

Interrelations of Green Oak Leaf Roller Population and Common Oak: Results of 30-year Monitoring and Mathematical Modeling

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Abstract

Long-term monitoring followed by mathematical modelling was used to describe the population dynamics of the green oak leaf roller *Tortrix viridana* L. over a period of 30 years and to study reactions of oak stands to different levels of defoliation. The mathematical model allows us to forecast the population dynamics of the green oak leaf roller and main characteristics of its development: survival, fecundity, and propagation coefficient. The model demonstrated that oak stands in various sites differ in their response to severe defoliation. The responses of absorbing roots of damaged trees are most intense after the first year of damage and decrease gradually if subsequent defoliation occurs. The analysis of weather characteristics over 50 years revealed that the hydro-thermic coefficient of growing seasons increased 1.7 times during the last 30 years; this may be favorable for oak stands growing in the observed region.

Introduction

The green oak leaf roller *Tortrix viridana* L. is a widely distributed leaf-eating monophagous species in oak stands that is well-adapted to its host tree specie, *Quercus robur* var. *praecox* Czern. It also damages other oak species both deciduous (*Q. petraea*, *Q. cerris*, *Q. suber*, *Q. rubra*) and evergreen (*Q. ilicifolia*). The green oak leaf roller is distributed throughout the European part of Russia and in many European countries, though it prefers conditions that occur in the steppe and forest-steppe zones. Outbreaks of mass propagations of the green oak roller are durable and larvae and egg masses are very tolerant to unfavourable biotic and abiotic factors. Larvae hatch over a period of 7 to 12 days. The lack of synchrony between hatching and oak budbreak or injury to young leaves caused by spring frosts can cause reinforced migrations of larvae looking for food and therefore impact significantly on their numbers. Larvae of both older and younger ages are not very mobile and move within a crown only if food is absent. Nearly 90% of larvae often die because of this discrepancy and are killed by predators and entomophages. A significant portion of the larval population is killed by diseases caused by entomopathogens, however the magnitude of this mortality is usually not catastrophic for the population. Males pupate before females (2-3 days) so when over-population occurs, mortality of male pupae is less than what is incurred by female pupae. The total number of pupae is an index of the state of the population and of the stage of an outbreak and depends on food quality, weather conditions and population density. The total number of female pupae of the green oak leaf roller depends directly on the level of crown defoliation.

The development of *T. viridiana* outbreaks depends significantly on survival in the larval and pupal stages and consequently on weather conditions, the condition of the host tree, and biotic factors. A delay in the development of larvae and pupae due to unfavorable conditions causes their increased mortality and therefore is an important factor in the population dynamics of this species.

Materials and Methods

This study of *T. viridana* populations was conducted on permanent trees in the Tellerman oak grove (the southern part of the forest-steppe zone, Voronezh oblast the Central Black Soil region of Russia), an area characterized by a dry continental climate. Observations were initiated in 1969 by N.N. Rubtsova and have been continued since 1975 by the authors.

Observations of the condition of trees and their crowns are made every year on 26 permanent plots located over the area of the Tellerman Forest Experimental Station, Institute of Forest Science, to reveal the locations of mass outbreaks of phyllophagous insects and to evaluate the status of crown defoliation.

