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Autor: Baltensweiler, W. / Fischlin, A.

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MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE

52, 259–271, 1979

The rôle of migration for the population dynamics of the larch bud moth, Zeiraphera diniana Gn. (Lep. Tortricidae)^{1,2}

W. Baltensweiler and A. Fischlin Dept. of Entomology, Swiss Federal Institute of Technology, CH-8092 Zürich

The rôle of migration for the population dynamics of the larch bud moth, Zeiraphera diniana GN. (Lep., Tortricidae) – Moth flight of Z. diniana was monitored during the last population cycle by means of pheromone and light traps in an area of approx. 20000 km^2 . The relationship between larval density and male moth catch is quantified by means of the power function $y = ax^b$. It is postulated that long range migration over several 100 km may contribute to the remarkable synchronization of outbreaks along the alpine arch, but that this stochastic form of migration cannot influence the regularity of the cycles. Rather, this regularity appears to stem from regional migration phenomena; i.e. moths immigrate annually by positive anemotactic behaviour from lower altitudes into the upper reagion of alpine mountain valleys. A verbal model of migration is outlined in view of simulation studies in the future.

Population dynamics has to be looked upon in a holistic view. There are no single processes or factors responsible for its outcome, even when we have to deal with the apparently most simple ecological situation: the cyclic population fluctuation. This statement, however, should not divert from careful evaluation of single processes as only their relative impacts defined in time and space provide the necessary base for a general understanding of a species' population dynamics. The recent verbal model of the larch bud moth system (Baltensweiler, 1977) is presented to provide the necessary background for the discussion of the rôle of moth migration and the formulation of a new enlarged model.

The larch bud moth (Zeiraphera diniana Gn., Lep., Tortricidae), is the most serious forest defoliator of the larch stands in the European Alps. Since 1850 it devastated the Engadine area in south-eastern Switzerland 15 times. Its population dynamics has been investigated in details by the Department of Entomology, Swiss Federal Institute of Technology, Zürich, since 1949 throughout the Alps and especially in the Engadine valley. Z. diniana exhibits in the subalpine region between 1700 m and 2000 m a cyclic fluctuation of great regularity and amplitude (Auer, 1977; Baltensweiler, 1978). Larval density increases on the average from 1 to 30000 per larch tree within 4 generations, then defoliation occurs. Outbreaks last 1 to 3 years and occur at intervals of 8.64 ± 0.29 years (5% confidence interval). They may cause economic losses (reduction of larch growth, tree mortality) and are locally detrimental the to recreational use of the forests.

The cyclic fluctuation of the bud moth results from the interaction of the bud moth and its host, the larch tree, within an abiotic environment which in general favours population growth continuously. Defoliation of the larch induces a

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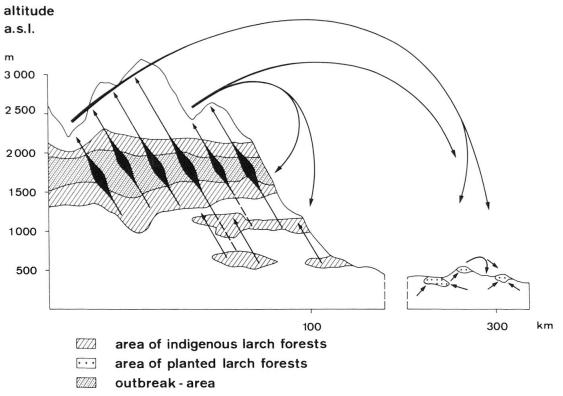


