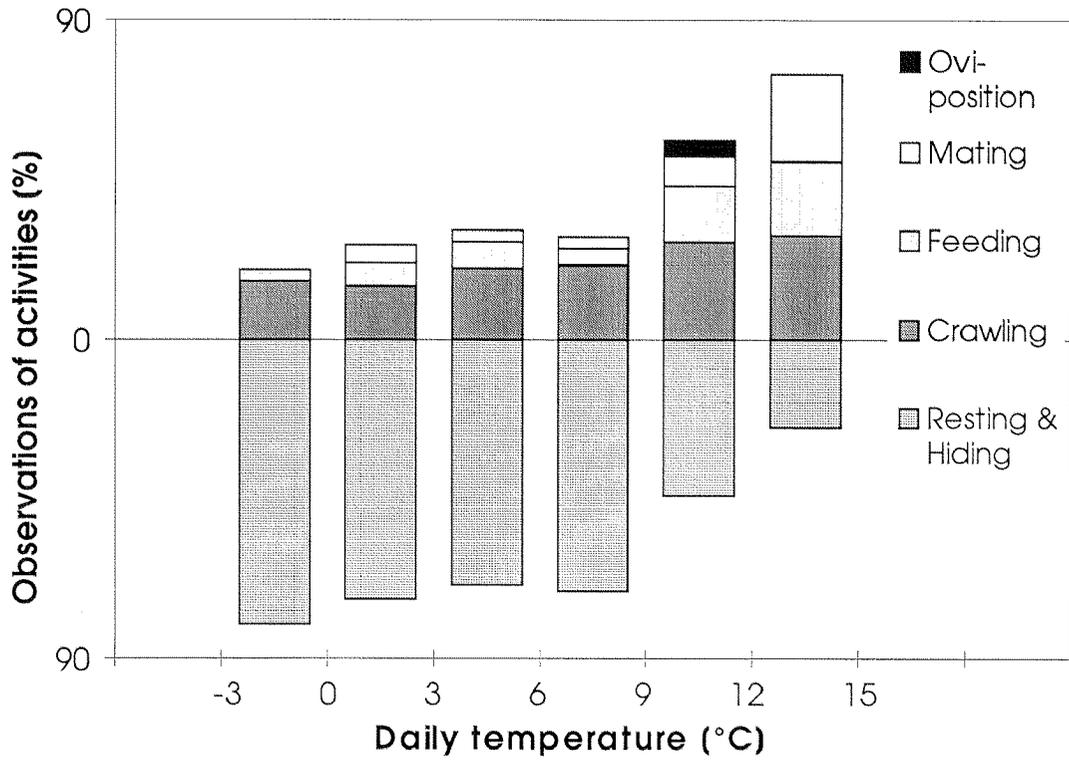


Fig.A.5.10. Behavioural patterns (y) of overwintered *Anthonomus pomorum* in relation to mean daily temperature (y) under field conditions two hours after sunset in spring (n=25)

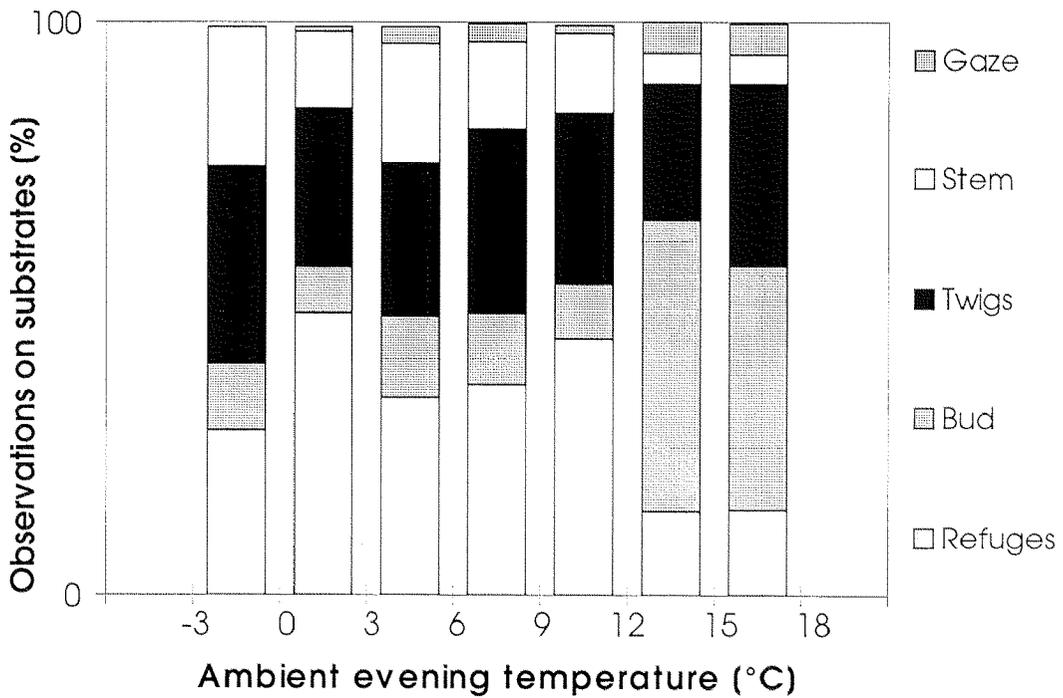


Fig.A.5.11. Occupation of microhabitats (y) by overwintered *Anthonomus pomorum* in relation to ambient evening temperature (x) under field conditions two hours after sunset in spring (<2% of weevils in ground and foliage)

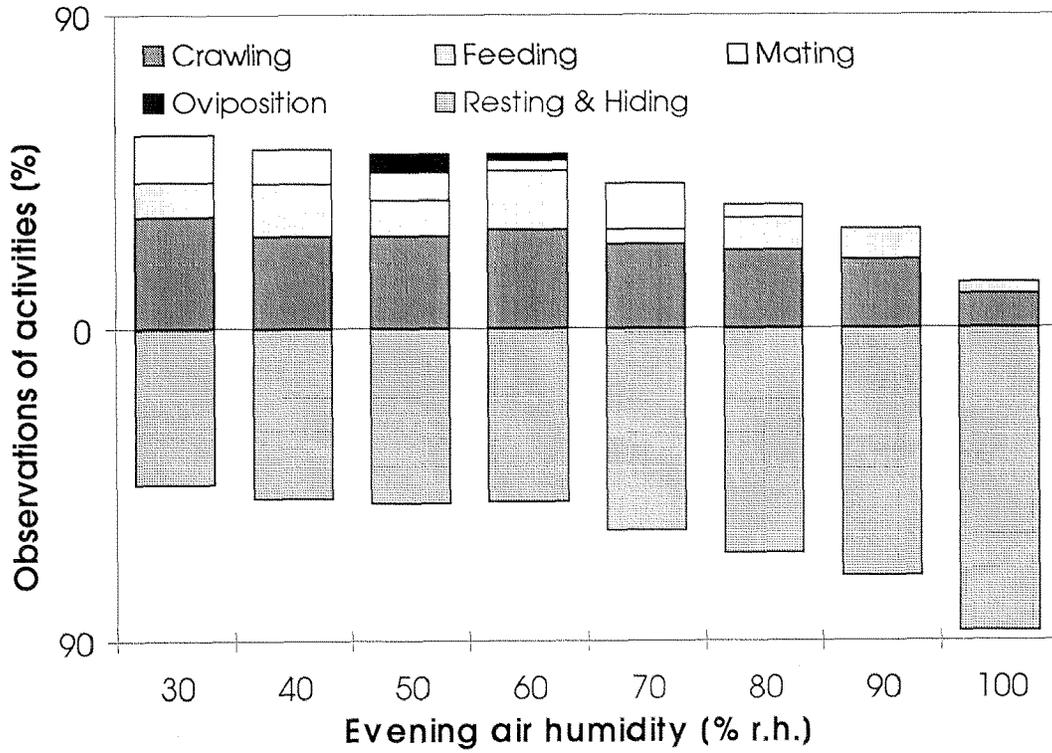


Fig.A.5.12. Behavioural patterns (y) of overwintered *Anthonomus pomorum* in relation to evening air humidity (x) under field conditions two hours after sunset (n=25)

