

Short note

Influence of repeated defoliations by insects on wood increment in common oak (*Quercus robur* L)

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Summary — The dynamics of radial wood increments were analysed over a 30 year period in oak stands (*Quercus robur*) of the forest-steppe zone in the Voronezh region (eastern-central Russia). Relative losses in wood increment, due to insect-caused defoliations of diverse extents and periodicity, were quantitatively assessed. Such estimates were made for trees with early and late phenology, as well as with respect to growth classes and to local forest types. The intensity of the responses of dominant and codominant trees were shown to vary in different forest types. No differences in increment losses were detected between early and late oaks after one to three moderate defoliations. A factor two variation was observed in the intensity of the responses, depending on actual climate. In response to repeated defoliations, the ratio latewood to earlywood was reduced by a factor 5–8 in a stand and even 20 in an individual tree. This suggests that insect defoliation severely affects oak growth.

radial increment / wood / leaf feeders / oaks / growth / defoliation

Résumé — Effets de défoliateurs sur la croissance de chênes (*Quercus robur* L). Les dynamiques de croissance radiale ont été suivies sur une période de 30 ans sur des chênes pédonculés (*Quercus robur* L) de la steppe forestière de la région de Voronezh (Russie centre-orientale). Les pertes relatives de croissance radiale dues à des défoliations par des insectes ont été évaluées quantitativement. Ces estimations ont concerné à la fois des chênes tardifs et précoces, ainsi que différentes classes de dominance, et divers types forestiers. L'intensité des réponses d'arbres dominants et codominants variait en fonction de la station. En revanche, aucune différence de sensibilité n'a été détectée entre variétés précoces et tardives en réponses à des séries d'une à trois défoliations modérées. L'intensité des réponses variait d'un facteur 2 en fonction des conditions microclimatiques. En réponse à des défoliations répétées, le rapport bois de printemps bois d'été était diminué d'un facteur 5–8 dans un des peuplements, et même de 20 sur un arbre isolé.

défoliations / croissance radiale / chêne / dépérissement

INTRODUCTION

Wood increment is a complex process, depending on tree age and phenology, site conditions and the many hazards that may happen in a forest ecosystem. The effects of insect defoliations on stem wood increment have been studied by many investigators. Results and techniques used can be found for common oaks in Russia in Ilyinski and Kobozev (1939), Yerusalimov (1965), Vorontsov (1967), Semevsky (1971) and Kucherov (1990) and many others. Vorontsov (1967) noted that many students still considered current increment to be the best vitality index in heavily defoliated stands. However, the problem of assessing quantitatively increment losses following insect damage is far from being solved. As a result of the diversity of the sampling and data processing techniques used, the interpretations and conclusions from different authors diverge significantly.

The main aim of the present work was to analyse the dynamics of radial increment in forest-steppe oak stands during a 30 year period (1958–1987) and to build a mathematical simulation allowing a quantitative estimate of increment losses due to defoliations by phyllophagous insects. We used not only current defoliation, but also an index of combined defoliation over 2–3 years. This may also reveal some biological and physiological features of the formation of annual wood-rings in oaks.

MATERIALS AND METHODS

Trees were sampled in an oak grove in the Tellerman Forest, close to Borisoglebsk, Voronezh region in eastern-central Russia, during 1980 and 1990. During 1980 and 1990, 376 and 300 oaks, respectively, were selected in four forest types on 26 permanent plots. The health status of these trees had been monitored once a year since

1969–1973, including an interannual estimation by eye of the degree of defoliation in the crowns. Two phenofoms were distinguished: late (*Q robur* var *tardiflora* Czern) and early oaks (*Q robur* var *praecox* Czern). The delay in bud-burst between both could reach 15–25 days according to years.

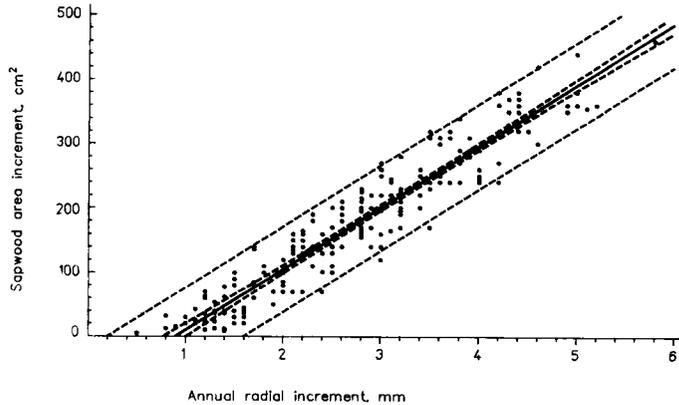
The permanent plots were located in four main stand types: i) an upland stand, site index I–II, aged between 55 and 85 years, dominated by late oaks, and prone to water deficits; ii) a flood-plain stand, site index II, aged 90 years, with only early oaks; soil water content varied from completely waterlogged to relatively dry; iii) a river-bank stand, site index IV–V, aged 80 years, with only early oaks; heavy lateral runoff resulted in unfavourable water supply; iv) a solonetz (salinified) stand, site index IV–V, aged 80–95 years, with early oaks only.

