EFFECT OF DEFOLIATION LEVELS ON RECOVERY OF LEAF AREA, ON YIELD AND AGRONOMIC TRAITS OF SOYBEANS[1]

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ABSTRACT - Four levels of defoliation (0, 33, 67 and 100%) were applied at four stages of development (V_3, V_8, R_2 and R_6) of soybeans (*Glycine max* (L.) Merrill) cv. Paraná, at the Embrapa-Centro Nacional de Pesquisa de Soja experimental station in Londrina, PR, Brazil. Plants were defoliated by hand, cutting off one leaflet of each leaf for each 33% of defoliation. Recovery of leaf area was measured at five and twelve days after defoliation, and mathematical simulations were made to study parameters of recovery. Results indicated intense recovery measured by liquid daily rate of leaf area increase (dr) and recovery time (rt) for low defoliation levels, specially when applied at vegetative stages. During the reproductive period, levels of defoliation reduced the rate of the soybean natural trend of losing leaf area. Yield was affected only by 67 and 100% defoliation applied at R_6, while main agronomic traits such as date of harvesting maturity, plant lodging and height were not affected by the treatments.

Index terms: economic damage, artificial defoliation, recovery parameters.

EFEITO DE NÍVEIS DE DESFOLHAMENTO NA RECUPERAÇÃO DE ÁREA FOLIAR E NA PRODUÇÃO E CARACTERÍSTICAS AGRONÔMICAS DA SOJA

RESUMO - Quatro níveis de desfolhamento (0, 33, 67 e 100%) foram aplicados em quatro estádios de desenvolvimento (V_3, V_8, R_2 e R_6) de soja, cv. Paraná, na estação experimental da Embrapa-Soja, em Londrina, PR. O desfolhamento foi efetuado cortando-se manualmente um folíolo de cada folha, em cada 33% de desfolhamento aplicado. A recuperação da área foliar foi medida cinco e doze dias após o desfolhamento, e foram feitas simulações matemáticas para estudar os parâmetros de recuperação. Os resultados indicaram recuperação intensa da área foliar, medida pela taxa líqüida de aumento da área foliar (dr) e pelo tempo de recuperação (rt) em baixos níveis de desfolhamento, especialmente no período vegetativo. Durante o período reprodutivo, os níveis de desfolhamento reduziram a taxa de perda natural da área foliar da soja. A produção de grãos foi afetada somente por desfolhamentos de 67 e 100% aplicados em R_6, enquanto as principais características agronômicas, como data de maturação para colheita, acamamento, e altura de plantas, não foram afetadas pelos tratamentos.

Termos para indexação: danos econômicos, desfolhamento artificial, parâmetros de recuperação.

INTRODUCTION

Earlier studies on the effects of artificial defoliation on soybean aimed to simulate weather phenomena like hail, thunderstorms or heavy rains accompanied by gusty winds (Gibson et al., 1943; Kalton et al., 1949; Weber & Caldwell, 1966). More recent investigations were directed to the relationships between foliage feeders and yield. According to these studies, defoliation levels of less than one third of leaf area did not affect soybean yield (Gould, 1960; Rosas, 1967; Daugherty, 1969; Turnipseed, 1972; Gazzoni & Minor, 1979). Yield reduction was reported with 33% of defoliation, associated with critical soybean stages or long duration of the period of stress (Daugherty, 1969; Todd & Morgan, 1972; Gazzoni, 1974; Gazzoni & Minor, 1979), while Begun & Eden (1965) and Rosas (1967) refer no yield reduction due to this defoliation level. Weber (1955) found that 50% defoliation between V_1 and full bloom had little effect on yield, and that significant yield loss occurred only with 100% defoliation during this

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period. On the other hand, Pickle & Caviness (1984) reported no yield loss with 100% defoliation at V_5. Turnipseed & Kogan (1987) indicated that soybean response to defoliation from emergence to R_3 has been consistent across environments and cultivars.

McAlister & Krober (1958) demonstrated that 40% defoliation near seed initiation resulted in only a 9% reduction in yield, whereas an 80% defoliation caused a 32% yield loss. With 50% of defoliation during the reproductive period Camery & Weber (1953), Gould (1960), Daugherty (1969) and Turnipseed (1972) encountered yield reduction, whereas during the vegetative stage soybean yield was not affected (Hanway & Thompson, 1967; Todd & Morgan, 1972).

Higher defoliation levels (67 and 100%) also interacted with the development stage of soybean, as Begun & Eden (1965), Gazzoni (1974) and Gazzoni & Minor (1979) reported no yield reduction on vegetative stages, while progressive reduction on reproductive stage was found, as also reported by Hanway & Thompson (1967) and Todd & Morgan (1972). Fehr et al. (1981) demonstrated that, in both determinate and indeterminate cultivars, the most sensitive stages to defoliation were R_5 or $R_{5.5}$, with 80% yield loss when 100% defoliation was applied at these stages. With total defoliation, Goli & Weaver (1986) found greater yield reduction with 100% defoliation applied at R_4 or R_5, than at R_6. Caviness & Thomas (1980) reported only 13-17% yield loss for defoliation at R_4 to $R_{5.5}$, showing that even at critical stages, soybean plants can stand considerable leaf loss. A defoliation of 70% at R_6 reduced yield by 20% (Turnipseed & Kogan, 1987). Board et al. (1994) reported that 100% defoliation at $R_{6.3}$ resulted in 40% yield reduction, whereas defoliation at $R_{6.6}$ caused 20% yield loss.

Soybean yield can be decomposed in terms of plant stand, pods per node, seeds per pod and seed weight. Several studies reported that lower yield was correlated to reduced seed or pod number (McAlister & Krober, 1958; Thomas et al., 1976; Caviness & Thomas, 1980; Hammond & Pedigo, 1982; Higgins et al., 1984; Ostlie & Pedigo, 1985; Board & Harville, 1993), whereas others found an effect on seed size (Egli et al., 1976; Fehr et al., 1981; Ingram et al., 1981; Ostlie & Pedigo, 1985; Goli & Weaver, 1986) or seed number (Fehr et al., 1977; Hammond & Pedigo, 1982; Higgins et al., 1984), but Ostlie & Pedigo (1985) referred no differences on number of seeds/pod due to defoliation treatments. Kalton et al. (1949), Teigen & Vorst (1975), Hinson et al., 1978, Fehr et al. (1981), Higgins et al. (1983) and Ostlie & Pedigo (1985) reported a shortening of plant height linearly associated to defoliation intensity. Higgins et al. (1983) also found fewer nodes on the main stem, but no reduction in plant stands or rates of branching of soybeans defoliated by *Plathypena scabra*. Moreover, there was a significant inverse linear relationship between the lodging score and density of larvae causing defoliation, also reported by Kalton et al. (1949), Fehr et al. (1977), Ostlie & Pedigo (1985).

