Comparison of the Photosynthetic Capacity between Intact Leaves of Triazine-Resistant and -Susceptible Biotypes of Six Weed Species

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Photosynthesis of Intact Leaves, Triazine-Resistant Biotypes, *Amaranthus, Chenopodium, Poa, Polygonum, Solanum, Stellaria*

The rate of photosynthesis in intact leaves of a triazine-resistant biotype of *Amaranthus retroflexus* was about 15% lower than that of a triazine-susceptible biotype. Differences in photosynthesis between resistant and susceptible biotypes of *Polygonum lapathifolium*, *Poa annua* and *Solanum nigrum* were not significant, and absent in *Chenopodium album* and *Stellaria media*. The results are brought in relation to the appearance of resistant biotypes in the field.

Introduction

Repeated applications of triazines have resulted in herbicide resistance in an increasing number of weed species [1]. Gressel and Segel [2] suggested that the relatively slow appearance of resistance in natural, mainly susceptible populations is partly due to lower ecological fitness of resistant biotypes. That appearance might be faster at high selection pressure such as repeated use of persistent triazines. This view is supported by data on lower biomass production or competitive ability of resistant biotypes [3–5], and lower rates of photosynthesis [6].

A comparison of the photosynthetic capacity between resistant and susceptible biotypes of some weed species could be included in a program to determine the influence of different herbicides on photosynthesis in intact leaves of these biotypes. Before the herbicide treatments (on which will be reported separately [7]), the photosynthetic rates of untreated resistant and susceptible biotypes were determined in light intensity series.

Materials and Methods

The origin of the seeds of resistant and susceptible biotypes of the 6 weed species is indicated in Table I. The seeds were germinated in fine quartz sand moistened with 0.2% KNO_3, and subjected to alternating temperatures for 2–3 weeks. In the early cotyledon stage the seedlings were transferred to nutrient solution, placed in a climate room at about 21 °C and 60–70% relative humidity, and irradiated for 17 $h \cdot d^{-1}$ with HPI/T 400-W lamps at a light intensity of 110 $W \cdot m^{-2}$ (400–700 nm).

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The measurements were made after 28–46 days (Table I). A number of attached, just full-grown leaves were mounted in a horizontal position in flat leaf chambers (25 × 15 cm), except for *S. media* of which complete branches were inserted (leading to overestimation of leaf area). The CO_2 uptake of these leaves was determined in an open system [8] modified by using a computer to regulate and record gas flows, CO_2 concentration (340 vpm) and air humidity, and to calculate continuously the rates of photosynthesis and transpiration taking account of the dilution effect [9]. The temperature was kept at about 23 °C. The full light intensity from HPI/T 400-W lamps filtered through 5 cm of water was about 250 $W \cdot m^{-2}$ (400–700 nm). It was lowered by inserting iron screens of different light transmission, following a sequence from darkness to full light.

All light response curves of net photosynthesis (P_N) were first drawn separately. The mean curve for each biotype was obtained by averaging the P_N values in these curves at fixed intervals of 50 $W \cdot m^{-2}$. The 95% confidence limits (+ and −) were calculated as $(\sigma_{n-1}/\sqrt{n}) \cdot t$, where σ_{n-1} is sample standard deviation, $\sqrt{n}$ is the square root of the number of replicates, while t is derived from a probability distribution table [10], and depends on the degrees of freedom $(n-1)$ and the level of certainty.

Table I. Origin and growth period of the weed species.

Weed species	Origin	Period (d)
Amaranthus retroflexus L.	Dijon, F	36–38
Polygonum lapathifolium L.	Dijon, F	39–40
Chenopodium album L.	Oplo, NL	28–30
Solanum nigrum L.	Wageningen, NL	32–37
Poa annua L.	Kapelle, NL	36–40
Stellaria media (L.) Vill.	München, GFR	38–46

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Results

The results are compiled in Fig. 1. The photosynthetic rates in leaves of the atrazine-resistant biotype of *Amaranthus retroflexus* were significantly lower than those of the susceptible biotype. The rates were about 15% lower within most of the light range, but somewhat less at the highest intensity. The photosynthetic rates in leaves of resistant biotypes of *Polygonum lapathifolium*, *Poa annua* and *Solanum nigrum* were not significantly lower than those of the susceptible biotypes, while no differences were found for either *Chenopodium album* or *Stellaria media*. In most cases the variability was rather large.