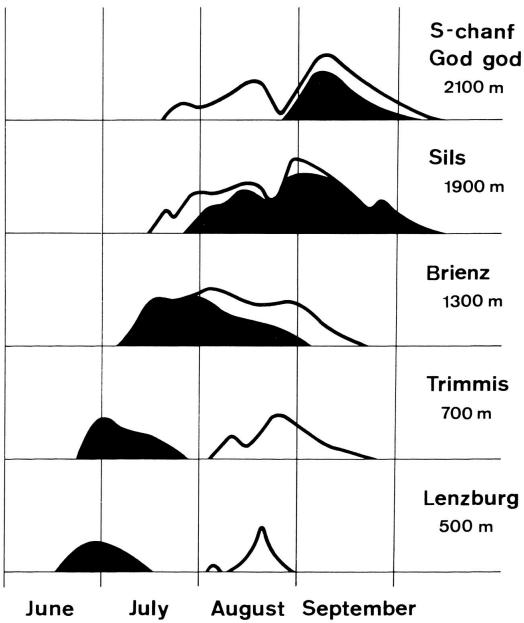
Fig. 1: Migration pattern of Zeiraphera diniana in the European Alps.

deterioration of the food quality and a decrease in food quantity, which in turn causes a decline in population density and selects for a more resistant ecotype. Thus a remarkable resilience is confered to the system by the recovery of the host plant and directional selection processes through their time lags and the fixed carrying capacity of the biotope.

Accounts of migrating masses of larch bud moth are quite frequent (Andrinschev, 1947; Burmann, 1965; Escherich & Bär, 1909; Schabunevitsch, 1967); invariably they are mentioned in relation to outbreaks with their large tracts of defoliated larch stands. Thus they were considered as anecdotal phenomena. Concern about migration arose only when the magnitude of moths which swamped the extensive area of the latent fluctuation type outside the Alps at low altitude was recognized (Graf, 1974; Baltensweiler & von Salis, 1975). The probability of influx in anyone area by long range dispersal would depend on the predominant weather pattern and the relative geographic position with respect to the exodus area. Because weather patterns vary with regards to locations rather stochastically the impact of long range dispersal on a specific area is not predictable.

From this it was deduced that long range dispersal may contribute to the conspicuous time sequence of defoliating densities throughout the Alps, but would not determine the regularity of regional cycles. Rather, this regularity of cycles appears to be partly the result of migration on a regional scale. This hypothesis is discussed in the following and supplemented with a verbal model which displays our approach to test this conception.

The following definitions as formulated by Baker (1978) are used throughout this paper. Migration is defined as the act moving from one spatial unit to another. In this context dispersal means to increase the distance between the individual members of a group whereas convergence describes the opposite process.



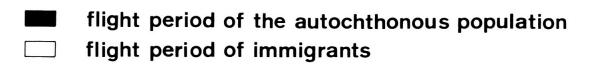


Fig. 2: Flight periods of Zeiraphera diniana at various sites in Switzerland.

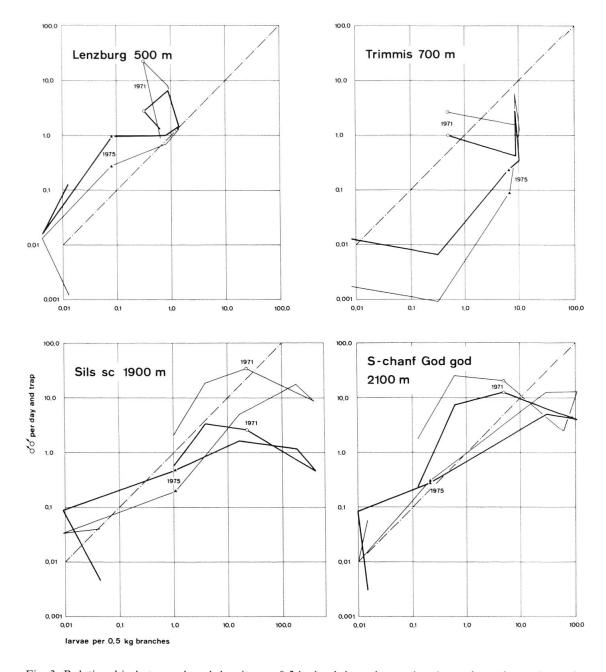


Fig. 3: Relationship between larval density per 0.5 kg larch branches and male moth catch per day and trap during the period 1970–1977 at 4 sites. Thick line: first flight per season; thin line: second flight per season.