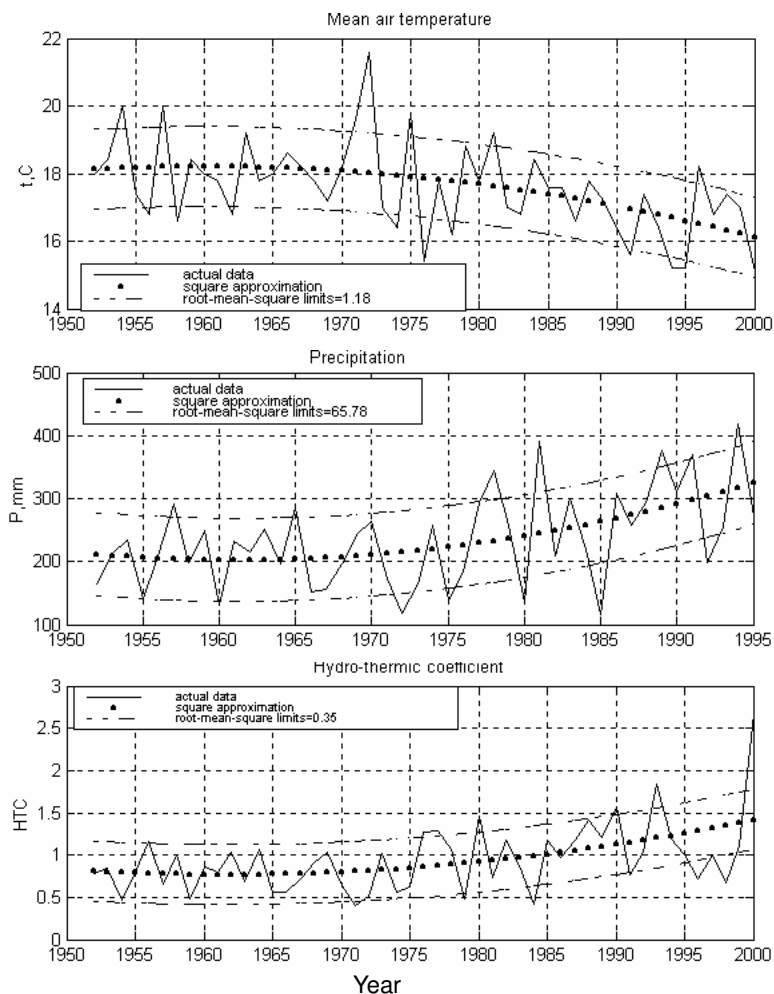


Figure 1.—Some weather characteristics over a growing season (May-September)

The most detailed study was conducted mainly in two types of forest: a) the floodplain lily-of-the-valley / dewberry oak stand (site index II, relative density 0.6-0.8, aged 85 years); b) the upland solonchaks oak stand (site index IV-V, relative density 0.6-0.8, aged 80-95 years).

Counts of larvae and pupae were made individually on marked trees, by cutting sample branches from the upper and lower parts of the crown. Butterflies and entomophages were raised in glass containers in the laboratory. Counts of egg masses of *T. viridana* L. in the forest were made twice a year, in October and March. In order to determine the mortality of eggs, larvae were allowed to hatch from eggs that were sampled at different periods during their development (Rubtsov et al. 1989b).

Before discussing some features of the population dynamics of *T. viridana* and other phyllophages and their impact on the condition of oak stands, we offer some discussion about the changing weather conditions over the last 30 years. This is meaningful for understanding the potential impact of climate and its relation to phyllophages and their host trees.

It is known that significant changes in weather and climate are occurring. We have analyzed various weather parameters recorded in the vicinity of our investigations for last 50 years in order to reveal some trends. Fig. 1 shows changes in three parameters selected for a growing season (from May to September): mean air temperature, precipitation and hydro-thermal coefficient (the sum of precipitation in mm divided by sum of air temperatures above 10°C multiplied by 0.1). It is evident that mean air temperature has decreased by 2°C during the last 30 years, whereas precipitation over the same period has increased by 110 mm. Consequently, the average hydro-thermic coefficient of a growing season has increased by a factor of 1.7. Since the southern forest-steppe zone is a region with