Ten outbreaks of phyllophagous insects were recorded between 1958 and 1987. Green oak roller (*Tortrix viridana* L), gypsy moth (*Lymantria dispar* L) and winter moth (*Operophtera brumata* L) were the most common defoliators. A defoliation index was recorded as the relative leaf area loss estimated by soil-born observers. It was cumulated when successive defoliations occurred, resulting in values above 100%.

Wood cores were collected during autumn 1980 and 1990 from the northern and southern sides of the stems at 1.3 m. The width of the 30 last annual rings was measured (± 0.05 mm), and latewood (LW) distinguished from earlywood (EW). Sampled trees were divided into groups according to i) stand type, ii) phenotype, and iii) growth and vigour, that is, dominant and codominant trees, and intermediate and suppressed trees. The search for potential correlations between annual increment and degree of defoliation was restricted to years with defoliation rates above 35% and devoid of additional stresses such as late frost or drought.

Losses in increment were estimated from the following procedure: An optimal increment was computed as a function of annual climate recorded every year (Rubstov and Rubstova, 1984); the difference between this optimal increment and the actual one recorded on the cores was taken as the increment loss due to defoliation. Sixteen to 51 trees were analysed in each group. A close relationship was found between radial increment and sapwood basal increment (fig 1); we therefore used the former one alone to describe annual wood increment.

Fig 1. Relationship between sapwood basal area increment, and annual radial increment of oaks from a floodplain stand during 1982–1990.



RESULTS AND DISCUSSION

The following main results were obtained from a statistical correlation analysis between crown defoliation degree and losses of radial increment in the early phenophase of *Quercus robur*:

- i) the relationship between increment loss and index of combined defoliation increased with the number of successive defoliations;
- ii) the relationship between increment loss and index of defoliation was closer in suppressed and intermediate trees than in dominant and codominant ones;
- iii) latewood increment was more closely related to defoliation than earlywood increment, with the exception of the Solonetz stand, where it was similar in early- and latewood;
- iv) the relationship between radial increment and a single defoliation was much closer in the upland and floodplain stands (correlation coefficients around 0.48 and 0.62, respectively) than in the riverbank and solonetz stands (0.36 and 0.35); when successive defoliations occurred, these differences were reduced.

Common oak displays a fairly adequate reaction to defoliation, with important compensation growth after a single defoliation.

As a consequence, the relationship between the intensity of such a defoliation and increment loss was rather loose. However, the degree of significance improved readily in response to two and even more, three successive defoliations.

In the floodplain and upland stands, the annual increment was more closely related to the rate of defoliation than to climate factors, even after a single defoliation; this difference increased after two and three successive defoliations. In the solonetz and riverbank stands, the relationship with climate was better than with defoliation; however, after two or three successive impacts, it was better with the latter than with the microclimate.

An estimate of the increment loss due to defoliation was calculated for every year, and represented as a function of the cumulated defoliation index (fig 2). Upland and solonetz stands appeared to be more sensitive to defoliations; a 100% loss, accompanied by severe dieback, occurred in response to heavy defoliation during 3 successive years. Floodplain and riverbank oaks were less sensitive, even if floodplain oaks were more frequently damaged, specially during early spring. These stands probably displayed a defence against early damage through a quick recovery of leaf area. This

defence was probably effective only in healthy stands and under favourable conditions (Utkina and Rubstov, 1994).