Long range migration for most airborne organisms is generally downwind orientated; in contrast to this, local and regional flight of the larch bud moth is upwind. Green's (1962) analysis of the flight behaviour of the European pine shoot moth, *Rhyacionia buolianae* (Schiff.), was the first showing that upwind flight turned into downwind flight at windspeeds in the range of 2.7 to 3.6 m/sec. This phenomenon, at that time appreciated only in terms of energetics, gained a biological aspect when knowledge about pheromone communication between the sexes added a new dimension to ecological studies since the late 1960's. From carefully controlled laboratory experiments, Kennedy (1974) reports on phero-

mone-regulated anemotaxis in day-flying moth, whereby the anemotactic angle is considered to be a function of the odor stimulation: odour causes positive anemotaxis whereas clean wind induced a typical searching or casting behaviour at right angles to the wind direction. With a dicontinuous odour plume, the typical flight

Table 1: Population densities of the grey larch bud moth in the larval and moth stage in non-outbreak areas during the last population cycle, 1969–1978. Larval density N: Data 1969–1974 from Auer, 1975: Data Sils Maria, S-chanf unpublished; 0: number of kg branches sampled; 1: $\frac{1}{2}N = \text{number of larvae per}$ 1 kg branches corrected for sex-ratio 0.5; 2,5,8: number of traps x days; 3,6,9: number of $\frac{1}{2}C$ captured per trap and day; 4,7,10: number of $\frac{1}{2}C$ captured per trap and day in unbaited traps in % of columns 3,6 and 9 respectively.

locality	year	Larva1		Moth densities								
		nsity N	Fi	First flight period		Second flight period		Total flight period				
		0	1	2	3	4	5	6	7	8	9	10
Lenzburg	1970 1971 1972 1973 1974 1975 1976 1977 1978	30 40 30 30 30 39.5 48	0.640 0.320 0.870 1.316 0.784 0.070 0.006 0.011	30 270 283 562 355	1.057 2.707 6.300 1.428 1.012 0.972 0.016 0.125		224 77 819 632 871 871 593 846	0.893 21.262 7.781 1.236 0.685 0.028 0.014 0.001		400 107 1089 915 1433 1226 782 1126	0.965 16.060 7.414 1.300 0.814 0.301 0.014 0.031	
Trimmis	1971 1972 1973 1974 1975 1976 1977 1978	40 30 30 30 30 30 18.5 30 60	0.512 8.916 8.666 10.666 6.700 0.324 0.008 0.008	148 136 599 229 616	0.992 0.419 2.698 0.354 0.227 0.006 0.012		421 749 336 1044 456 2156 602	2.634 1.534 5.631 1.301 0.086 0.001 0.002		549 897 472 1643 685 2772 922	2.251 1.350 4.786 0.956 0.133 0.002 0.005	
Sils sc	1971 1972 1973 1974 1975	63 63 42 22 22 22 15 60	1.091	364 442 252	0.557 3.382 2.568 0.429 1.128 1.634 0.473 0.086 0.004	16.7 1.2 1.6	704 500 704 866 441 339 278 240 125	2.094 18.448 34.152 8.426 17.095 5.060 0.194 0.033 0.040	63.7 0.9 0.2	1146 1118	1.726 12.101 21.970 6.623 11.088 3.668 0.273 0.058 0.017	75.4 0.9 0.4
Sils Maria	1974 1975 1976	15 15 15 15 15 30	245.400 4.170 0.016	206 280 284 305 304 290	5.262 2.911 0.507 0.157 0.030 0.002	1.7	140 413 368 380 112 110	1.686 9.460 5.448 0.087 0.018 0.009	7.3 5.6 3.1	346 693 652 685 416 400	3.815 6.814 3.300 0.118 0.026 0.002	- 4.0 3.3
S-chanf	1970 1971 1972 1973 1974 1975 1976	90 7.5 7.5 7.5 7.5 7.5 6 24	0.208	418 214 845 185 218 349	0.235 7.187 12.145 4.895 4.005 5.005 0.278 0.082 0.003	52.3 1.7 0.0	667 652 357 698 300 212 612 504 434	1.756 25.534 20.535 2.481 13.017 12.533 0.291 0.010 0.058	56.2 2.8 0.3		1.290 18.367 17.390 3.803 9.580 8.716 0.286 0.048 0.025	54.0 2.6