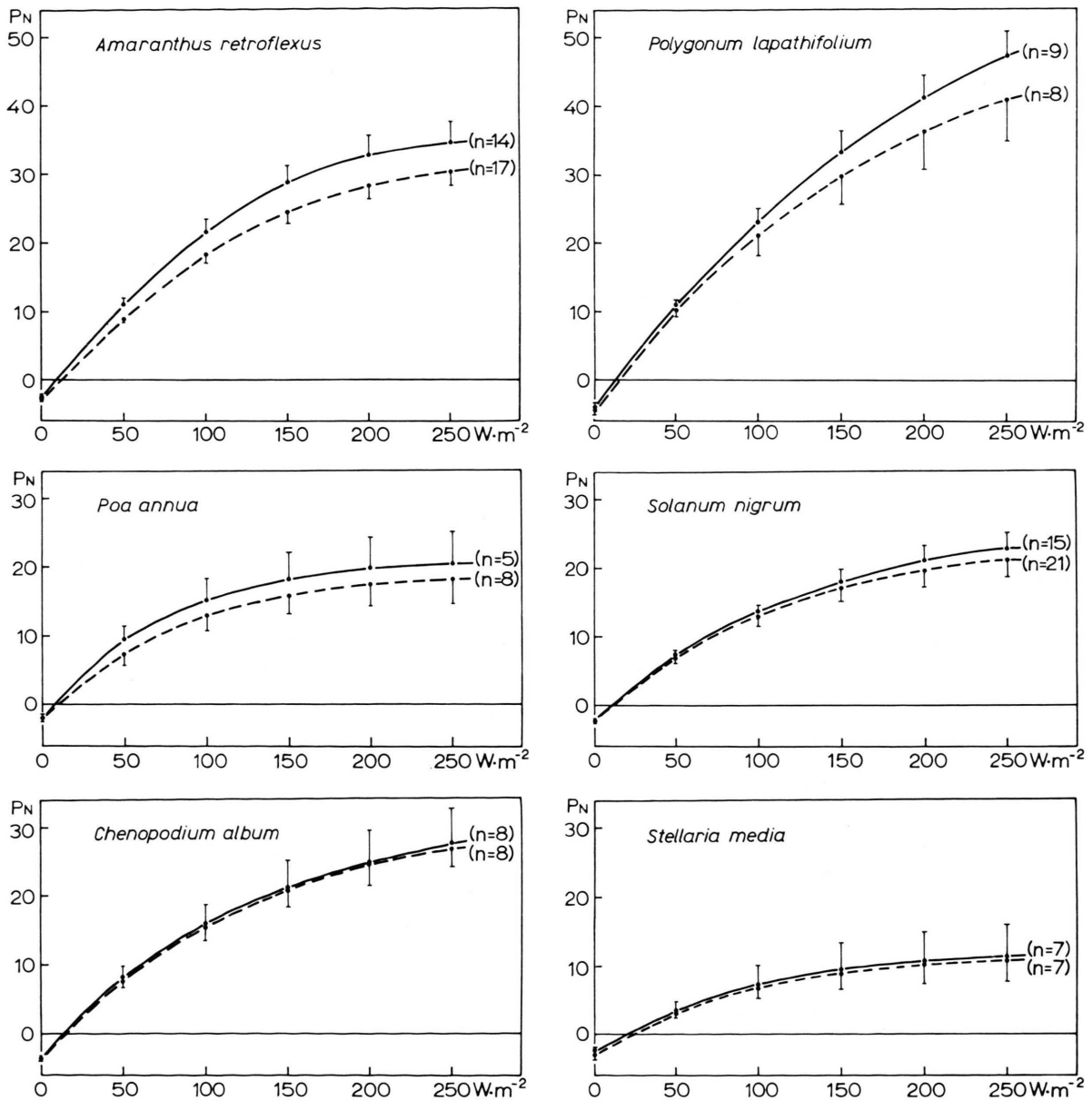

Fig. 1. Mean rates of net photosynthesis (P_N, in mg $CO_2 \cdot dm^{-2} \cdot h^{-1}$) of intact triazine-susceptible (——) and -resistant (– – –) biotypes of six weed species in relation to light intensity (400 – 700 nm). Vertical lines indicate 95% confidence limits (+ and –, but drawn at one side only); between brackets the number of replicates.

Discussion

The small difference in photosynthetic rate between resistant and susceptible biotypes of *Amaranthus retroflexus* might be a factor in competition, especially because this rate differs also under light limitation. Recently, a lower photosynthetic rate in resistant biotypes was also reported for *A. hybridus*, but this was not limited by electron transfer capacity [11]. Lower photosynthesis in resistant biotypes of *A. retroflexus* would be in agreement with the competition experiments by Conrad and Radosevich [3], and growth records by Gasquez, Darmency and Compoint [12]. On the other hand, Weaver, Warwick and Thomson [13] found no significant differences in growth characteristics between resistant and susceptible biotypes of *A. retroflexus*, although they did for *A. powellii*.

Differences in photosynthetic rates between resistant and susceptible biotypes were also observed for *Senecio vulgaris* [6], but here they were ascribed to reduced chloroplast efficiency in the resistant biotype [14]. Its growth was smaller [4, 15] and its competitive ability lower [3].

In this study the differences in photosynthesis between resistant and susceptible biotypes of the 5 other weed species were not significant. Other data on photosynthesis of biotypes of these species are not available. Our results on *Chenopodium album* disagree with most growth records [5, 12, 16, 17], while the susceptible biotype was also superior in competition experiments [5]. Similar growth differences were found for *Solanum nigrum* and *Polygonum lapathifolium*, although in the latter species these differences were also determined by temperature [12].

The variability in most of our experiments makes it impossible to distinguish between relatively small differences in the rate of photosynthesis. Both susceptible and resistant biotypes were rather variable, and this contrasts with some data on biomass production where resistant biotypes were more homogeneous [18, 19].

However, it remains to be seen whether even at lower variability true differences in the rate of photosynthesis can be assessed betweeen resistant and susceptible biotypes. This is because these biotypes were collected at random in the field, and probably differ not only in triazine resistance, but also in other characteristics which may influence photosynthesis can be assessed between resistant the availability of isogenic lines which genetically differ in herbicide resistance only [12].

It should also be mentioned that lower competitive ability is not *per se* based upon lower photosynthetic rates, since other factors such as germination temperature [16, 18, 20] and plant height may also be involved. Gasquez [18] pointed out also that low competitive ability of resistant biotypes is not the only hypothesis to explain their low initial incidence in a natural population. It is also possible that resistance is only present latently in the population, but developing slower and less coercive under the action of triazines.

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