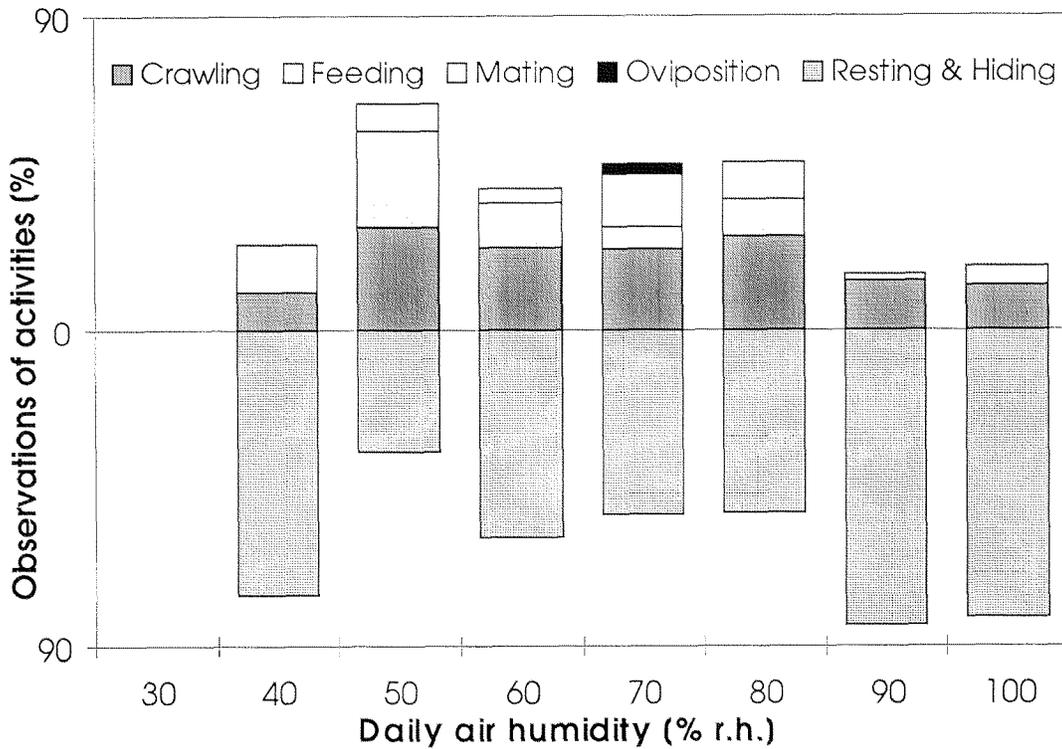


Fig.A.5.13. Behavioural patterns (y) of overwintered *Anthonomus pomorum* in relation to mean daily air humidity (x) under field conditions (n=25)

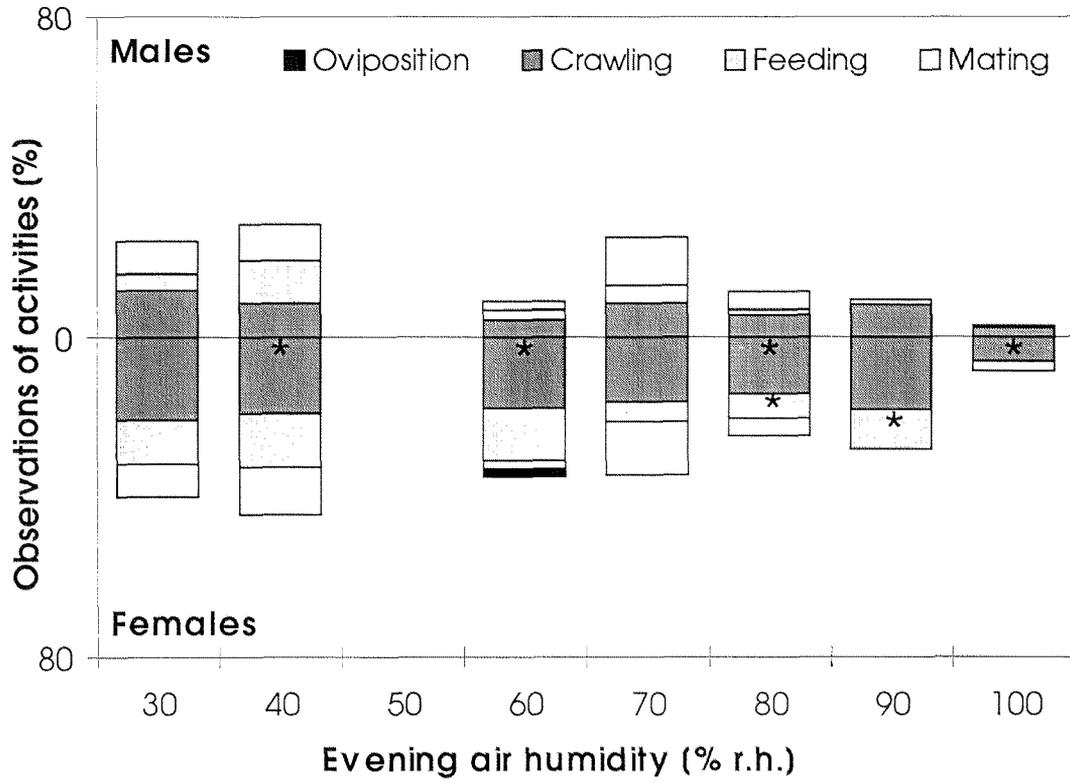


Fig.A.5.14. Behavioural patterns of overwintered male and female *Anthonomus pomorum* in relation to evening air humidity in the field in spring (n=25, M.-Whitney-signed-rank-test, P<0.05)