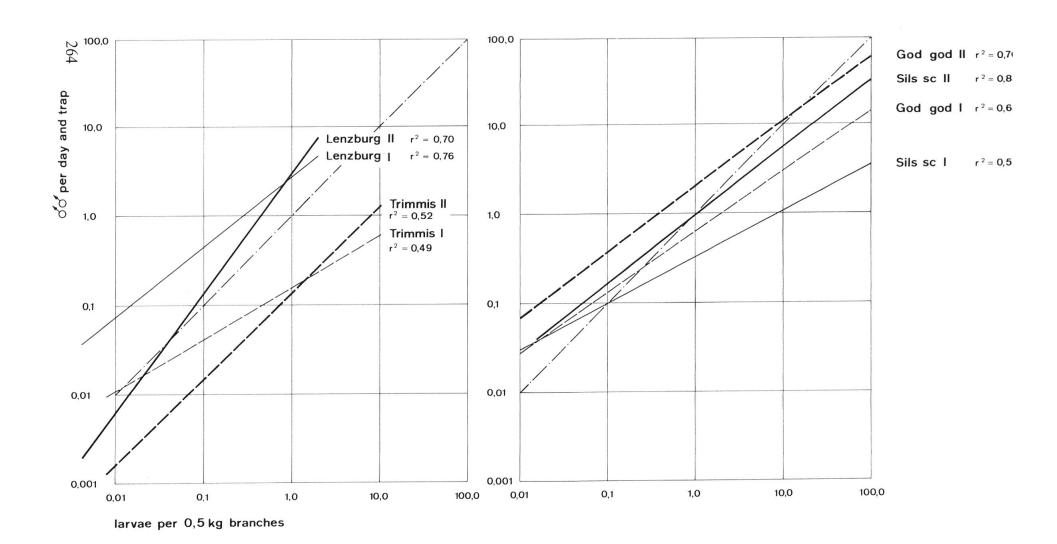


Fig. 4: Relationship between larval density (x) and male moth catch (y). The thin lines depict the regression of the densities of the first flight on larval density, the thick lines those of the second flight. Regression formula: $\ln \hat{y} = b \ln x + \ln a$.

track consists of irregular zigzags obliquely upwind along the plume. Outdoors, and especially in forests, wind turbulence tends to interrupt the pheromone plume irregularly which brings about a forward movement of the moth at various rates.

In its subalpine habitat the larch bud moth is most active during the first half of the night in July and August at temperatures above 7 °C (Vačlena & Baltensweiler, 1978). At this time cold air drainage from the upper regions of the mountains occurs. These laminar winds rarely exceed velocities of 3 m/sec and they are characterized by a surprisingly high degree of periodicity (Buettner & Thyer, 1965; Gerig, 1978; Urfer-Henneberger, 1964) This is due to either temperature conditions, i.e. the mutual fluctuation of temperature gradients and inversions, and the accentuated orography. These conditions may lead to very different windsystems at local or regional scales; in its most extreme forms, we may find either a very steady down-slope or down-valley wind from high ridges or mountain-passes or wind-convergence zones with increased turbulence in places where lateral down-slope winds and valley-bottom winds impinge on each other.

Positive anemotactic behaviour leads moths against down-slope and down-valley winds to the upper regions of mountain valleys. This is easily monitored by pheromone traps spread out along the altitudinal profile. Pheromone traps fixed parallel to the contour-lines catch in general considerably more moths on the valley oriented lee-side of the trap than on the upper luv-side. The fact that moths are caught at the upper timber line at 2100 m just when the local population enters the pupal stage, supports this reasoning. Although we are still ignorant about the mechanisms which cause the moths to continue their flight after having passed the timberline, informations from light traps show that males and females reach mountain ridges and passes by active flight. At these places conditions are optimal for windborne moths to be taken up into the gradient wind and then long-range migration starts (fig. 1).