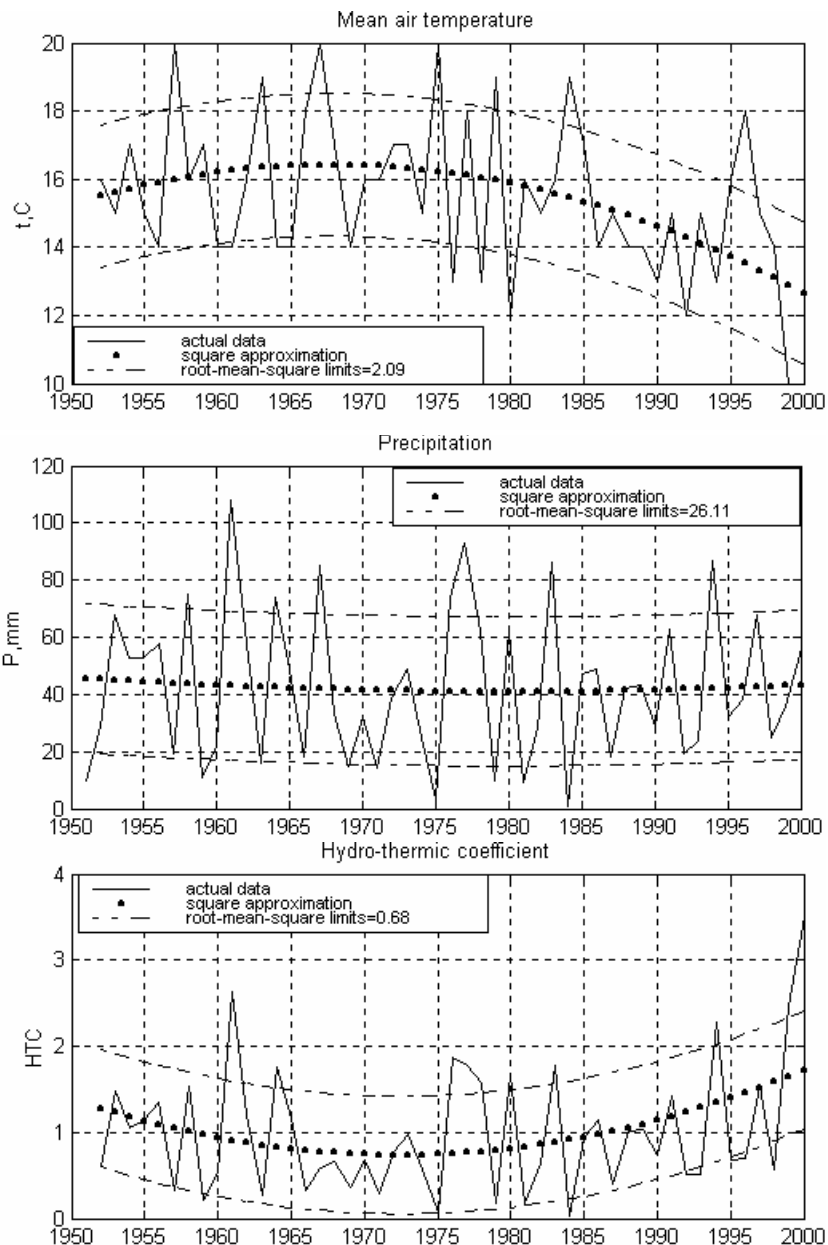


Figure 2.—Some weather characteristics in May

deficient moisture, the changing hydro-thermic regime during the growing season may be considered favorable for vegetation. The consequences of these climatic changes have also influenced the state and productivity of oak stands. Figure 2 illustrates the trend in the same three parameters for the month of May. It is obvious that the mean air temperature and the hydro-thermic Coefficient has declined by a factor of 2.4. Because May is the period when intensive feeding by larvae of *T. viridana* and other early-spring phyllophagous insects occurs, these changing weather conditions should clearly influence the relationship between phyllophagous insects and their host trees.

Results and Discussion

A mathematical model of the development of *T. viridana* populations was developed on the basis of data obtained from the literature and from studies conducted by one of the authors (Rubtsov 1983, 1990). It interprets the mechanism of outbreak development in accordance with the synthetic theory (Victorov 1965, Schwerdtfeger 1968). The model is non-linear, non-stationary, has alternating structure and dimensions, and reflects the results of a series of complex interactions within the modeled system. The mathematical model can be used to describe the dynamics of *T. viridana*