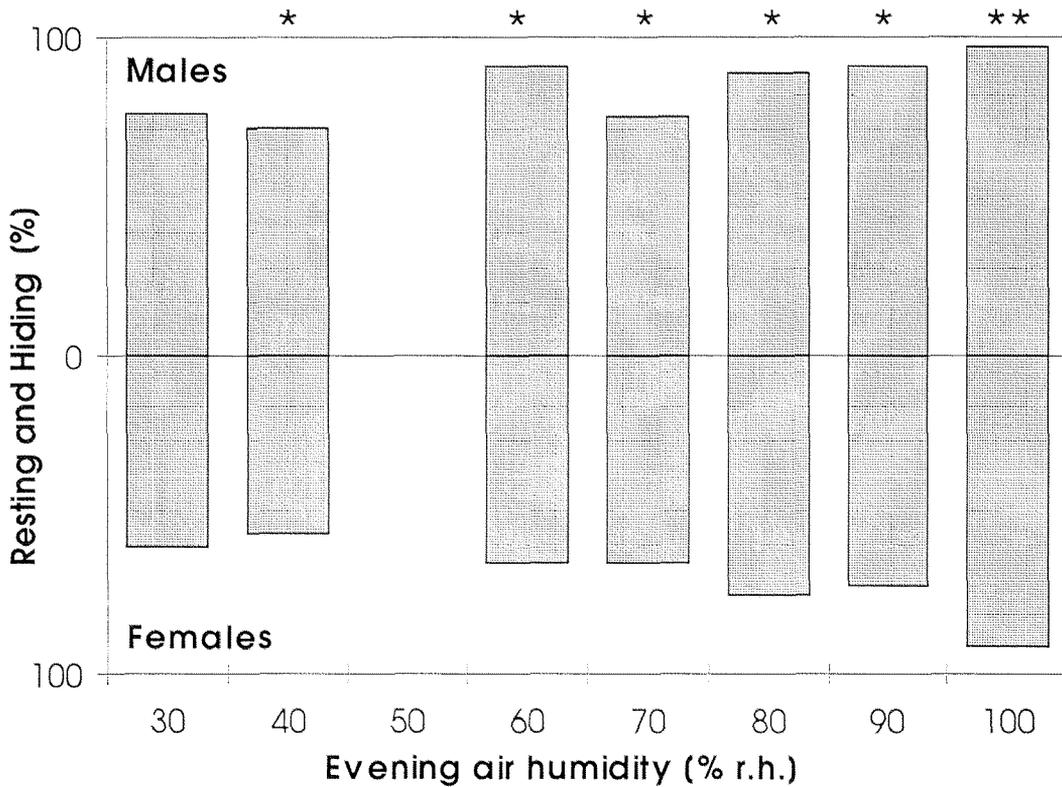


Fig.A.5.15. Resting and hiding of overwintered male and female *A. pomorum* in relation to evening air humidity in the field two hours after sunset (n=25, M.-Whitney-signed-rank, P<0.05)

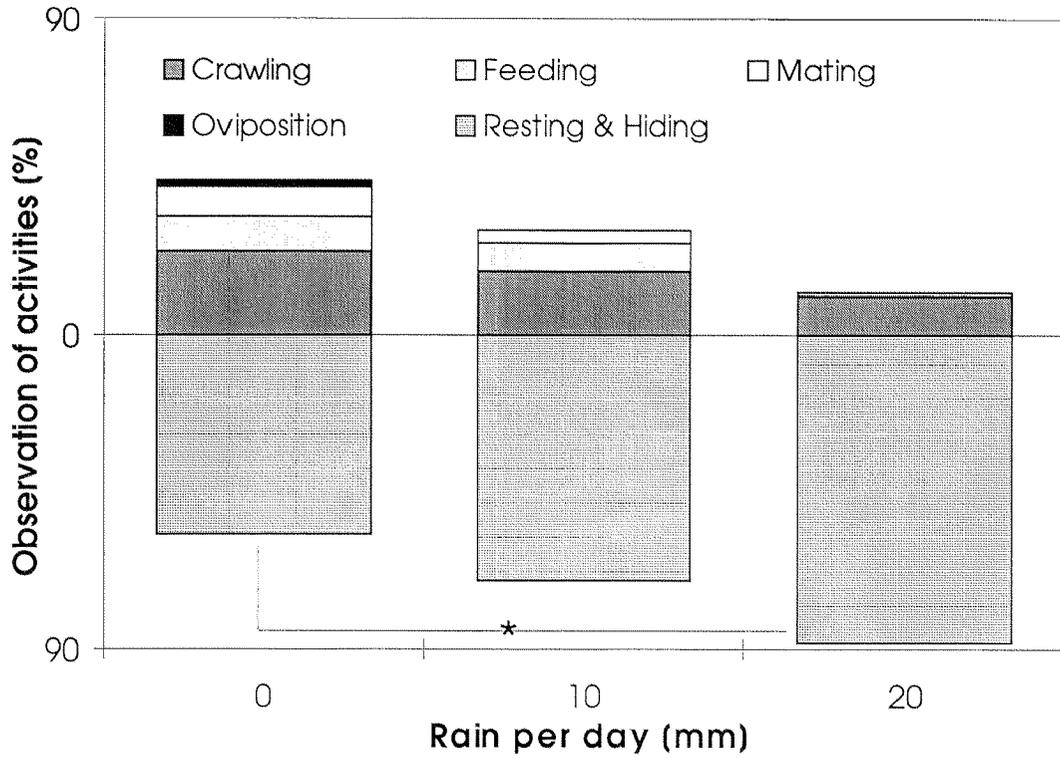


Fig.A.5.16. Behavioural patterns (y) of overwintered male and female *Anthonomus pomorum* in relation to mean daily rainfall (x) in the field in spring (n=25, Mann-Whitney-U-Test at P<0.05)

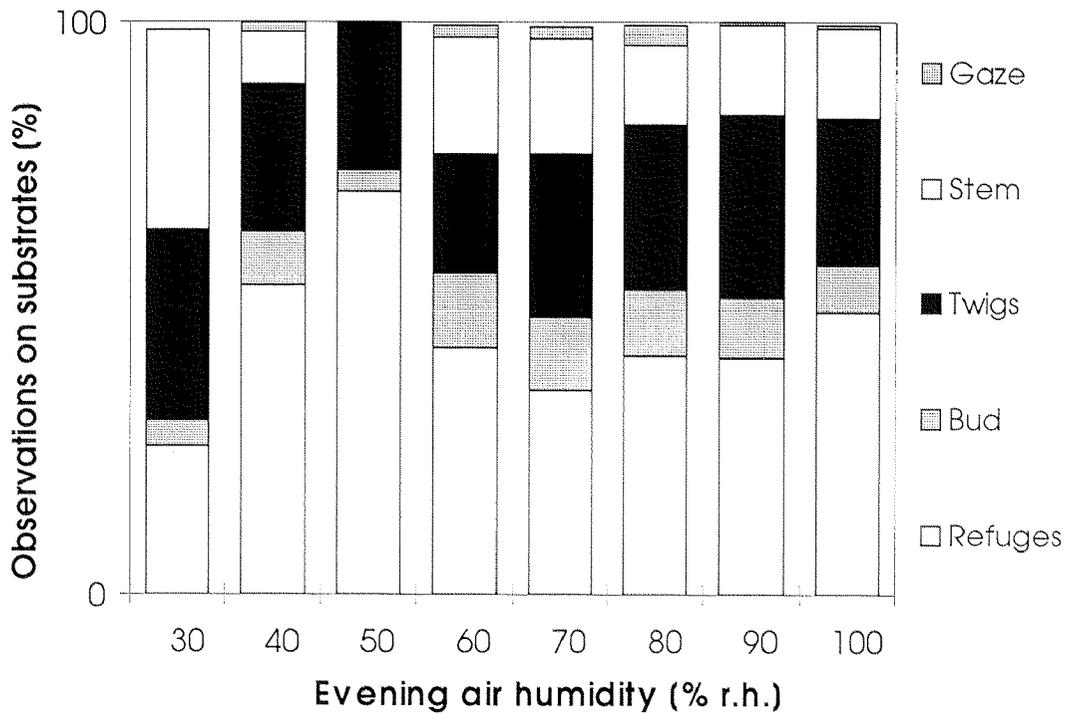


Fig.A.5.17. Occupation of microhabitats (y) by overwintered *Anthonomus pomorum* in relation to evening air humidity (x) under field conditions two hours after sunset in spring (<2% of weevils in ground and foliage)