Larch stands at the upper timber line which gain moths from lower source areas but lose moths to higher regions due to a steady down slope windfield are called transition sites (fig. 5: e.g. site 10). In contrast to this type of sites larch stands in areas with high wind turbulence are termed convergence sites since the males are trapped within the site by odour plumes changing continuously in their direction (fig. 5: e.g. site 1).

RELATIVE EVALUATION OF MOTH CATCH

It is generally known that pheromone trapping of males is not very well suited to measure population density as the mutual competition between traps and females varies in relation to the density of the females. However by relating male counts to larval density over the entire density range at a given site, moth catch can be interpreted in a relative sense. In addition important phenological differences between sites at different altitudes allow to separate immigrants from the autochthonous moths (fig. 2). The following discussion relies on census data collected at four sites in Switzerland: Lenzburg near Zürich and Trimmis in the Rhine river valley near Chur lie both in the area of latent fluctuation below 1000 m altitude. The localities Sils sc and S-chanf God god in the Engadine valley belong to the cyclic fluctuation area, they lie in site 1 and 10 resp. (fig. 5).

In the area of latent fluctuation the flight curve is bimodal, the two maxima are separated by nearly one month. The first flight represents the flight of the

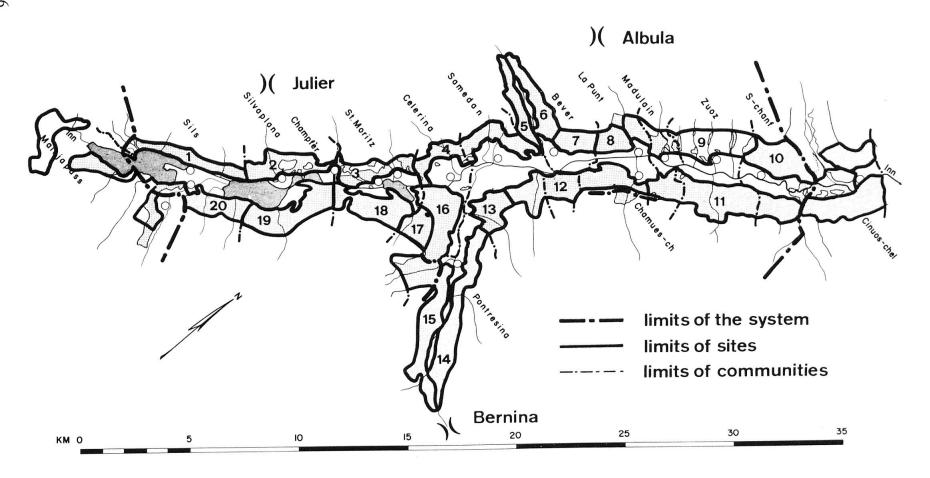


Fig. 5: Map of the upper Engadine with the outline of the sites 1-20.

Table 2. Relationship between densities of bud moth larvae and male moths catch at various sites expressed by the function y = axb.

Regression calculus for the function $\ln \hat{y} = b \ln x + \ln a$:

- n: number of samples, a: intercept, b: slope,
- r²: coefficient of determination.
- I: Male moth density of the first flight regressed on larval density
- II: Male moth density of the second flight regressed on larval density.

Relationship		Area of l fluctua		Area of cyclic fluctuation				
		Lenzburg	Trimmis	Sils sc	Sils Maria	S-chanf God god		
I	n	8	7	8	5	8		
	a	2.698	0.156	0.330	0.165	0.627		
	b	0.781	0.581	0.513	0.710	0.739		
	r ²	0.758	0.487	0.592	0.874	0.677		
II	n	8	7	8	4	8		
	a	3.060	3.060	0.967	0.125	1.999		
	b	1.350	1.350	0.956	0.563	0.732		
	r ²	0.700	0.523	0.810	0.920	0.695		

resident population, whereas the second flight curve displays the flight of immigrants. The seasonal timing and the magnitude of this second flight depend on the large scale synoptic weather pattern and the defoliation status in the cyclic fluctuation area.