Leaf area compensation for defoliation may be expressed through changes in new leaf area expansion or in normal plant senescence. Experimental data measuring leaf area recovery were reported by Gazzoni (1974), who found a general trend of high recovery when treatments were applied on vegetative stages, with recovery indexes being more intense at high defoliation levels. Low and medium defoliation levels applied at reproductive stages provoked reduction of leaf area beyond natural senescence, while total defoliation induced a light recovery of leaf area. However, this investigation was based on leaf area present near physiological maturity, without reference to leaf area recovery just after the application of the treatments. Fehr et al. (1981) reported that development of new leaf area after defoliation at R_4 and $R_{4.5}$ was greater for the undeterminate variety and negligible for defoliations at $R_{5.5}$ and R_6, stating that the difference in leaf area recovery could not account for all the difference in yield reduction. Board et al. (1994) commented that defoliation during the vegetative period usually has shown little effect on yield, largely due to leaf regrowth potential at this time. Contrarily, Boote (1981) contested what he called "the widely accepted concept of compensatory regrowth", stating that it was largely a myth. Higgins et al. (1983) agreed with this statement, as their study did not detect any compensatory regrowth in leaf area. Also, Ostlie & Pedigo (1985) stated that compensation was minimal, as defoliated plants had greater leaf area in the lower abscission stratum in contrast to little evidence of compensation on the higher stratum, exception made to one year of more intense defoliation, when plants had more trifoliates following defoliation.

There are several references to plant species producing more leaf area than actually needed for maximum interception of solar radiation (Brougham, 1956, 1958; Davidson & Donald, 1958; Watson, 1958; Murata, 1961; Stern & Donald, 1962). Plant leaves are not only photosynthesizing organs, but also act as transitory storage tissue. Primary accumulation of photosynthates and absorbed nutrients in soybeans particularly occur in leaves, to be translocated afterwards to pods and seeds. Studies made by Henderson & Kamprath (1970) showed a peak in nutrient and dry matter accumulation in the transition between R_5 and R_6 stages of soybean development. The rate of dry matter accumulation in both vegetative tissue and total plant decreased following the peak, due to reduced growth and leaf fall. The decrease in nitrogen content in the leaves and stems after bloom indicated translocation to pods and seeds, in spite of total nitrogen accumulation persisting late in the growth cycle. Also, phosphorus and potassium reached a peak during pod filling stage when translocation to pods and seeds provoked reduction of their content in vegetative parts of the plants. These results can largely explain yield reductions associated with medium to high defoliations applied between pod fill and physiological maturity. They can also help explain the low impact of defoliation when applied early in the vegetative stage, when the plants have the ability and the time to rebuild any loss of photosynthates stored in lost leaf area.

Seed size is determined by seed filling rate and the effective seed filling period, according to Gbikpi & Crookston (1981). Kaplan & Koller (1974) found yield to be influenced by seed filling rate during the effective filling period, while Egli et al. (1976) cited that yield was correlated with genetic and environmental effects on the length of the effective filling period. Defoliation decreases yield by reduction of plant photosynthesis, reduced light interception, reduction of stored dry matter caused by leaf area loss and reduction of the filling period (Hinson et al., 1978; Ingram et al., 1981). The relationship of dry matter production and accumulation rate on leaf area index (LAI) is well understood, specially for pasture and rice (Brougham, 1956; Davidson & Donald, 1958; Watson, 1958; Murata, 1961). Meanwhile, different approaches of plant response to LAI were found exceeding effective photosynthetic leaf area. Kasanaga & Monsi (1954) referred to the "optimum LAI" approach, when the dry matter accumulation reaches a maximum. Brougham (1956) and Williams et al. (1965a, 1965b), defined a point called critical LAI, when plants still produced and accumulated dry matter at the maximum rate, even when maximum radiation interception rate had declined. Shibles & Weber (1965) defined soybeans as a species following the critical LAI theory. Sakamoto & Shaw (1967a, 1967b) reported that light interception occurs primarily at the top and periphery of the canopy, and that distribution of solar radiation inside the canopy had an exponential adjustment, indicating that effective LAI is solely a portion of observed LAI and that lower leaves had more of a storage than a photosynthetic function. This observation can help to explain why reduction of leaf area had presented no direct correspondence with soybean yield before the plant starts filling the seeds and why during pod filling, loss of leaf area can affect the yield.

Ostlie & Pedigo (1985) proposed that final yield is related to soybean accumulation of photosynthetic energy, and the way this energy is divided between structural and reproductive components. Through their data, the authors concluded that yield reductions were proportional to reduction in total plant weight, therefore soybean compensation evaluated by increased partitioning of energy was not present.

Hammond & Pedigo (1982) stated that dry weather conditions produced very small leaf areas and resulted in much greater yield reductions, in contrast to other study conducted on abundant moisture conditions. The same results were found by Kincade et al. (1971) and Smith & Bass (1972), indicating that adequate moisture was a pre-requisite to recovery of soybeans from insect damage. Ostlie & Pedigo (1985) noted that soybeans compensated for development retarded by drought through the rapid addition of new leaves and increased leaf area expansion when normal rain resumed.

The main purpose of this study was to quantify the recovery of soybean leaf area upon short and medium time range after defoliation, based on parameters of daily increase of leaf area and time required to recover potential LAI.

MATERIAL AND METHODS

The experiment was conducted at the experimental station of the Embrapa-Centro Nacional de Pesquisa de Soja, located in Londrina, PR, Brazil, using soybean cv. Paraná, planted on November 21, with 0.5 m between rows and 25 seeds per meter of row. One week after germination the density of plants was equalized to 20 per meter of row. Experimental plots measured 2x7 m with four rows of plants; the two outer rows were considered borders rows. The two central lines were divided into six sections of 0.5 m each and another of 4 m of row (Fig. 1).