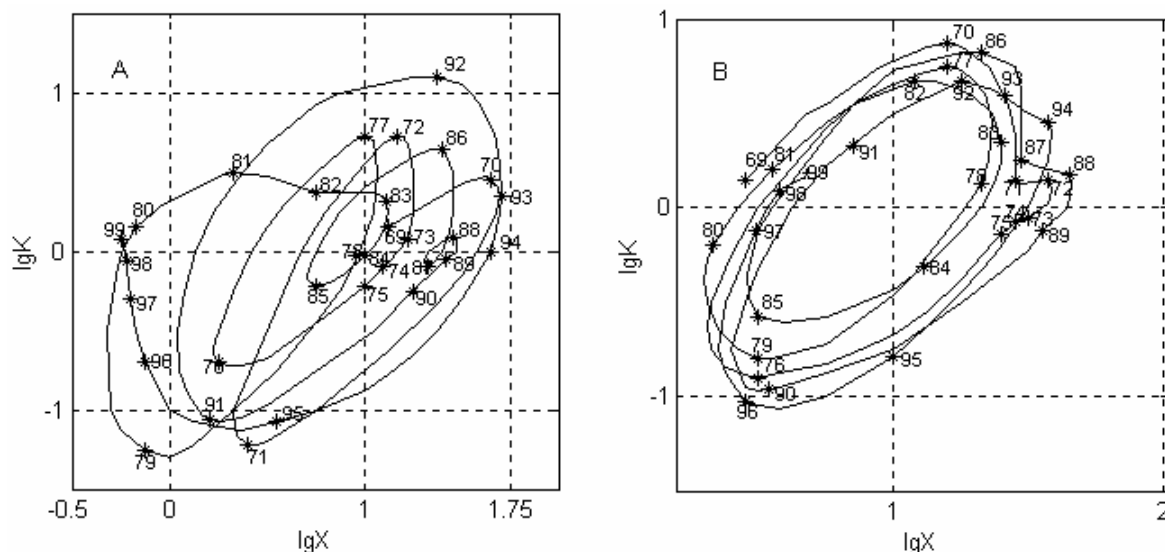


Figure 3.—Phase trajectories of green leaf roller's population in floodplain oak stand (A) and solonets oak stand (B). X — population density, K — propagation coefficient.

populations and can be used to estimate the following parameters: the density, survival, fecundity, and propagation coefficient of the population in each generation; defoliation and refoliation of crowns in a stand; value and loss of stem increment, and some other parameters. The model demonstrates that weather has a relative impact on the development of larvae and that the level of crown defoliation decreases at higher population densities; if the population continues to increase, i.e. a significant over-population occurs, the importance of weather factors again increases. Results of the modeling demonstrate also that when severe over-population occurs, discrepancy (lack of synchrony) between bud break and larval hatching can be favorable for survival of *T. viridana* populations because it reduces the over-population; the extended period of hatching provides for the successful development and survival of the remainder of the population. The results of our modeling indicate that there is the possibility of large amplitudes of fluctuations in *T. viridana* population density under certain conditions not only in the period of its mass propagation, but also when populations are at low densities.

The main factors that are responsible for modifying and regulating populations of *T. viridana* were considered in detail in earlier publications (Rubtsov 1990, Rubtsov and Utkina 2001, and others). Here we discuss only the importance of larval and pupal entomophages in regulating populations of the green oak leaf roller. The species composition of these organisms in the Tellerman oak grove is very rich. This can be explained in part by the complex composition of stands, their many-tiered stratification, and the presence of many glades with flowering plants including cruciferous species. The most abundant entomophagous species are as follows: *Phaeogenes invisor* Thunb., *Itopectis alternans* Grav., *Apectis resinator* Thunb., *Apectis rufata* Gm., *Trichomma enecatur* Rossi., *Lissonota* sp., *Meniscus bilineator* Grav., *Elodia tragica* Mg., *Bessa fugas* Rd., *Dibrachys cavus* Walker., *Habrocytus* sp., *Brachymeria intermedia* Nees., *Monodontomerus minor* Ratz., *Apanteles* sp. aff. *albipennis* Nees., *Apanteles* sp., *Microgaster laevisenta* Thans. (Rubtsov and Rubtsova 1984).

The regulation of the population density of phyllophages can often be well described by means of mathematical modelling. However, it is very difficult to forecast changes in population density due to their stochastic and non-stationary nature. This decreases significantly the accuracy of forecasting. After analyzing the features of fluctuating population numbers, we conclude that the green oak leaf roller can be described as an eruptive species in accordance with Isaev et al. (1984). Figure 3 shows the phase trajectories of *T. viridana* populations in the floodplain oak stand (A) and in the upland solonets oak stand (B). The development of outbreaks in an eruptive pattern was observed in 1968-1976, 1979-1987 in the floodplain stand. In the latter case, *T. viridana* was affected by a modifying

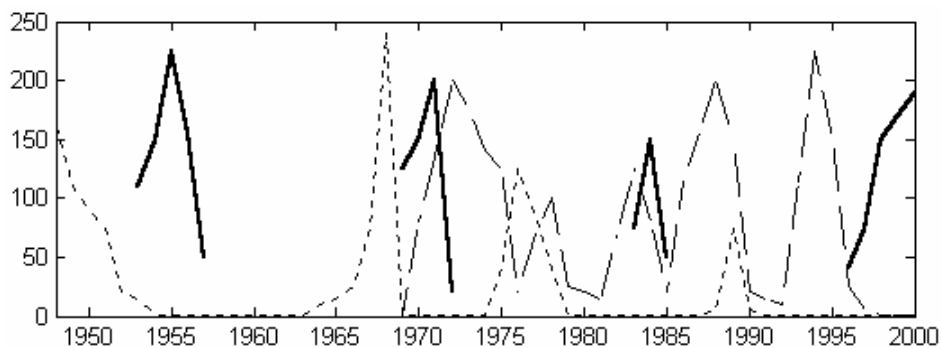


Figure 4.—Population dynamics of some phyllophagous insects in the Tellerman oak grove,

.....*Lymantria dispar* L. : number of egg-masses per 50 trees
 ———*Tortrix viridana* L. : number of egg-masses per 5m of branch length
 ———*Operophtera brumata* L. : number of imago females per 1 tree

factor, a significant drought which occurred in 1979; the population expanded rapidly after this occurrence.