Dominant and suppressed trees responded differently to defoliation in different stand types. In the floodplain stands,

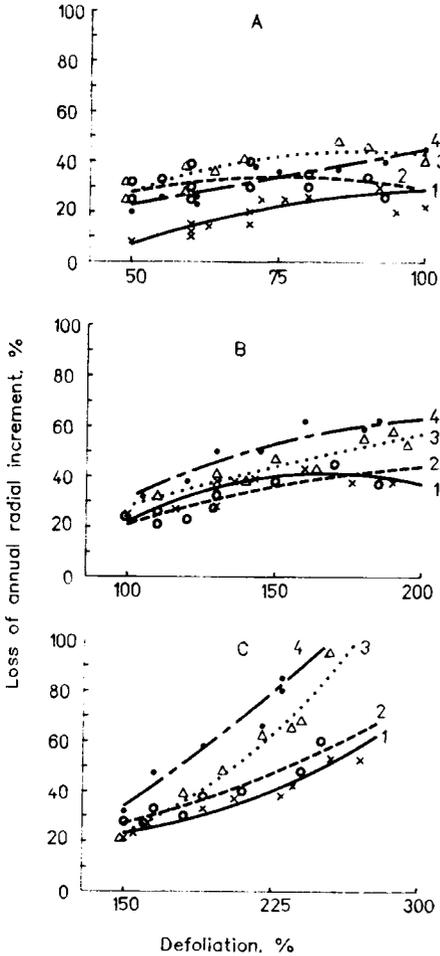


Fig 2. Loss of radial increment in different oak stands in response to various intensities of defoliation resulting from: (A) a single defoliation; (B) repeated defoliation during 2 successive years; (C) repeated defoliation during 3 successive years. Numbers and different symbols indicate stand type (1: floodplain; 2: riverbank; 3: solonetz; 4: upland).

the reduction in increment was higher on dominant than on suppressed trees after a single defoliation. This difference vanished after three successive defoliations (fig 3). In the solonetz stand, suppressed trees presented a slightly higher loss of increment, whatever the frequency of the defoliations (fig 4).

Finally, figure 5 demonstrates the interactions between sensitivity to defoliation and actual weather. Two classes of climate conditions were distinguished, based on the

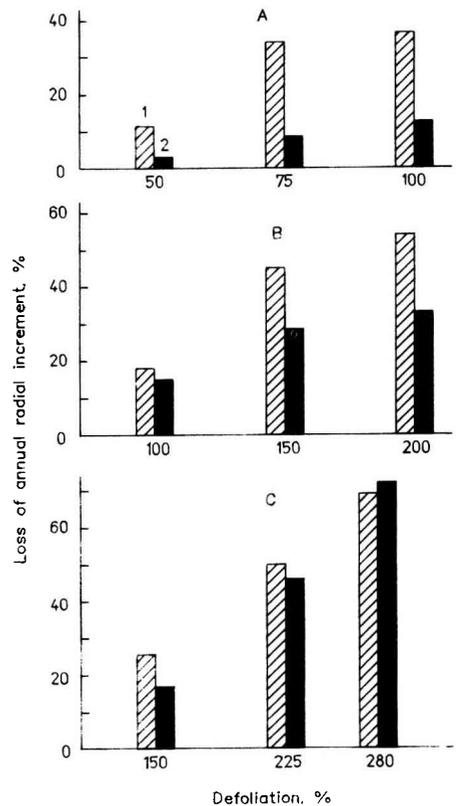


Fig 3. Loss of annual radial increment in a floodplain stand of oaks in response to various intensities of defoliation resulting from: (A) a single defoliation; (B) repeated defoliation during 2 successive years; (C) repeated defoliation during 3 successive years, in (1) dominant trees and (2) suppressed trees.

cumulated precipitation during July and August: favourable (above 200 mm rainfall) and unfavourable (below 50 mm) to radial increment. The increment loss varied by a factor up to 1.8 between the two conditions.

The ratio latewood/earlywood (LW/EW) has been proposed as an index for cambial activity during the summer period (Tikhomirov, 1989). Figure 6 displays the

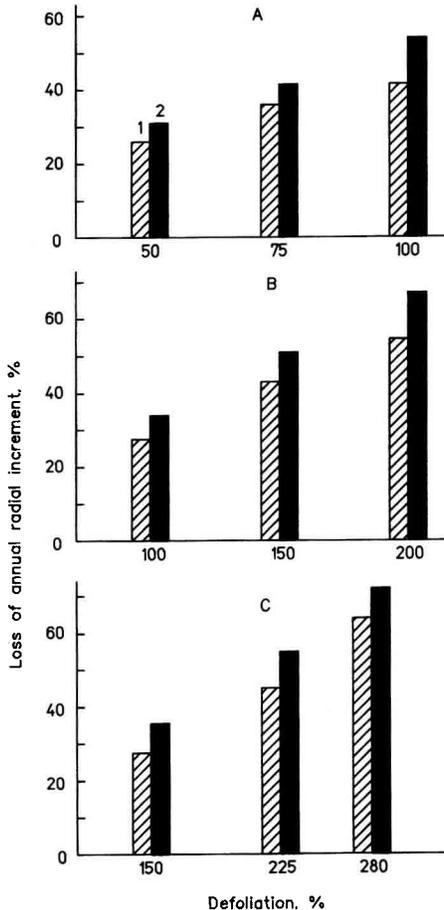


Fig 4. Loss of annual radial increment in a solonetz oak stand in response to various intensities of defoliation resulting from: (A) a single defoliation; (B) repeated defoliation during 2 successive years; (C) repeated defoliation during 3 successive years, in (1) dominant trees and (2) suppressed trees.