Treatments consisted of four defoliation levels (0=check; 33%; 67% and 100%), applied at stages V_3 (three leaves completely unrolled), V_8 (eight leaves completely unrolled), R_2 (full bloom) and R_6 (seed filling), according to Fehr et al. (1971). These stages were chosen because the key defoliator of Brazilian soybeans (*Anticarsia gemmatalis* Hübner) attacks plants from the early vegetative to mid-reproductive stages. In total, the experiment comprised 16 treatments and the experimental design was a randomized complete block, with three replications. Plants were hand defoliated, and each 33% of defoliation corresponded to one leaflet of each partial or totally unrolled leaf to be cut. For the 33% level, the leftmost leaflet of the lower leaf was cut, the central leaflet of the above leaf, the rightmost leaflet of the next leaf, starting again with the left one for the fourth leaf. For the 67% treatment, the left and central leaflet of the lowest leaf were cut, followed by the central and right leaflet of the second leaf, the outer leaflets for the third leaf, and starting the cycle again with the next leaf. Defoliation was first applied to borders during the first day and to the rest of the plot on the next day, since the application of treatments to all plots could not be performed in a single day. From the two central rows of each plot leaflets were collected from 2 m of the center of the rows to measure leaf area through a leaf area meter (Hayashi Dekoh Co. Ltd, Model AAC-400). Previous studies (Gazzoni, 1974; Gazzoni & Minor, 1979) demonstrated that defoliation induced opening of new leaves after 3-5 days, so two evaluations of leaf area were made at five and 12 days after defoliation, by cutting and measuring all leaves present in 0.5 m of the two inner rows.

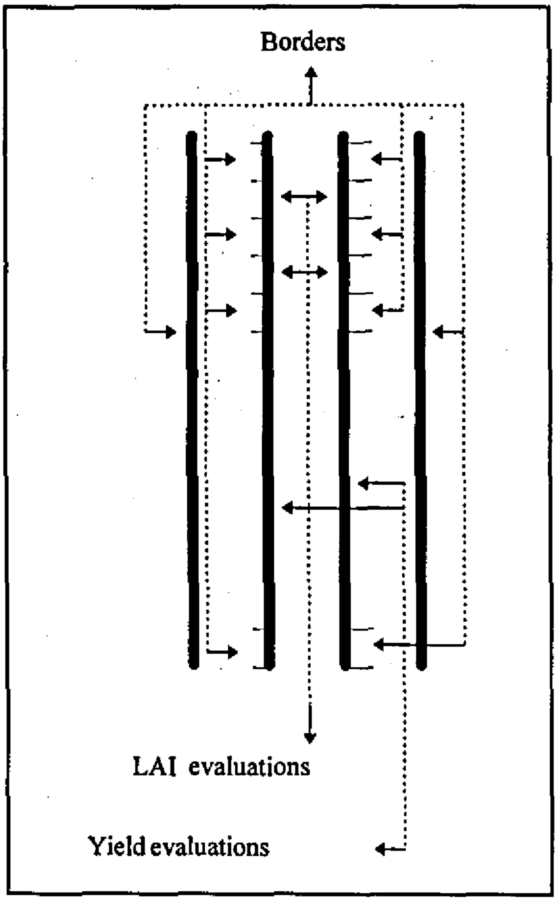

FIG. 1. Schematic representation of an experimental plot. Thicker lines represent soybean rows.

The index of linear daily rate of leaf area growth (dr) was obtained through the following formula:

dr=LA/GA/TP, where

LA= leaf area recovered in square meters;

GA= ground area corresponding to the LA sampling area, in square meters;

TP= number of days from defoliation to the measurement of the recovered leaf area.

The recovery time index (rt) was established with the help of mathematical equations, looking for the number of days that would be necessary for a defoliated soybean plant to reach, for the first time, the same LAI of a non-defoliated plant, with the same age. It represented a measure of the speed of leaf area recovery, expressed in days.

At the end of the soybean cycle, plots were harvested by hand, using 4 m of each central row for yield evaluation and 0.5 m of the same row for other characteristics. For adjustment of fitness equations 16 different mathematical models were tested, and statistical analysis were made using the Statistical Analysis System (Barr & Goodnight, 1972)

RESULTS AND DISCUSSION

The soybean cycle lasted 110 days from planting to harvest. The leaf area index (LAI) was measured at several stages of development, and results are presented in Fig 2. The highest LAI value (5.0) was attained five days after full bloom, when determinate soybeans naturally stop growing and start reducing the amount of leaves in the plant. Very close LAI values (5.69-5.73) were also obtained by Higgins et al. (1983), but were different from those of Gazzoni (1974), probably due to lower soil fertility of this last experiment. A cubic exponential equation was the best fit (r^2=0,99) found to describe the relationship between days after planting and LAI:

$$Y=0.012*2.718281^{(0.24x-0.00297x^2+0.0000096x^3)}$$

being Y the LAI at the x day after planting date.

Analysis by growth stage

In mid-December a 20 day drought, accompanied by high mean temperatures probably was the reason for stable LAI verified just after V_3. This condition might also have affected the shape and intensity of leaf area recovery during this period. From stages V_3 to V_6 the linear daily rate of leaf area growth (dr) for non-defoliated soybeans was 0.068 (Table 1), meaning an increase of 680 cm^2 of leaf per square meter of soil. When 33% defoliation was applied at V_3, the dr was 0.083, showing that leaf area grew 20% faster than the check (Fig. 3). Defoliation of 67% at this stage resulted in a similar growing rate (dr=0.069) to the check, while 100% defoliation reduced the speed of leaf area development by 58% (dr=0.04). The best fit equations describing the relationships between days after defoliation and leaf area index are shown in Table 1. These equations are very useful for prognosis of short and medium time leaf area recovery, and have special application on mathematical simulation models of both soybean growth and insects attacking leaf area, specially for the Brazilian key defoliator of soybean, *Anticarsia gemmatalis* (Gazzoni et al., 1998). For this early de-