However, the population did not reach its maximum due to the significant impact of another modifying factor, severe winter frosts that occurred in 1984/1985 and affected populations of both *T. viridana* and the entomophages that normally regulate its numbers. This is represented by the formation of a loop in the phase portrait (Fig. 3A, 1984-1985). When studying phase portraits, a conclusion can be made about the permanent character of outbreaks of the green oak leaf roller since the population does not usually stabilize its numbers when the gradation cycle is over and a new outbreak begins. Attention is drawn to the relative stability of population density and propagation coefficients at similar stages of different gradation cycles in the solonets oak stand (Fig. 3B). The highest population density is 20-32 and the lowest is 2-3.5 egg-masses per 1 m of a sample branch; the maximum propagation coefficient is 5-7 and the minimum is 0.1-0.25. These features suggest that the solonets oak stand is representative of a stable ecological regime and simplifies forecasting the population development.

Before proceeding to the influence of phyllophagous insects on oaks, we should note that other leaf-eating insects, such as the gypsy moth and the winter moth occur also in stands of the Tellerman oak grove. Their population dynamics are presented in Figure 4. Four outbreaks of both the gypsy moth and the winter moth were recognized after the Second World War (Rubtsov et al. 1989a); permanent monitoring of *T. viridana* populations began in 1969. The impact of *T. viridana* on the state and growth of oak trees in a floodplain oak stand is shown in Figure 5. Values of stem increment and percentage loss of increment averaged for a stand are plotted along with data on the population density of *T. viridana* and defoliation estimates on individual trees. Figure 6 shows the results of modeling the loss of increment of oaks as a function of a single and cumulative defoliation index in four different stands by means of statistical regression analysis.

The most loss occurred in the upland and solonets stands: 40% after a single defoliation and 60% after two consecutive defoliations. The cumulative defoliation, equal to 250-270% over three years, caused nearly 100% loss of increment and significant mortality of trees. The least loss of increment occurred in oaks of the floodplain stand, which can be explained by their tolerance of frequent and significant insect defoliations and their increased ability to refoliate (Utkina and Rubtsov 1994).

The impact of crown defoliations on the seasonal growth activity of absorbing roots in oaks has been studied during the past five year in collaboration with V.V. Mamaev (Mamaev et al. 2001, 2002). Figure 7 shows the relation between the growth of absorbing roots of defoliated and non-defoliated oak trees in 1998 in the floodplain stand. The defoliated trees incurred up to 90% defoliation while