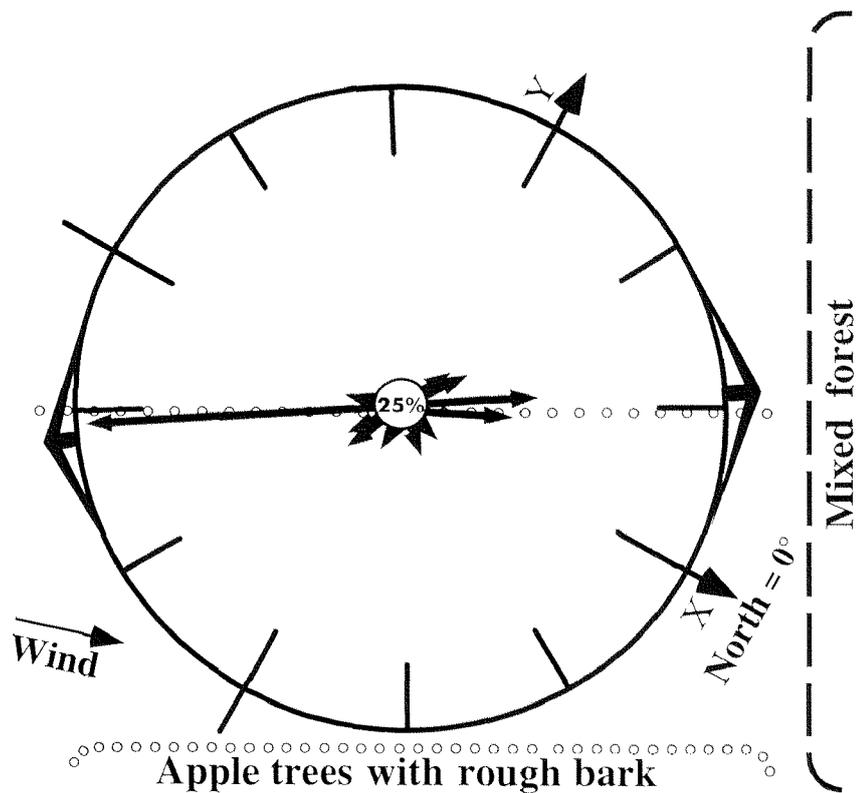


Fig.A.6.1 Direction of dispersal of marked *A. pomorum* from release point in the **area of smooth bark trees** of orchard B in autumn 1996 ($n=377$). Orientation of weevils mainly along the apple tree rows (°°°°Dotted line in the circle is the direction of tree rows). 25% stayed at the tree of release. Arrows represent a resultant vector of orientation according to a number of moving weevils in an interval of 15° . Length of resultant vectors with $R = n \cdot r$ (mean vectors length). Arrows on the outline of the circle show the two mean angles of the mean axis of bimodal dispersal ($\varphi_1 = 323 \pm 21^\circ$, $\varphi_2 = 143 \pm 21^\circ$). The mean angle of the whole data is $286 \pm 41^\circ$ with a length of $r_{\text{all}} = 0.74$, indicating a high level of concentration of dispersing weevils at $P < 0.005$, Rayleigh-test).

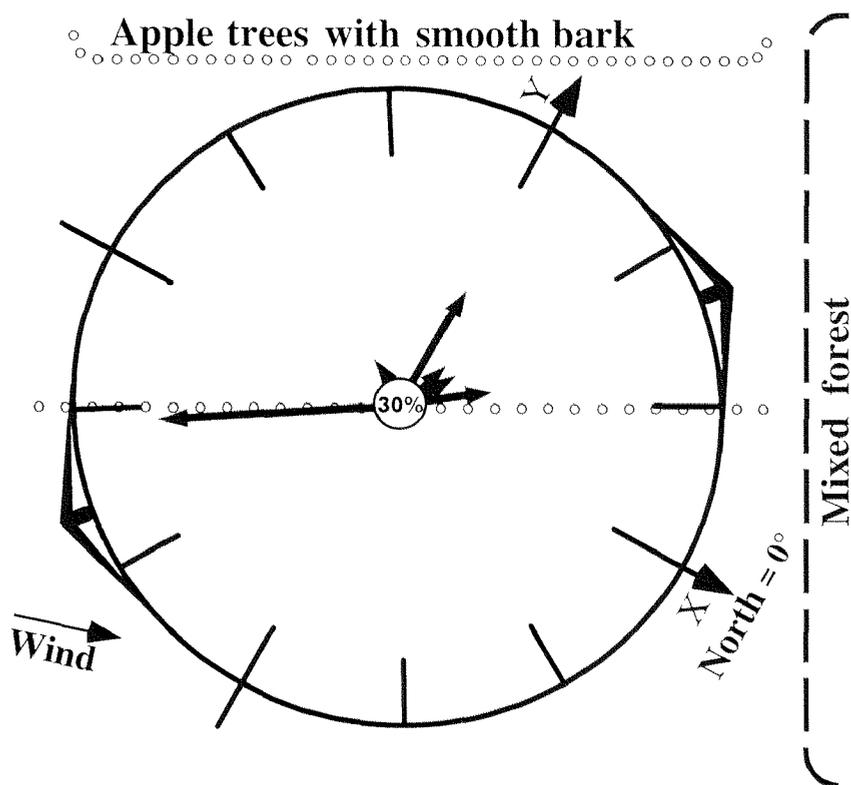


Fig.A.6.2 Direction of dispersal of marked *A. pomorum* from release point in the **area of rough bark trees** of orchard B in autumn **1996** ($n=167$). Orientation of weevils mainly along the apple tree rows (°°°Dotted line in the circle is the direction of tree rows). 30% stayed at the tree of release. Arrows represent a resultant vector of orientation according to a number of moving weevils in an interval of 15° . Length of resultant vectors with $R= n \cdot r$ (mean vectors length). Arrows on the outline of the circle show the two mean angles of the mean axis of bimodal dispersal ($\varphi_1= 312 \pm 25^\circ$, $\varphi_2= 132 \pm 25^\circ$). The mean angle of the whole data is $286 \pm 41^\circ$ with a length of $r_{all}= 0.61$, indicating a medium level of concentration of dispersing weevils at $P < 0.005$, Rayleigh-test).

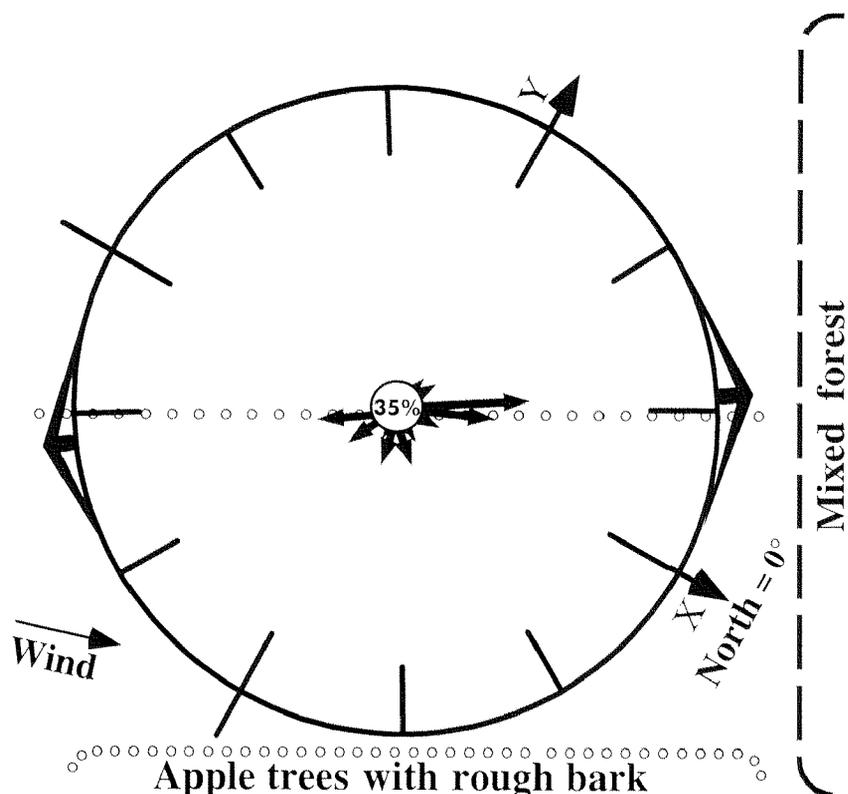


Fig.A.6.3 Direction of dispersal of marked *A. pomorum* from release point in the **area of smooth bark trees** of orchard B in summer and autumn 1997 ($n=82$). Orientation of weevils mainly along the tree rows, to the adjacent forest and to the apple trees with rough bark. 35% stayed at the tree of release. Arrows represent a resultant vector of orientation according to a number of moving weevils in an interval of 15° . Length of resultant vectors with $R= n \cdot r$ (mean vectors length). Arrows on the outline of the circle show the two mean angles of the mean axis of a bimodal dispersal ($\varphi_1= 325 \pm 28^\circ$, $\varphi_2= 145 \pm 28^\circ$). The mean angle of the whole data is $290 \pm 55^\circ$ with a length of $r_{\text{all}}= 0.54$, indicating a low level of concentration of dispersing weevils at $P < 0.005$, Rayleigh-test). °°°Dotted line in the circle is the direction of tree rows.