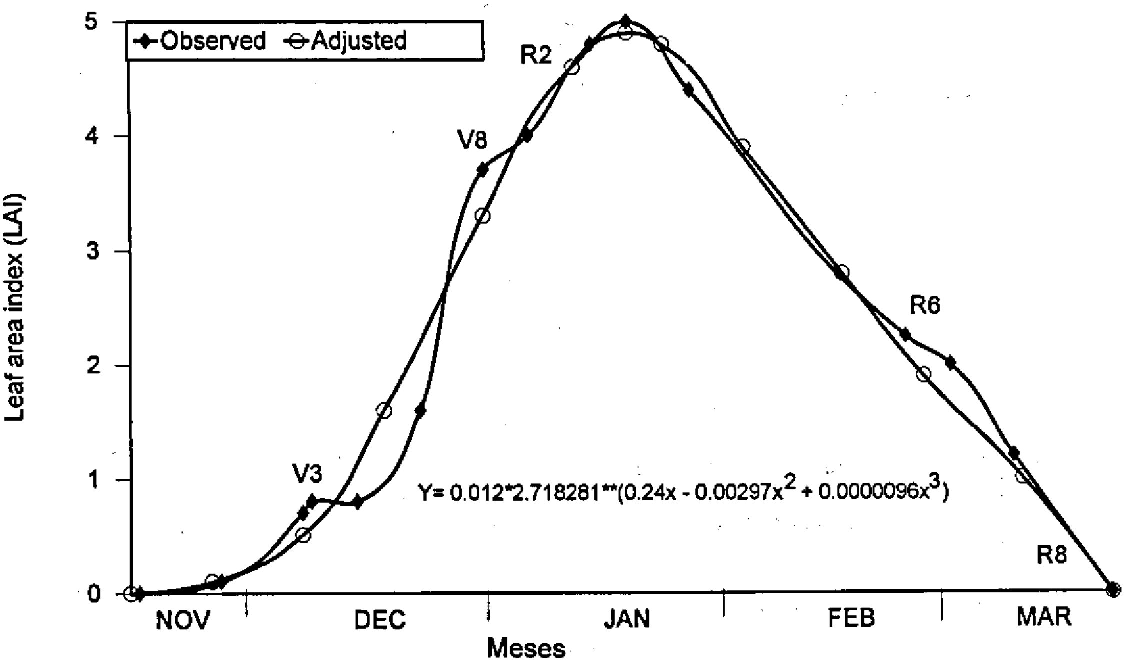

FIG. 2. Leaf area index of soybeans cv. Paraná.

TABLE 1. Regression equations and coefficient of determination (r^2) between days after application of treatments and leaf area index of soybeans with different degrees of defoliation[1].

Stage	Defoliation %	Equation	r^2
V_3	0	$Y=0.86-0.067X+0.0095X^2$	1.0
	33	$Y=0.6-0.062X+0.01X^2$	1.0
	67	$Y=0.29-0.025X+0.0067X^2$	1.0
	100	$Y=-0.04+0.04X$	1.0
V_8	0	$Y=3.67+0.028X+0.0045X^2$	1.0
	33	$Y=2.16+0.24X-0.00595X^2$	1.0
	67	$Y=0.95+0.28X-0.076X^2$	1.0
	100	$Y=0.009+0.089X+0.0028X^2$	1.0
R_2	0	$Y=4.31+0.21X-0.015X^2$	1.0
	33	$Y=2.89+0.11X-0.043X^2$	1.0
	67	$Y=1.41+0.14X-0.053X^2$	0.97
	100	$Y=-0.097-0.0017X+0.0045X^2$	1.0
R_6	0	$Y=2.27-0.012X-0.0054X^2$	1.0
	33	$Y=1.66-0.165X+0.007X^2$	1.0
	67	$Y=0.79-0.045X+0.001X^2$	1.0
	100	$Y=0.09+0.0075X+0.00036X^2$	1.0

[1] All equations were statistically significant for $p=0.05$; as some fitness models required $X <> 0$, for these calculations the day of defoliation was considered $X = 1$; values of $r^2=1$ are frequently found when adjusting data with only three sampling points.

velopment stage (V_3), the dr of treatments varied between 40% below and 14% above the check (Table 2), indicating that: a) the plant was unable to react adequately to defoliation by intrinsic characteristics or due to the lack of optimal soil moisture; b) it had no need of an intense reaction, as the new LAI standards were adequate for producing enough seeds of good reproductive quality; c) the relatively long period of vegetative stage still remaining triggered a reaction of soybeans so as to recover leaf area at slower rates, based on medium time strategy, or d) a combination of the three possibilities.

From V_8 to R_1 the dr was 0.092, growing faster than during the V_3 to V_6 period (Fig. 4). Applying 33% defoliation to soybeans at V_8 represented a change to dr = 0.158, ca. 70% higher than the check, indicating a positive reaction of the plants to recover full leaf area in a short time. This was a 'wise decision' considering the proximity of the natural inflection of the soybean LAI curve. Even more intense was the recovery rate when 67% defoliation was applied at V_6 (dr = 0.175); however, in this case initial leaf area reduction was high enough to im-