For sites in the cyclic fluctuation area above 1700 m the reverse is true: moth emerging at altitudes between 1200 m to 1600 m reach by regional migration sites at higher altitudes some time before the autochthonous flight begins. As long as moth emerge and fly at lower altitudes regional migration towards higher altitudes will occur. Later in the season, moths immigrating into forests at higher altitude cannot be distinguished from flying residents. For this analysis we defined as the flight of immigrants the particular portion of the seasonal flight curve which occured before the mean temperature sum for 50% emergence is reached in a particular site and season. Immigration occuring at a later date was neglected.

The mean number of males caught per trap and season in relation to larval density is shown on double logarithmic scale (fig. 3; tab. 1). For Lenzburg and Trimmis moth- and larval-densities are presented for each year since 1970 and 1971 respectively until 1977. It is evident that at equal larval densities significantly more moths were caught at Lenzburg than at Trimmis. At both sites however, more males were caught during the autochthonous flight than in the second flight, except for peak densities from 1971 to 1973 when defoliation occurred in the Alps. The most striking feature in the two graphs Sils and God god is the fact that at highest larval densities the moth catch is considerably reduced. As the density threshold for the defoliation lies at a density of 50 of larvae, this reduction is a quantitative measure of desorientation.

For ease of comparison of the relationship below the defoliation threshold the data were expressed by the power function y = axb, which, after transfor-

The outline of the recursive formula is depicted in fig. 5. The flight period and the processes which stimulate or constraint flight behaviour are defined as follows:

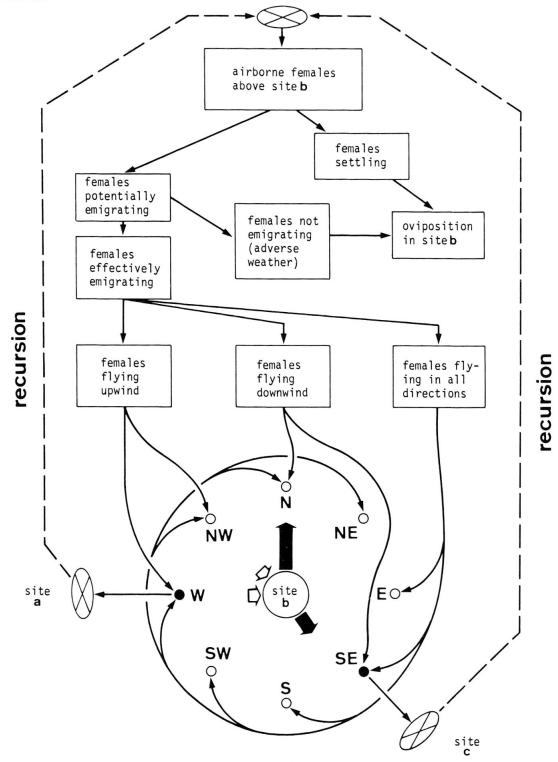


Fig. 6: Recursive formula for the migration applicable to any site. Here site b is depicted with two neighbouring sites to the west and southeast. Wind vectors: length proportional to average velocity during cyclonic () weather. o: sinks for females lost to the system.

mation in logarithms, may be solved by linear regression (fig. 3, tab. 2). At low densities moth catch is generally higher in the Engadine area than at the Lenzburg and Trimmis sites. It was not investigated whether the regression lines for the Engadine area differ significantly from each other; however the fact that moth catch at the God god site is highest at all larval densities, is in agreement with the idea of continuous moth immigration from lower altitudes (fig. 4).