Tab.A.6.1 Differences between numbers of hibernating weevils in substrates of a simulated apple orchard with rough bark trees and an adjacent forest. (Chapt.6.4 Fig.4, $n=6$ with 6×30 weevils, conditions: 70%RF, L:D 8:16, 0° - 15° , Fisher's LSD test at $P < 0.05$)

	Smooth Bark	Rough Bark	Litter of Leaves	Soil
Grass	0.026*	0.005*	0.000**	0.42
Smooth Bark		0.000**	0.000**	0.119
Rough Bark			0.000**	0.001**
Litter of Leaves				0.000**

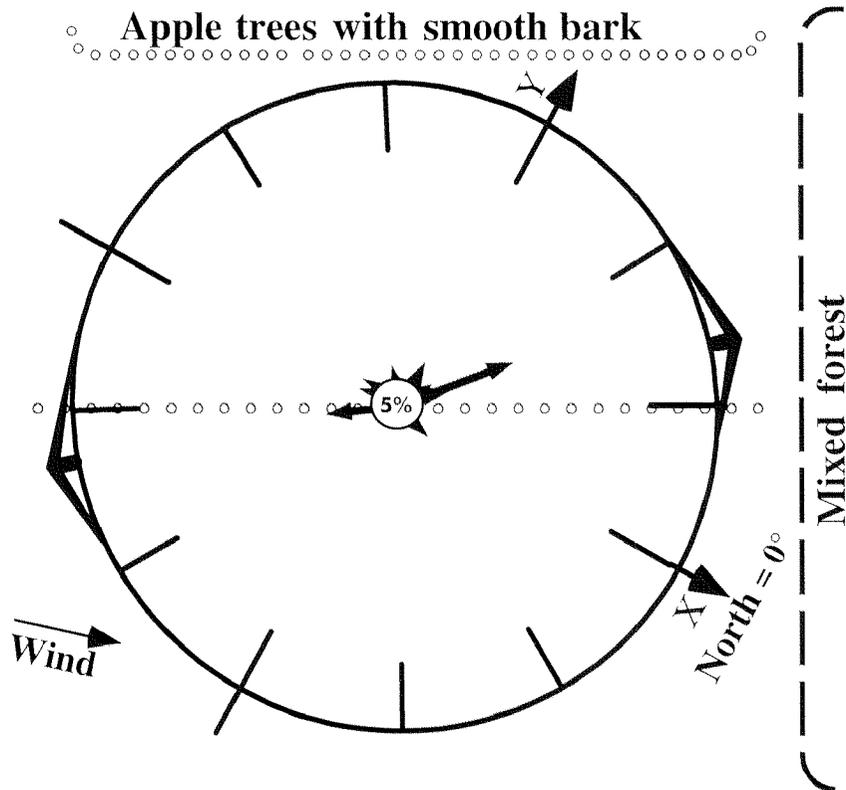


Fig.A.6.4 Directions of dispersal of marked *A. pomorum* from release point in the **area of rough bark trees** of orchard B in summer and autumn **1997** ($n=27$). The data pool is limited but shows a slight preferred orientation of weevils along the tree rows, and to the adjacent forest. 5% stayed at the tree of release. Arrows represent a resultant vector of orientation according to a number of moving weevils in an interval of 15° . Length of resultant vectors with $R = n \cdot r$ (mean vectors length). Arrows on the outline of the circle show the two mean angles of the mean axis of bimodal dispersal ($\varphi_1 = 322 \pm 25^\circ$, $\varphi_2 = 142 \pm 25^\circ$). The mean angle of the whole data is $284 \pm 50^\circ$ with a length of $r_{\text{all}} = 0.62$, indicating a medium level of concentration of dispersing weevils at $P < 0.005$, Rayleigh-test). °°°Dotted line in the circle is the direction of tree rows.
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Tab.A.6.2 Differences between numbers of hibernating weevils in substrates of a simulated modern apple orchard with dwarf smooth bark trees. (Fig.A.6.5, $n=6$ with 6×30 weevils, conditions: 70%RF, L:D 8:16, 0° - 15° , Fisher's LSD test at $P < 0.05$)

	Smooth Bark	Litter of Leaves	Soil
Grass	1.00	0.000**	0.147
Smooth Bark		0.000**	0.147
Litter of Leaves			0.000**

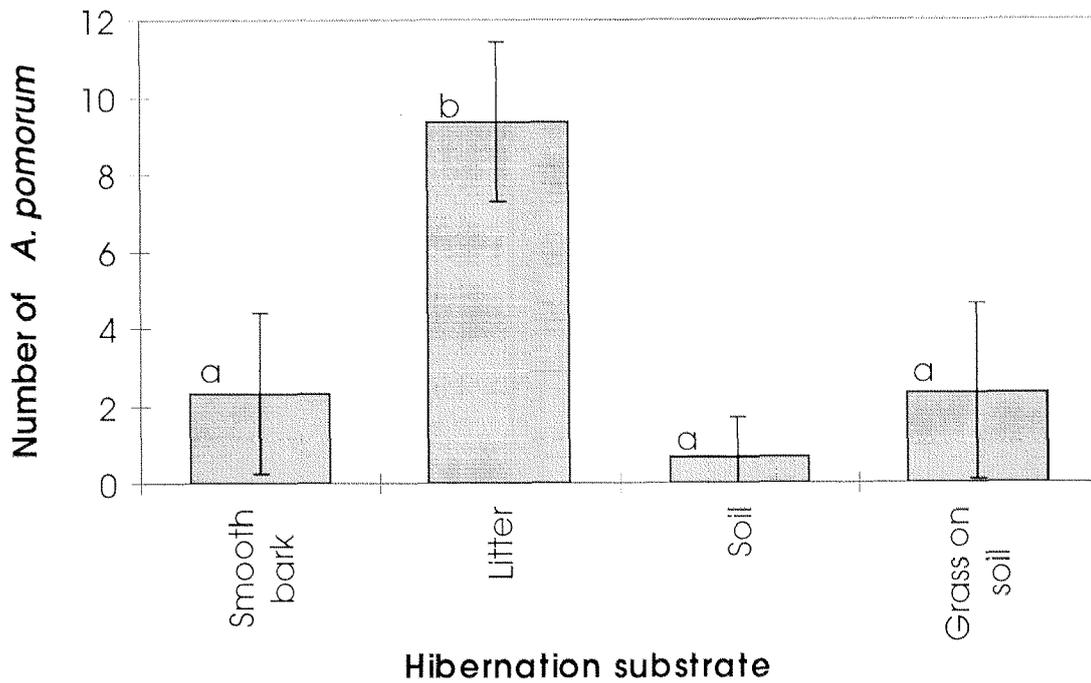


Fig.A.6.5 Hibernation of *Anthonomus pomorum* (y) in different substrates (x) of a simulated orchard without rough bark and without adjacent forest. Litter of leaves has highest importance for the hibernation of *A. pomorum*. (n=6 with 6x30 weevils, conditions: 70%RF, L:D 8:16, 0°-15°, Fisher's LSD test at P< 0.05))