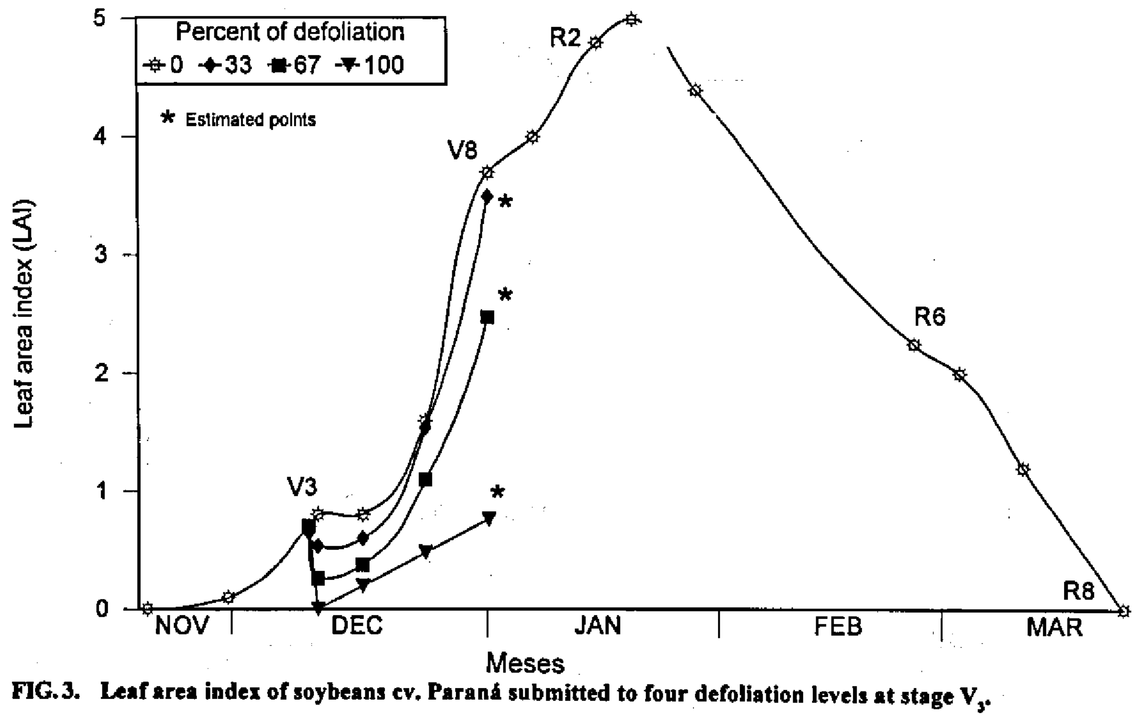

FIG. 3. Leaf area index of soybeans cv. Paraná submitted to four defoliation levels at stage V_3.

pede LAI from reaching its potential. In the most severe treatment (100%), recovery was close to linear against time, with a dr = 0.14, almost 50% higher than the rate of the check, indicating again that the plant reaction was slightly more intense with low and medium defoliation levels, and that absolute values for each defoliation level were higher than that obtained with defoliation at V_3.

TABLE 2. Index of linear daily rate of leaf area growth (dr) of soybeans with different degrees of defoliation.

Stage	Defoliation %	0-5 days	6-12 days	0-12 days
V_3	0	0.00	0.11	0.07
	33	0.02	0.13	0.08
	67	0.02	0.10	0.07
	100	0.04	0.04	0.04
V_8	0	0.06	0.11	0.09
	33	0.20	0.13	0.16
	67	0.25	0.12	0.18
	100	0.13	0.14	0.14
R_2	0	0.10	-0.09	0.00
	33	0.08	0.03	0.05
	67	0.14	0.01	0.07
	100	0.05	0.08	0.07
R_6	0	-0.05	-0.11	-0.09
	33	-0.12	-0.03	-0.07
	67	-0.05	-0.02	-0.03
	100	0.02	0.02	0.02

LAI peaked five days after full bloom (Fig 2), and then started to decrease until plants reached complete senescence. In this case, the dr of the check was positive before the LAI peak, and negative after that. For the five days following R_2, plants grew at maximum speed, being the highest value obtained with 67% defoliation, while from 6 to 12 days after R_2 the check had a dr = -0.086, implying that lower leaves were yellowing and falling off the plants. Overall dr of the period for the non-defoliated plants was null. A reduction of 33% of leaf area produced a dr=0.05, showing an increase in leaf area even while non-defoliated soybean plants were losing leaf area. This kind of behavior was also observed for defoliations of 67 and 100% (dr=0.07). Nevertheless, looking at the partial indexes for 0-5 and 6-12 days after R_2, the ones for the first five days are higher, exception made to 100% defoliation, meaning that, in spite of the continued increase in leaf area, physiological changes were triggered, what reduced the rate of LAI increase (Fig. 5). In the case of 100% defolia-

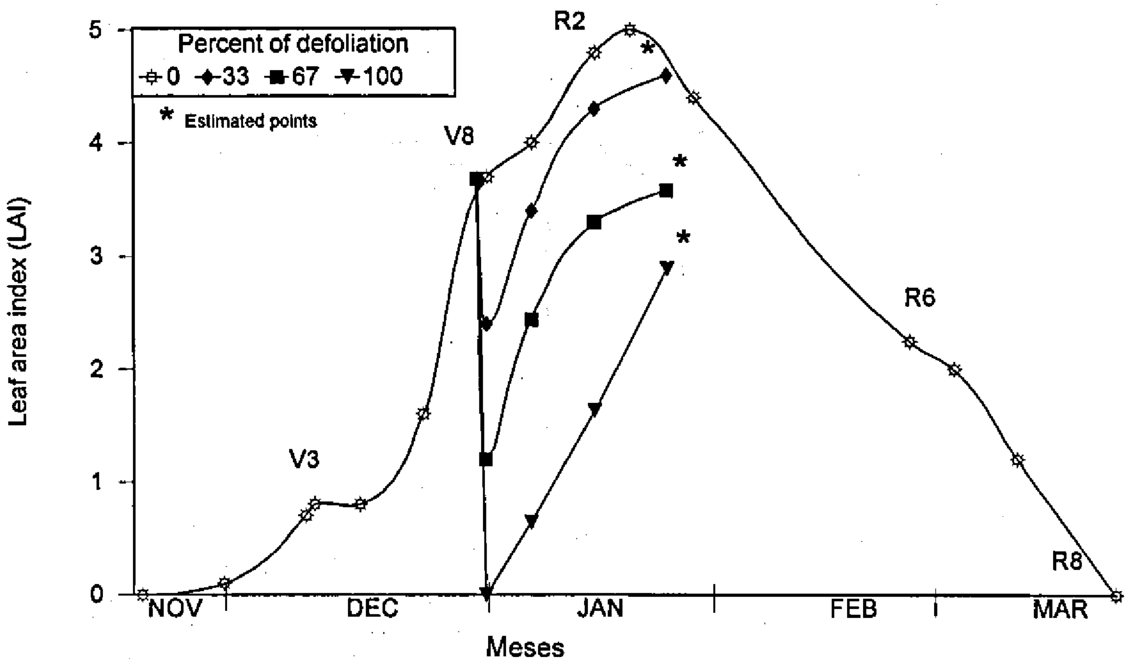

FIG. 4. Leaf area index of soybeans cv. Paraná submitted to four defoliation levels at stage V_8.

tion, evidence was that: a) the need for fast leaf area recovery overcame the plant process of loosing area (there was no additional leaf area to loose), extending the period of vegetative growth beyond the date it would normally stop growing; b) the biochemical pathways for triggering the mechanism of leaf recovery were strongly dependent on chemicals produced or stored by leaves, that were absent; or c) a combination of both hypothesis.