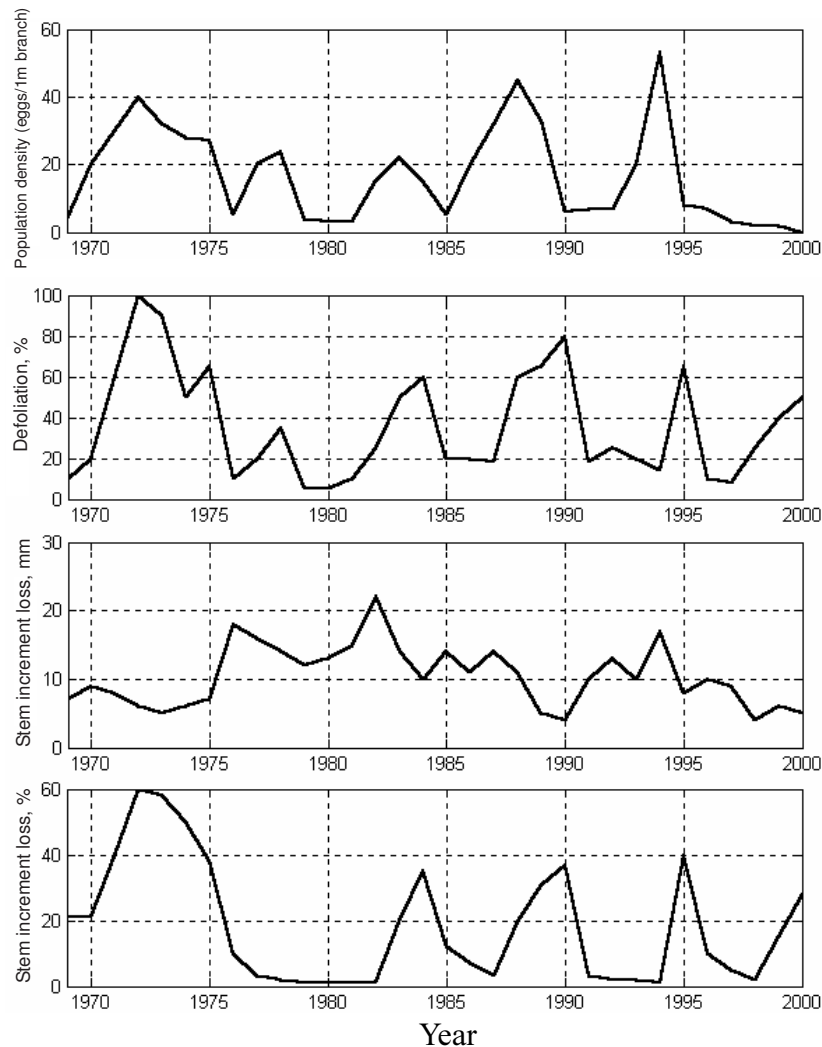


Figure 5.—Population dynamics of *Tortrix viridana* L. and its impact on defoliation and stem increment in the floodplain oak stand.

the control trees were practically undamaged. The winter moth was the dominant leaf-eating insect species responsible for the defoliation. Active regrowth of foliage began on May 28 and occurred very rapidly. By June 18 the new foliage was very abundant and denser as compared to the foliage on the undamaged trees. New leaves were not damaged by insects and mildew, appeared to be rather fresh and were slightly different color as compared to spring foliage. The root system of the damaged trees responded immediately to defoliation by producing intensive mycorrhizae. However, as refoliation occurred in early June, the rate of growth declined. The least amount of root growth occurred during the period of most intense refoliation. The control trees experienced peak root activity during the same period. Additionally, the amount of newly generated mycorrhizae per 1 unit of soil volume was more comparable to that which occurred on the control trees over the entire growing season. The least difference between damaged and control trees was evident only in autumn.

The principal conclusions from this study suggest that the growth of new absorbing oak roots is closely related to the condition of the crown and responds keenly to a loss of foliage, however, the intensity of the response varies in trees that suffer single or repeated defoliations. In the first year of severe defoliation, the root systems of trees respond by rapidly producing a mass of new mycorrhizae roots, however after repeated defoliations, there was no increase in this root growth activity. When an abundance of oak mycorrhizae with well formed mycelia occurs in soil, this results in a significant increase in the volume of absorbing root surface. This suggests on one hand that the weakening of