negative effects of defoliation on this ratio, which decreases with increasing defoliation, suggesting a reduced cambial activity during summer. Both the optimal value of LW/EW, as well as the extent of the decrease, depended on the stand nature,

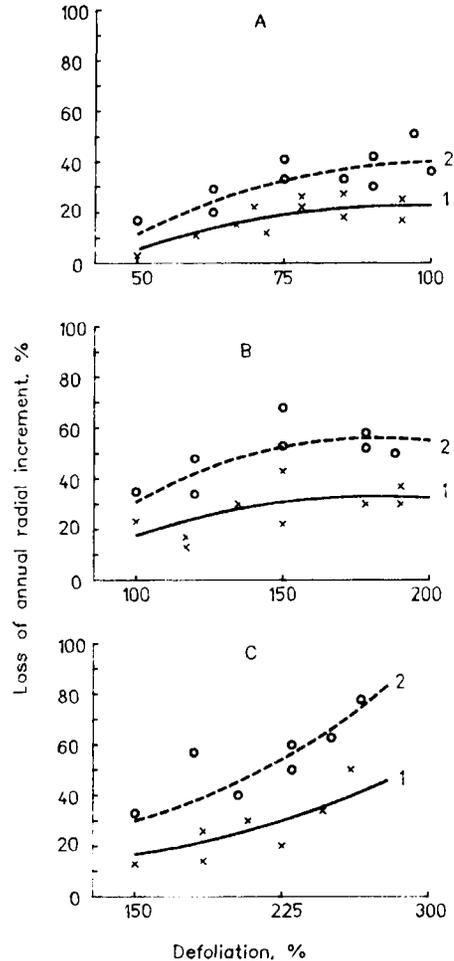


Fig 5. Influence of the amount of rainfall in July–August (1: below 50 mm; 2: above 200 mm) on the loss of radial increment in a floodplain oak stand in response to various intensities of defoliation resulting from: (A) a single defoliation; (B) repeated defoliation during 2 successive years; (C) repeated defoliation during 3 successive years.

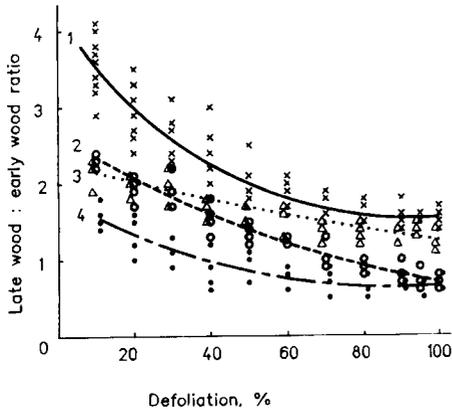


Fig 6. Effects of defoliation severity on the late-wood/earlywood ratio in different oak stands. (1: floodplain; 2: upland, 85-year-old trees; 3: upland, 55-year-old trees; 4: solonetz).

the floodplain stand presenting the highest ratios and most severe decreases, and the solonetz, the lowest ratios and limited decreases.

CONCLUSION

These investigations strongly suggested that, despite the ability of oaks to respond to defoliations, the repetition of attacks by phyllophagous insects can lead to severe reductions of growth and even dieback. The most important increment losses were observed in the upland and solonetz stands, and the lowest in the floodplain and riverbank stands. Since the crowns are more frequently damaged by insects in floodplain stands, these latter have probably developed a defence mechanism, in principle common to all oaks, but able to fully act under these favourable conditions, and providing a quick and complete recovery of photosynthetic leaf area.

The LW/EW ratio was severely reduced by defoliations, and this may be of severe consequences for wood quality. If defoliation repeats, this ratio may be diminished five to eight times at stand level, and even more in some individuals. This indicates that phyllophagous insects influence wood structure in oaks. Finally, the actual climate experienced by the trees, and in particular the water availability, strongly modulated the response to defoliation.

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