In the R_6 stage, the rate of natural leaf area reduction in check plants was quite similar to the second period (6-12 days) discussed above (dr=-0.09), as shown in Fig. 6. Application of treatments in this stage at first accelerated senescence for 33% defoliation (dr= -0.12), but from six to 12 days after defoliation the dr index was reduced to -0.03, similar to the reaction of plants receiving 67% defoliation. Complete defoliation led to a slight increase in soybean leaf area (dr = 0.02).

Results of intensity of leaf area recovery are apparently in contrast with those obtained by Higgins et al. (1983) and Ostlie & Pedigo (1985). But some different experimental conditions can partially explain different conclusions. In their study Higgins et al. (1983) had defoliation of soybeans only after bloom and in the upper stratum of soybean canopy, in order to mimic *Plathypena scabra* infestations. Also, the soybean variety used was Amsoy, an indeterminate soybean and, according to comparisons between leaf area/plant presented in their work, defoliation measured two weeks after bloom varied between ca. 20 to 35%, which are considered light defoliation in our work. Under the same conditions (low defoliation at reproductive stage) the dr was found to vary from low (0.03) to negative (-0.07). Ostlie & Pedigo (1985) did not mention the soybean variety used, but also applied defoliation treatments at fool bloom, and defoliation levels obtained, measured as percentage of leaf area reduction in relation to the check, were always under our lightest treatment, so the same considerations made above apply to this case. Furthermore, the authors mentioned that, in one year of more intense defoliation, the plants had more trifoliates following defoliation, meaning a kind of leaf area recovery, that would match with our findings (slight regrowth was observed following 33% defoliation on R_2).

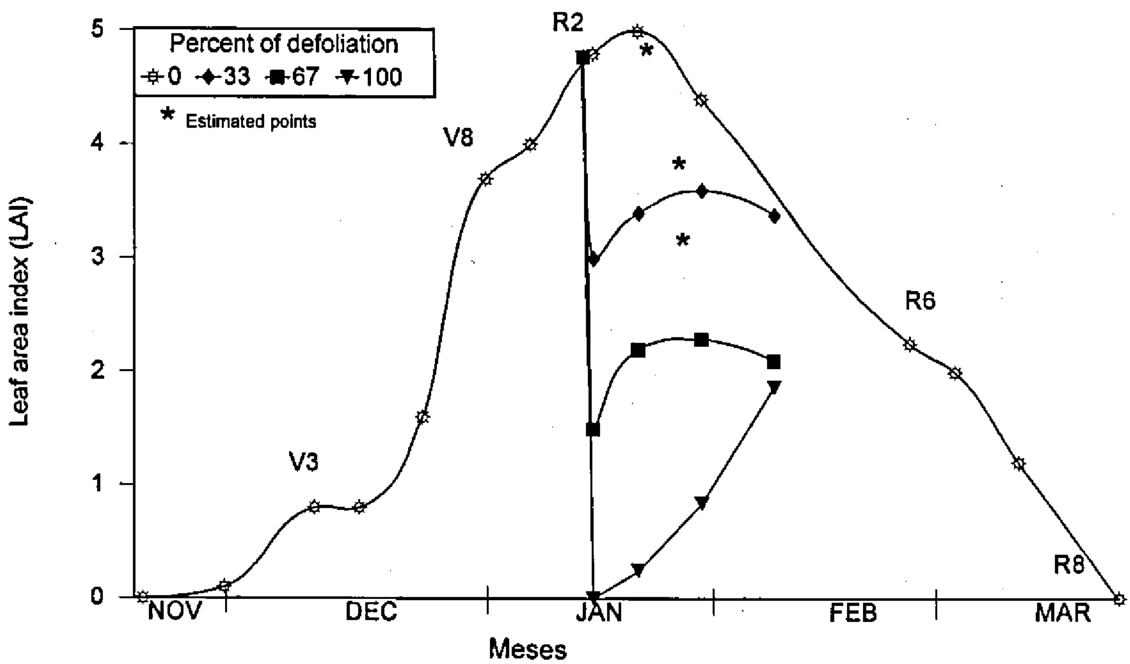

FIG. 5. Leaf area index of soybeans cv. Paraná submitted to four defoliation levels at stage R_2.

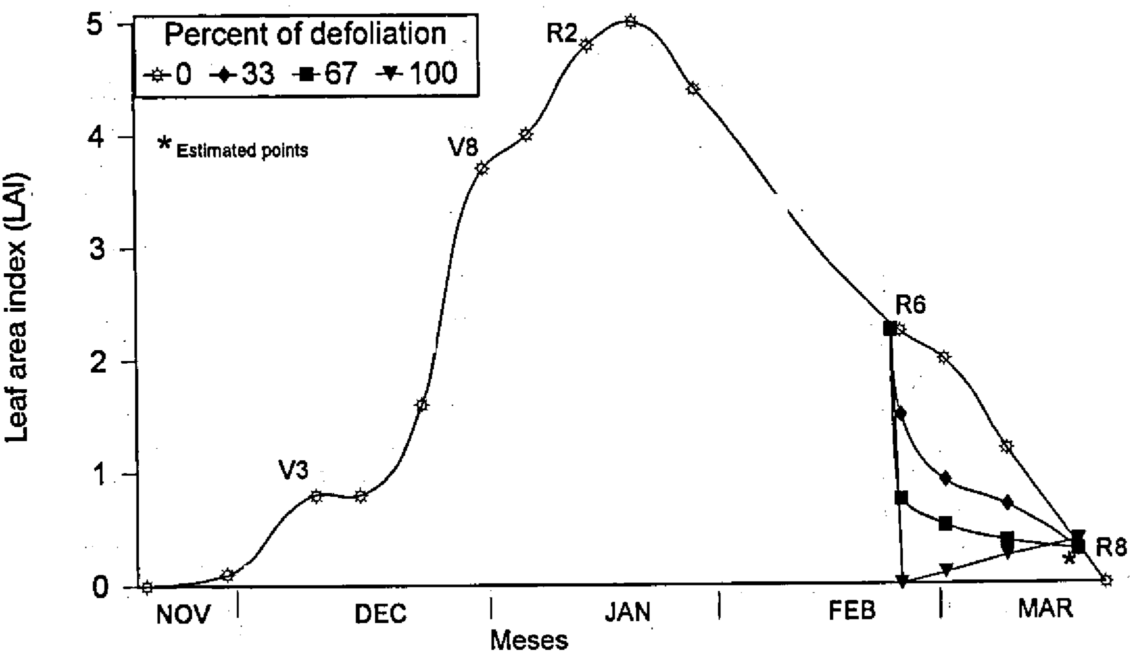

FIG. 6. Leaf area index of soybeans cv. Paraná submitted to four defoliation levels at stage R_6.