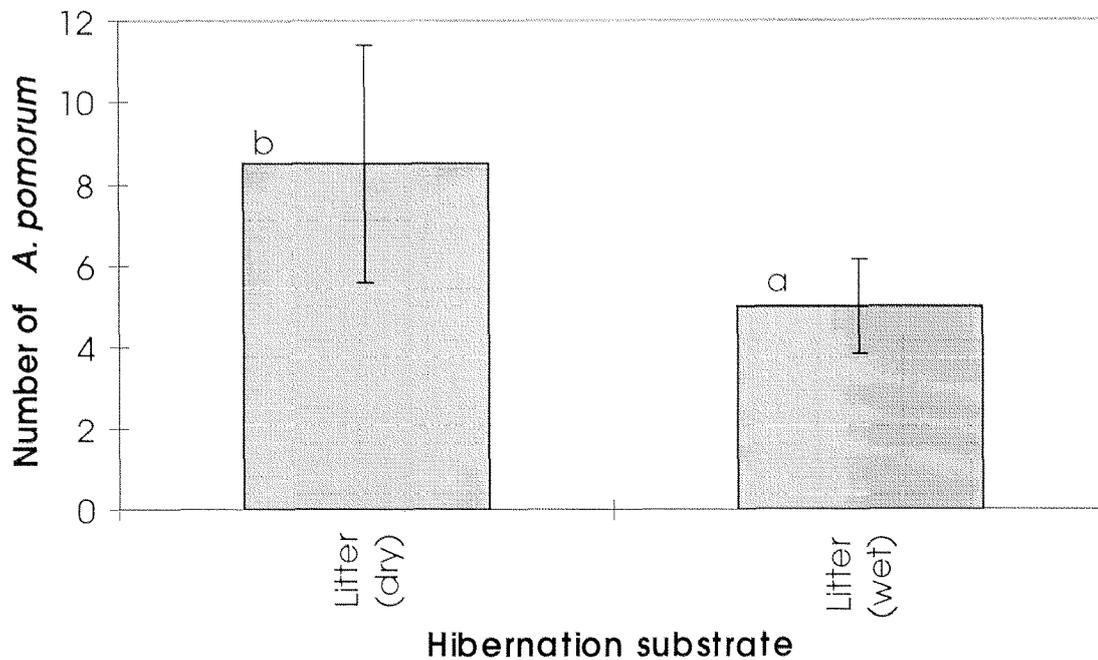


Fig.A.6.6 Hibernating *Anthonomus pomorum* (y) in dry and wet litter of leaves (x), (n=6 with 6x30 weevils, conditions: 70%RF, L:D 8:16, 0°-15°, Wilcoxon-Signed-Rank-test at P<0.05)

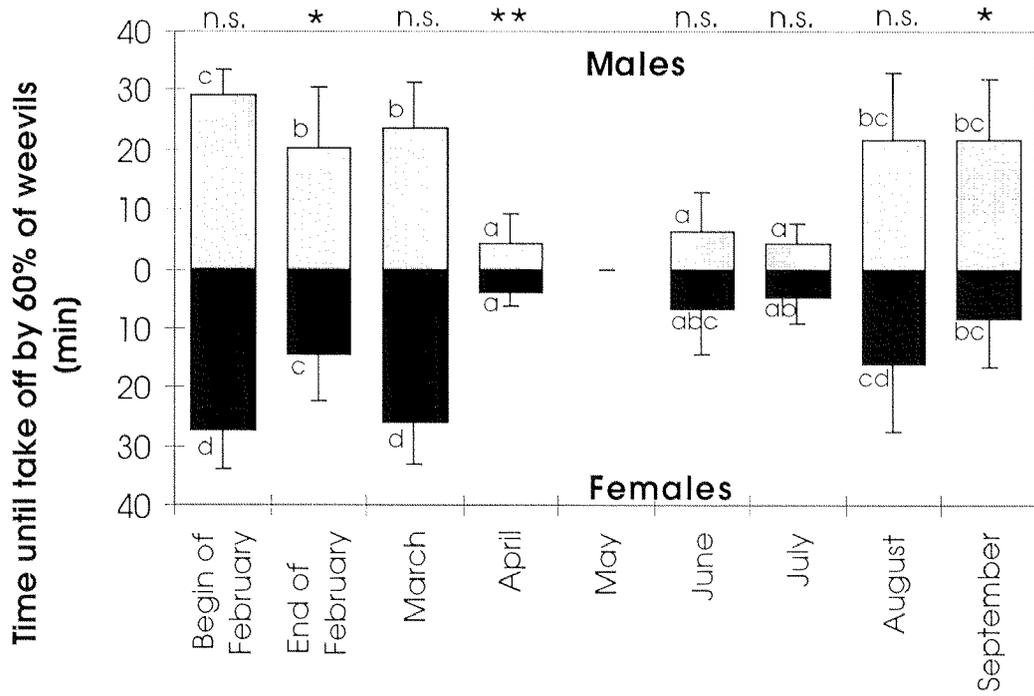


Fig.A.6.7 Seasonal fly proclivity of *A. pomorum* [time until 60% of weevils took off] in fly-stands (n=4x11 males & females, in afternoon, daylight 4,000 lux, spring 19°C, summer 23°C). Begin of February termination of diapause, from June on new generation. Kruskal-Wallis multiple comparison between months (letters on bars), M.-Whitney-U-test between males and females (letters on top) at P<0.05.

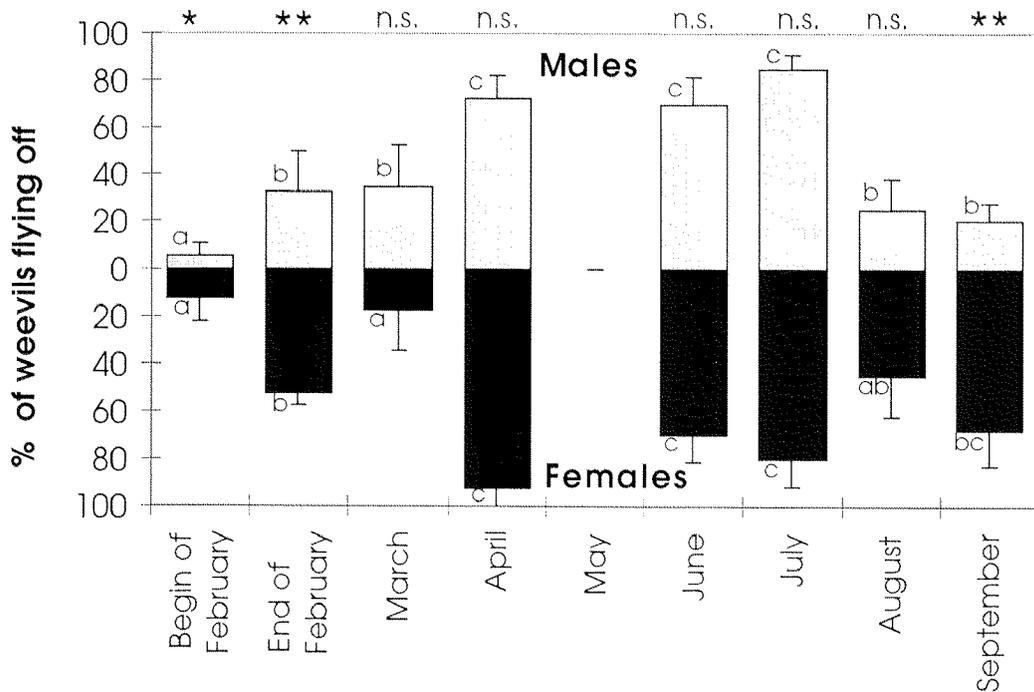


Fig.A.6.8 Seasonal fly take off response of *A. pomorum* [percentage of weevils flying off] in fly-stands (n=4x11 males & females, in afternoon, daylight 4000 lux, spring 19°C, summer 23°C). Begin of February termination of diapause, from June on new generation. Kruskal-Wallis multiple comparison between months (letters on bars), M.-Whitney-U-test between males and females (letters on top) at P<0.05.