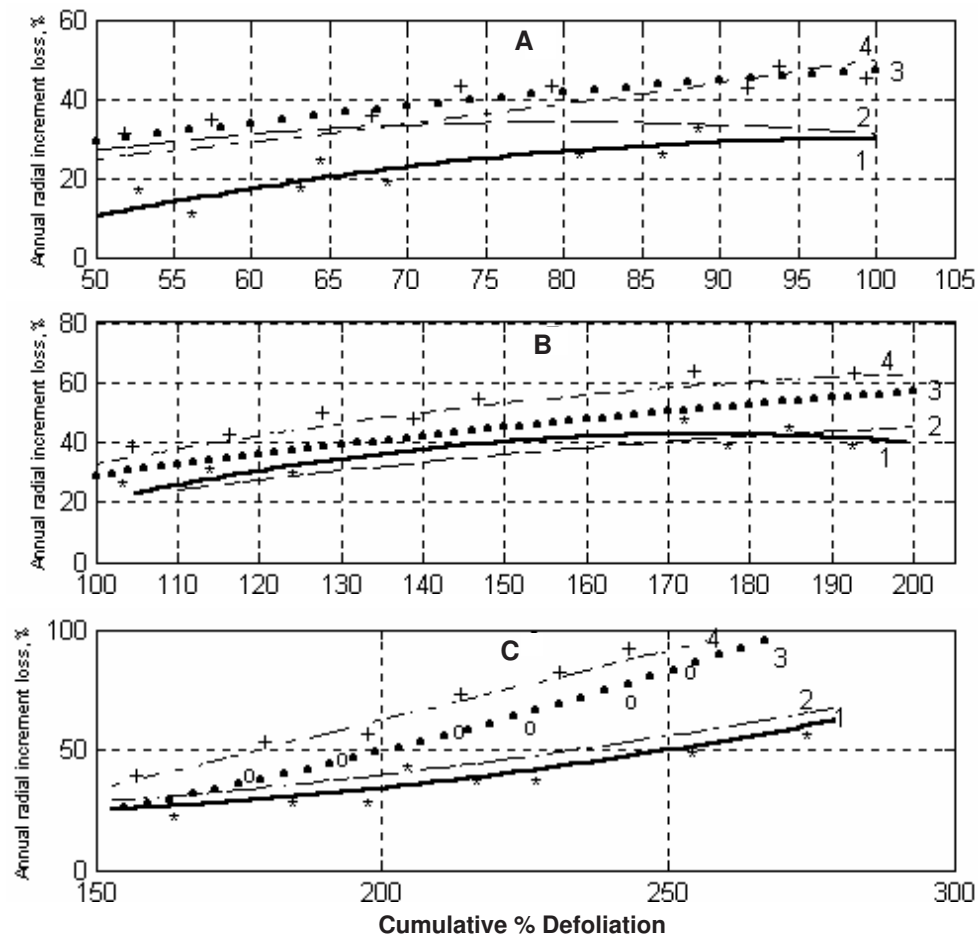


Figure 6.—Loss of radial increment in different oak stands in response to various level of defoliation: A - single defoliation; B - repeated defoliation during two successive years; C - repeated defoliation in three successive years. Numbers and different symbols indicate stand type: 1- floodplain; 2 - riverbank; 3 - solonetz; 4 - upland.

trees and reduction assimilates and reserves occurs and, on the other hand, that oak trees respond to the stress of repeated severe defoliations by engaging defensive mechanisms. It should be noted that healthy trees have the highest growth activity of roots after defoliation occurs, whereas growth activity of roots is less in weakened and suppressed trees and nearly absent in dying trees. The close relationship between the development of new absorbing roots and the condition of crowns is one of the ways by which trees survive under conditions of stress. During the last five years, oaks in the floodplain and solonets stands suffered severe defoliation caused by the winter moth. These defoliations combined with summer droughts in 2001 and especially in 2002, caused severe weakening of oak trees and produced a micro-focus of decline. We are forecasting that these foci of decline will expand next year since in the current year, the refoliation of trees and accumulation of energy reserves in damaged trees was poor.

Acknowledgments

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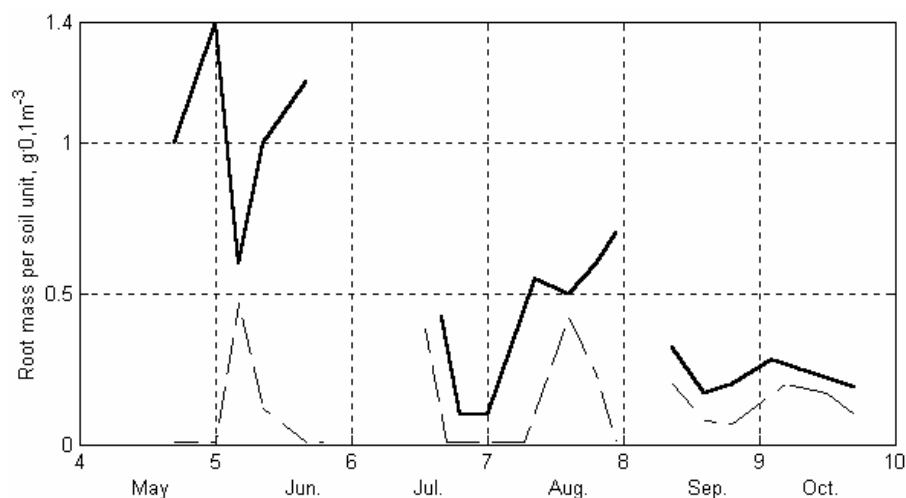


Figure 7.—Dynamics of new growth of young absorbing oak roots in the floodplain oak stand after insect defoliation in 1998

— — — — — trees without defoliation (control)
 - - - - - trees with 90 % defoliation

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