An important parameter to evaluate the reaction of the plant to different intensities of defoliation, which also affects the timing of treatment application, is the time that would be required to reach again potential LAI, as estimated by mathematical simulations. The recovery time index (rt) is a measure of the speed of leaf area recovery, in terms of number of days to overlap check values of LAI. Equations describing the relationship between days after defoliation and percent of leaf area recovery are shown in Table 3.

For early season defoliations, recovery time was an exclusive function of the degree of leaf reduction, as rt varied between 13-14 days for 33%, 19-26 days for 67% and 34-35 days for 100% defoliation. Evidence was that no matter in what stage of the vegetative period defoliation was applied, the key element for rt definition was the intensity of defoliation. These simulations are of theoretical importance because they did not consider the natural leaf area reduction for both defoliated and non-defoliated plots after full bloom, since recovery of leaf area from defoliation made at the end of vegetative period (V_8) continued in the beginning of the reproductive stage. During full bloom, calculated rt increased to 24 (33%) or 41 (67%) days, while the value calculated for complete defoliation was three days longer than the time between day of defoliation and expected day of complete senescence, indicating that 100% defoliation in this stage would not allow the plants to reach their potential LAI up to the end of the plant cycle. For defoliation applied at R_6, there

TABLE 3. Regression equations and coefficient of determination (r^2) between days after application of treatments and percent of leaf area recovery.

Stage	Defoliation %	Equation[1]	r^2	rt
V_3	33	$Y=-42.3+0.78X-0.0023X^2$	1.00	13
	67	$Y=-6.3+0.12X+0.0021X^2$	1.00	27
	100	$Y=-0.597+0.35X$	0.92	35
V_8	33	$Y=-31.6+0.46X$	0.96	15
	67	$Y=-10.31+0.295X$	0.91	19
	100	$Y=-0.23+0.35X$	0.99	35
R_2	33	$Y=-42.8+0.67X$	0.93	24
	67	$Y=-21.03+0.62X$	0.98	41
	100	$Y=0.53+0.61X$	0.99	62

[1] All equations were statistically significant for $p=0.05$.

were no mathematical models fitting the data that would generate acceptable rt values, indicating that any level of defoliation applied at reproductive stages would not result in soybean recovery to potential LAI before physiological maturity.

Analysis by level of defoliation

The lower level of defoliation (33%) normally induced a quick and positive plant response in order to recover lost leaf area. On V_3 calculated rt was 13.3 days, about the same as on V_8 (rt = 14.8); in this case helped by the fact that check plots were naturally losing leaf area, as also happened when defoliation occurred on R_2; however, at this stage rt was almost double of those required for vegetative stages. As shown on Fig. 5, not only was the rt longer, but the absolute leaf area was also intensely reduced, as the integration against time of difference between LAI of treatment and the check was lower than any of the treatments applied to vegetative stages. Furthermore, the dr was always positive when 33% of defoliation was applied up to bloom, becoming negative for the treatment applied at R_6.

Defoliation of 67% induced rt = 26,6 when applied at V_3 and V_8 stages. This surprising low recovery time was partially due to the highest individual daily rate (dr = 0.18), and also to the fact that check plants started losing leaf area 16 days after application of the treatment, making it difficult to adjust a mathematical equation that could take it into account. This low recovery time can be explained by the fact that the sampling period did not cover the moment of inflection of the LAI curve for the 67% defoliation, and that prognosis was not made on data effectively observed. Treatments of 67% defoliation applied at reproductive stages demanded high rt values, including unrealistic ones for the R_6 stage, and also produced negative dr values when the treatment was applied at R_6.

Complete defoliation would require rt = 34.8 when applied at V_3, similarly for V_8 (rt = 35), and would not reach the potential LAI again when applied after blooming. Values of rt for 100% defoliation were higher when the plants were still growing, as compared to other defoliation levels, and the highest value for defoliation of 100% was attained when the treatment was applied at V_8.

Analysis of grain yield, its components and agronomic traits

The effect of defoliation on the yield of soybeans is shown in Fig 7. There was no difference for any level of defoliation applied from V_3 to R_2 and for 33% applied at R_6, while 67 and 100% of defoliation applied at R_6 decreased soybean yield by 25 and 38%, respectively. Reports in the literature agreed that low to medium intensity defoliation applied at vegetative stages did not affect the yield (Gould, 1960; Begun & Eden, 1965; Rosas, 1967; Daugherty, 1969; Turnipseed, 1972; Gazzoni, 1974; Gazzoni & Minor, 1979), but contradictions were found with both high levels of defoliation applied at vegetative stages or low defoliation levels applied at reproductive stages, sometimes decreasing soybean yield (McAlister & Krober, 1958; Begun & Eden, 1965; Hanway & Thompson, 1967; Todd & Morgan, 1972; Gazzoni, 1974; Gazzoni & Minor, 1979; Pickle & Caviness, 1984). On the other hand, defoliation levels of 67 and 100% applied at vegetative stages did not reduce yield (Begun & Eden, 1965; Gazzoni, 1974; Gazzoni & Minor, 1979), but progressive reduction

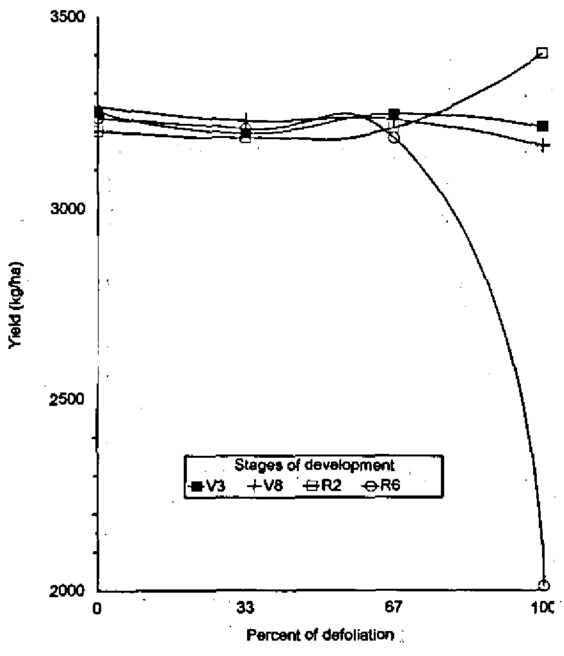

FIG. 7. Grain yield of soybenas cv. Paraná, submitted to four defoliation levels, applied on four stages of soybean development.