Tab.A.7.1. Different gonad development stages of the telotrophic ovary with 4 ovarioles of *Anthonomus pomorum*. After Ctvrticka and Zdarek (1992), B. Hirs (unpubl.).

Code	Gonad stage
A (1)	Ovarioles short, undifferentiated and entirely transparent or already a visible border between tropharium and region of formation of follicle (vittellarium)
B (2)	Starting pre-vitellogenesis, first start of egg growing (2-3 small but indistinct proximal oocytes), nuclei visible, no visible cell wall
C (2)	>4 pre-vitellogenetical oocytes, growing of eggs without nutriment inside, empty small cell with small lumen
D (3)	Increasing volume and number of oocytes, visible epithelium of follicle, big transparent lumen
E (4)	Starting vitellogenesis (production of dotter), nuclei still visible. Large number of eggs still undersized
F (5)	More nutriment and increasing of volume of cell, no nuclei visible. Terminated egg of full size
G (6)	Termination of vitellogenese, growing of chorion, very large eggs. A few eggs descended to calyx
H (7)	Weevils ready to oviposite, eggs in calyx and oviduct
J (8)	Calyx and oviduct are empty, vittellarium is larger than germarium

Tab.A.7.2. Growth stages of blossom buds of *Malus domestica* (scale after Fleckinger, 1948, BBCH numbers after Anonymous, 1992)

Code	Bud growth stage	BBCH-Scale
A	Closed bud, hibernation	00
B	Little silver greenish tip	52
C	Half inch green tip	53
C3	Mouse ear stage	54
D	Tight cluster of green bud	55
E	Pink bud	57
E2	Balloon stage	59
F	Pink, start of blooming	61
F2	Blooming	65
G	Last blooming period	67
H	Finish blooming, petal fall	69
J	June drop	73

Tab.A.7.3. Differences in feeding behaviour between male and female *Anthonomus pomorum* on buds of different growth stage in the field in Zürich, CH, in 1998 (t-test at *P<0.05)

Sex	Feeding behaviour [%] on buds of growth stages					
	A	B	C	C3	D	E
Males	0.4 ±0.9	1.0 ±2	3.2 ±3.3	1.1 ±2.4	2.3 ±4	9.2 ±12
Females	6.9 ±8.9	14 ±18.9	5.3 ±3.4	6.3 ±9.6	4.2 ±4.7	11 ±16.6
P < 0.05	*	*		*		

Tab.A.7.4. Feeding damage by *Anthonomus pomorum* on apple buds of different growth stage in multiple choice tests in laboratory (var. Boskoop, n= 12 pairs of weevils, damage is expressed as feeding holes).

Multiple choice experiment in laboratory 1996					
Exposure time first 10d					
Bud stage	A	B	C3	D	E(F)
Ø of damage	0.0	3.0	6.4		23.4
SD	0.0	5.3	5.9		10.5

Multiple choice experiment in laboratory 1997										
Bud stage	Exposure time first 10d					Exposure time second 10d				
	A	B	C3	D	E(F)	A	B	C3	D	E(F)
Ø of damage	4.2	6.5	23.0	23.0	56.0	1.0	3.8	9.5	45.0	83.0
s.d.	4.0	9.0	11.0	18.0	37.0	3.0	3.5	10.0	29.0	42.0

Tab.A.7.5. Differences between feeding damage by *Anthonomus pomorum* on different bud growth stages in multiple choice tests with P-values of Fisher's LSD (var. Boskoop, n= 15)

Blossom bud stages (first ten days):		Blossom bud stages (after 20 days):	
A vs.B:	0.5	A vs.B:	0.009
A vs.C3:	0.00	A vs.C3:	0.00
A vs.D:	0.00	A vs.D:	0.00
A vs.E(F):	0.00	A vs.E(F):	0.00
B vs.C3:	0.00	B vs.C3:	0.08
B vs.E(F):	0.00	B vs.E(F):	0.00
B vs.D:	0.002	B vs.D:	0.00
C3 vs.D:	0.59	C3 vs.D:	0.001
E(F) vs.C3:	0.09	E(F) vs.C3:	0.00
E(F) vs.D:	0.039	E(F) vs.D:	0.12

Tab.A.7.6. Feeding damage by *Anthonomus pomorum* on buds of different varieties of growth stage C3(54) in triple choice tests. Test always between 3 varieties with n= 12 pairs of weevils, ANOVA and multiple comparison by Fisher's LSD test at *P<0.05. Damage is expressed as feeding holes on 5 buds per variety, exposure time 10 d, LD 12:12, 80 % r.h., L 17°C, D 12°C,

Variety	Gold. Del.	Jona- gold	Idared	Gold. Del.	Ida- red	Gala
Fisher's LSD	Gold. Del.	1		Gold. Del.	1	
P<0.05	Jonagold	0.32	1	Idared	0.75	1
	Idared	0.61	0.18	1	Gala	0.55
						0.36
						1
Variety	Mai- gold	Gala	Glo- ster69	Jona- gold	Mai- gold	Glo- ster69
Fisher's LSD	Maigold	1		Jonagold	1	
P<0.05	Gala	0.00	1	Maigold	0.41	1
	Gloster 69	0.00	0.70	1	Gloster 69	0.02
						0.10
						1

Tab.A.7.7. Different groups of developmental speed of varieties in early spring (after Friedrich, 1993; Kellerhals, 1997).

Development of blossom buds	Varieties of <i>Malus domestica</i>
Early blooming	Alkmene, Boskoop, Gravensteiner, Idared, Summered
Accelerated	Arlet, Boskoop, Cox Orange, Idared, Maigold, Primerouge, Retina, Visla Bella
Medium	Glockenapfel
Retarded	Golden Delicious, Florina, Gloster, James Grieve, Jonathan, Jonagold, Gala, Rubinette, Spartan
Late varieties	Berlepsch, Gloster 69