By similar reasoning we may explain the discrepancy of moth catch for the autochthonous flight at Lenzburg (LZ I) and Trimmis (TR I). The traps at the Lenzburg site are located near the top of NE-facing slope which is covered by 100 ha of mature larch trees. Since on the Swiss Plateau westerly winds prevail, the high catch may be conceived as the result of a convergence-mechanism in a regional windsystem. In contrast to this, the traps at the Trimmis site sample the moths in a fringe of larch trees of about 200 m width at the lower end of an extensive pine-spruce forest and above an extensive range land. In the light of the proposed forms of migration, the Trimmis site cannot gain moths from lower altitudes, but loses constantly autochthonous moths to higher regions.

From this verbal model, supported by quantitative information, it is postulated that continuous moth immigration from source areas at 1200-1600 m contributes to switch the regression phase of the gradation cycle over to the progression phase. Thus regional moth immigration could represent an important prerequisite for the longterm regularity of the cyclic fluctuation.

VERBAL OUTLINE OF THE MODEL FOR SPATIAL DYNAMICS: THE MIGRATION MODEL

The long term studies of the population dynamics of the larch bud moth in the Upper Engadine have revealed consistent differences in local dynamics. Therefore the Engadine has been subdivided into 20 spatial units (fig. 5) by considering various ecological relevant aspects such as topographical features, exposure, forest stand composition and also the structure of the basic field data in relation to space. These spatial units are called sites. The dynamics of larch bud moth numbers within a site, the local dynamics, is described by FISCHLIN & BALTENSWEILER (1979).

This model yields for each site and each generation (year) a qualified number of mated females, which in turn provides the quantitative base to start the model of spatial dynamics, the migration-model. This migration model is conceived as a recursive process, i.e. the behaviour of all female moths in a site, either residents or immigrants, is defined by the recursive formula (fig. 6) relative to the specific site conditions. The recursive formula calculates the proportions of females which either lay their eggs in that particular site or leave it. Recursion is established as some of these emigrating females are accounted for as immigrants in neighbouring sites in just the same way as in the previous site until all of them are either ovipositing or lost to areas outside the system. The recursion is limited by the number of females and by the rule that no female may deposit eggs in more than three sites. Because it is assumed that only mated females become airborne, no interference between moths has to be considered, therefore this recursive formula may be repeated for the females of all sites in sequence. With this approach the two models for the local dynamics and migration are intimately linked and form a new system at a superior level.

- (1) The flight period is bound exclusively to the time of seasonal occurrence of the moth from July 15 to September 30 and within this period to diurnal moth activity from dusk to midnight (1800–2400).
- (2) Vačlena & Baltensweiler (1978) have shown that the defoliation status of a larch forest determines whether moths are attracted to stay and oviposit in the particular stand (site) or whether they avoid it.
 - (3) Weather affects flight behaviour by various parameters:
- the temperature of 7 °C determines the lower activity threshold (Vačlena & Baltensweiler, 1978)
- Winds determine moth flight and its orientation by their intensity and direction.

Anticyclonic weather induces a stable and very predictable nightly windfield and subsequent up wind flights of the moths. Cyclonic weather with its turbulent and strong winds often prohibit any flight. Indifferent pressure areas, characterized by warm airmasses and thunderstorms intensify moths activity and lead frequently to long range downwind migration. The local wind conditions are classified and quantified according to the synpotic weather pattern by adding up the duration of the various weather types.

Because weather types are assumed to determine by means of wind direction and intensity subsequent direction of moth migration as well, airborne females above a specific site can be allocated as immigrants to neighbouring sites. This allocation is assumed to be proportional to the duration of relevant weather types and the surface of neighbouring sites in any one of the 8 cardinal points. For the time being we assume that females flying in directions where no sites occur, will be lost to the system.

This approach which considers migration as recursive process offers many advantages, the most important is without doubt the profit in lucidity by reducing the migration process to what happens to females in a spatial unit, the site. This verbal model has been tested quantitatively with encouraging results (FISCHLIN, in prep.).

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