was observed when applied at reproductive stages (Hanway & Thompson, 1967; Todd & Morgan, 1972). Complete defoliation produced greater yield reduction when applied at R_5 (Fehr et al., 1981) or at R_4 and R_5 (Goli & Weaver, 1986). A defoliation of 70% at R_6 reduced yield by 20% (Turnipseed & Kogan, 1987), while Board et al. (1994) reported that a 100% defoliation at $R_{6.3}$ and $R_{6.6}$ resulted in 40 and 20% yield loss, respectively. It seems that these unmatched conclusions resulted from externalities like soybean variety (group, cycle, growth type, genetic potential), cultural practices (weed infestation, insect control, row spacing, plant density, time of planting), soil (fertility, structure, compactation, moisture), weather condition (radiation, temperature, precipitation, wind, hail), and other traits like plant height or lodging, which can interact with defoliation treatments and alter results according to prevalent conditions.

For the purpose of better understanding the contribution of yield components and their relationships to soybean yield, data are presented in terms of percent of variation relative to the check (Table 4). As a rule, yield components followed almost the same trend pattern of the grain yield. The yield/plant was very closely related to yield/hectare ($Y=0.026+0,97x$, $r^2=0.94$). All treatments applied at reproductive stages produced yield/plant lower than the check, but only 67 and 100% defoliation applied at R_6 significantly reduced the yield/plant in relation to the check. The number of pods/plant was the component most intensely affected by defoliation and the one mainly responsible for yield reduction. The relationship between pods/plant and yield/ha followed a linear model ($Y=0.21+0.87x$, $r^2=0.95$). From the slope of the equation it can be estimated that each 1% of reduction of pods/plant would reduce soybean yield by 0.87%. Several authors reported a reduction of the number of pods/plant associated with defoliation, resulting in soybean yield decrease (McAlister & Krober, 1958; Thomas et al., 1976; Caviness & Thomas, 1980; Hammond & Pedigo, 1982; Higgins et al., 1984; Ostlie & Pedigo, 1985; Board & Harville, 1993). According to Ostlie & Pedigo (1985), yield reduction due to defoliation reflected primarily in pod number reduc-

TABLE 4. Soybean grain yield and its components, expressed as percent of the check.

Stage	Defoliation (%)	Yield	Yield/plant	Pods/plant	Seeds/pod	Seed weight	Stand
V_3	33	2.1	1.0	3.3	-1.0	2.8	4.1
	67	-1.0	0.5	2.2	-1.7	1.1	2.2
	100	0.0	-0.2	1.4	-4.2	2.1	1.8
	Mean	0.4	0.4	2.3	-2.3	2.0	2.7
V_8	33	0.0	1.4	2.2	-2.1	1.4	-2.1
	67	-1.8	1.7	1.8	-3.2	-1.9	1.4
	100	-3.1	2.4	-3.1	-1.4	-2.4	-3.7
	Mean	-1.3	1.8	0.3	-2.2	-1.0	-1.5
R_2	33	0.2	-1.8	-2.8	-3.2	1.5	-2.2
	67	1.4	-2.5	-2.1	-1.8	0.3	4.5
	100	-2.8	-4.7	-3.7	-5.4*	-2.2	2.3
	Mean	-0.4	-3.0	-2.9	-3.5	-0.1	1.5
R_6	33	-2.3	-3.2	-5.2	-2.4	-0.7	2.8
	67	-25.0	-21.1*	-29.4*	-5.0*	-11.2*	-0.7
	100	-38.0	-40.7*	-42.1*	-5.8*	-17.5*	1.4
	Mean	-11.0	-10.8	-11.9	-4.2	-5.0	1.2
	33	0.0	-0.4	-0.6	-2.2	1.7	0.9
Mean	67	-6.7	-5.6	-6.9	-2.9	-2.9	0.4
	100	-11.0	-10.8	-11.9	-4.2	-5.0	1.2

* Significantly different from the check by Duncan's test at p=0.05.

tion and secondarily in a decrease in seed size, but the authors also referred that seed size, as a function of source to sink ratio, depended on external factors like lodging or precipitation. The seed weight (=seed size) was second in importance with respect to grain yield reduction, as found by other researchers (Egli et al., 1976; Fehr et al., 1981; Ingram et al., 1981; Goli & Weaver, 1986). Seed weight was consistently reduced by 100% defoliation, except when the treatment was applied at V_3, and by any level of defoliation applied at R_6, but the decrease was inferior to the number of pods/plant. The relation between seed weight and yield also was linear ($Y=0.95+2x, r^2=0.94$), but its contribution to yield reduction was half the value observed for pods/plants ($\beta=2$). The number of seeds per plant was reduced for all treatments, as the number of seeds/pod was consistently reduced, even for those treatments where pods/plant increased in relation to the check. However, significant differences among defoliation treatments and the non-defoliated check were found only for 100% applied at R_2 and R_6 and 67% applied at the later stage. In spite of being significant, regression between number of seeds/pod and yield/ha did not fit well on a linear model ($Y=11,21+5,37x$, $r^2=0.5$) and the relation was best explained by a quadratic equation ($Y=-10.69-11.04x-2.39x^2, r^2=0.7$). Ostlie & Pedigo (1985) observed no differences in number of seeds per pod due to defoliation treatments. Plant stand at the end of the soybean cycle was not affected by the treatments. The type of results observed with yield components indicated that the plant had chosen to produce fewer but more viable seeds. The treatments had no effect on soybean stand at harvest, leaf area retention after R_8, date of harvesting maturity, height of first viable pod, plant lodging and plant height.

CONCLUSIONS

1. Soybean plants present a trend to intense compensatory leaf growth when low (33%) to medium (67%) defoliations are applied at vegetative stages.
2. At full bloom only low levels of defoliation induce shorter recovery time, while defoliation applied at R_6 has the effect of reducing intensity of natural leaf area loss.
3. Effect of treatments upon yield is observed only with medium and intense defoliation applied at stage R_6.

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