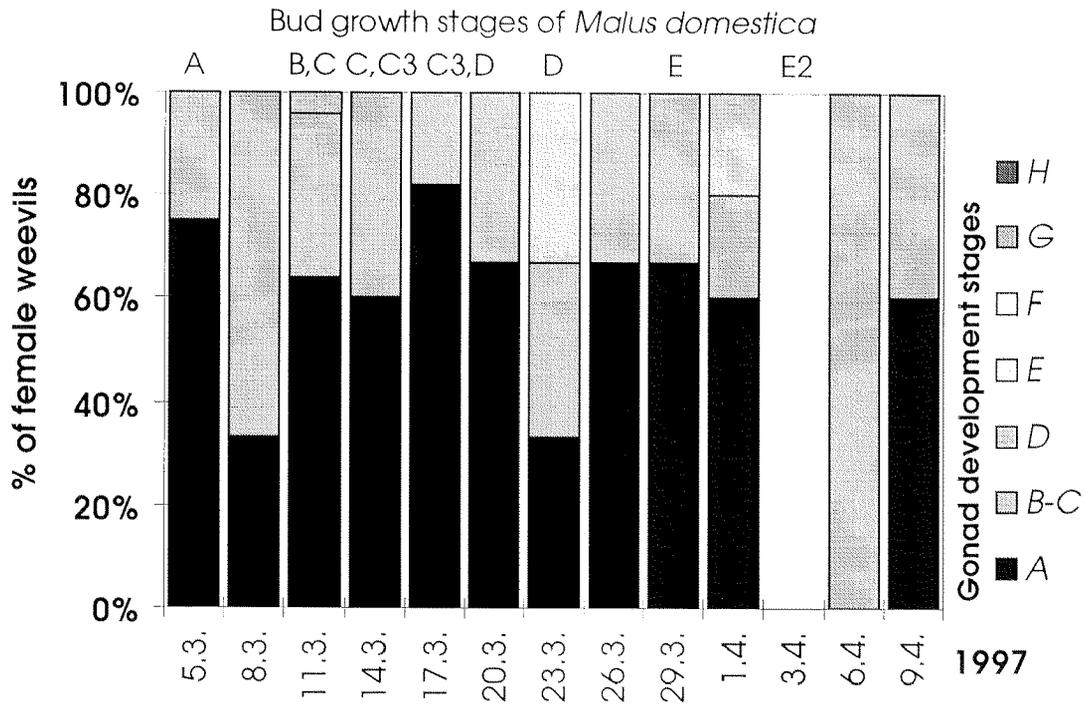


Fig.A.7.1. Gonad development of *Anthonomus pomorum*, which just emerged from overwintering substrate of leaf litter in spring 1997 (each date n= 15, April 3 no data, most developed ovarioles of gonads of individuals were recorded, gonad stage H= ready to oviposit)

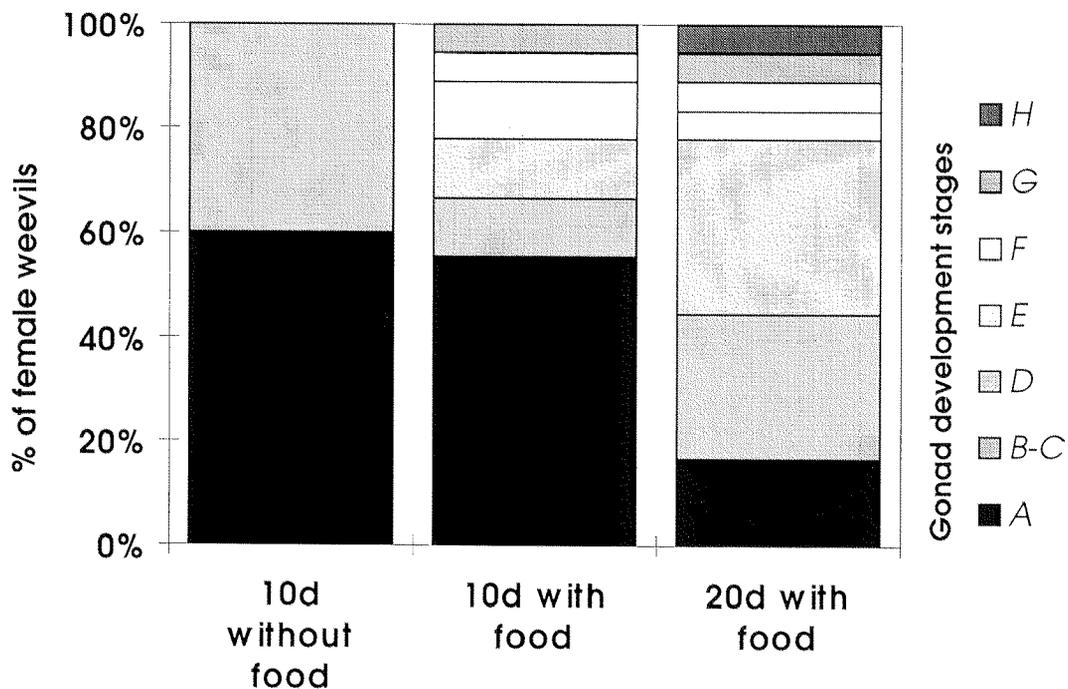


Fig.A.7.2. Gonad development of *Anthonomus pomorum* under different food regime (n= 20, 90% died, weevils just stopped diapause, LD 12:12, L 17°C, D 12°C, 80% RH, L 3500 lux, gonad stage H= ready to oviposit)

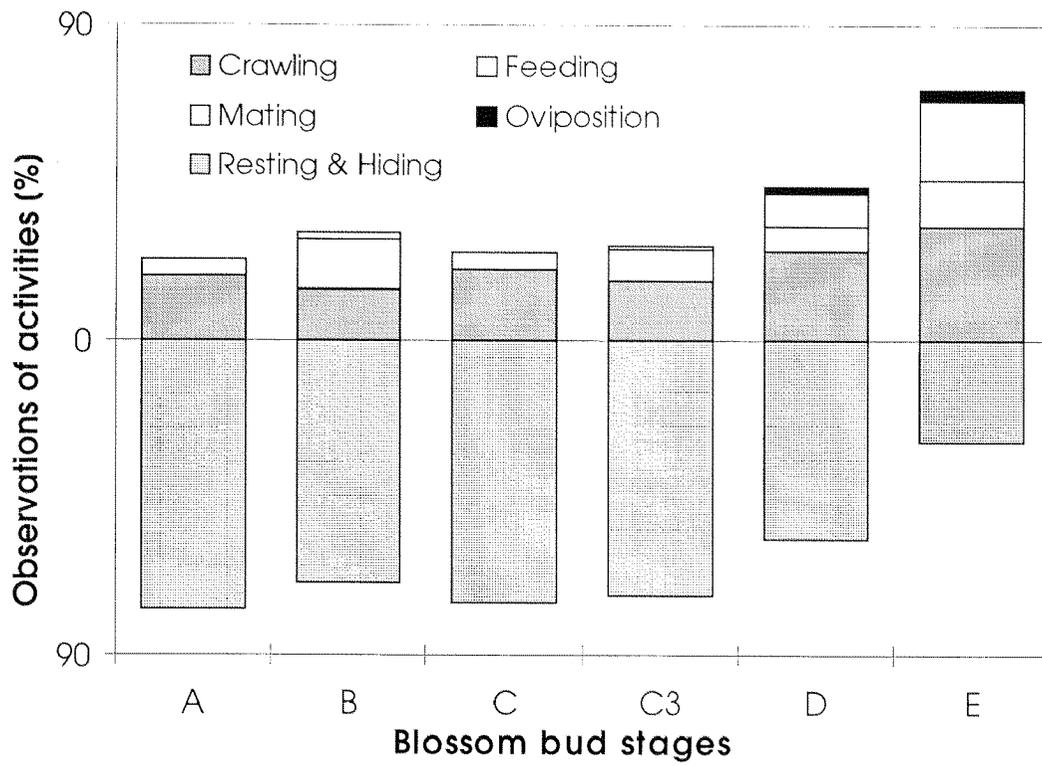


Fig.A.7.3. Crepuscular behaviour (y) of *Anthonomus pomorum* on the apple tree two hours after sunset and the blossom bud stages (x), (n= 25, bud stages after Fleckinger, 1948)

CURICULUM VITAE

Personal

Name	Stefan Töpfer
Birthday	22.04.1970
Place of birth	Berlin (German Democratic Republic)

Education

9/1984 - 8/1988	Extended secondary school with advanced language education
9/1990 - 2/1996	University of Halle-Wittenberg. Diploma degree in Biology. Specialisation: animal ecology, geobotany, microbiology and analytical chemistry
5/1993 - 9/1993	Semester work: The Aleutian Tern <i>Sterna aleutica</i> in the Kronotzky State Reserve on Kamtchatka (Russia)
1995	Diploma thesis in "Relations between landscape structure and avicoenosis in an agricultural area in the north of Harz mountains". Examiner: Prof. M.Stubbe, Dr. D.Heidecke at the Institute of Zoology, D-06099 Halle/S
2/1996 - 12/1999	Ph.D. student in Applied Entomology ETH Zürich (Switzerland) Assistant in laboratory courses