INTERFERENCE BETWEEN VELVETLEAF (*ABUTILON THEOPHRASTI* MEDIC.) AND SOYBEANS (*GLYCINE MAX* (L.) MERRILL)

By

John Dekker

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ABSTRACT

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Literature pertinent to the interaction between velvetleaf and soybean is reviewed. It shows that velvetleaf is associated with inconsistent soybean yield losses. Allelopathy by means of water relationship interference is implicated.

Methods of assessing crop-weed interference are also reviewed, and the limitations of traditional additive designs are discussed. The inherent confounding of effects due to changes in proportion and population are overcome with substitutive and density design methodologies presented. General analytical and graphical procedures are presented for the replacement series design. Interpretations of this design for plastic growth responses, mortality and changes in crop-weed reproductivity are also presented.

The data indicate, in terms of mortality, that soybean responds as if velvetleaf were not present, and exhibits very low mortality. Soybean therefore perpetuates smaller, less productive plants; while velvetleaf plants thin to more productive populations, which are severely interfering populations.

The presence of velvetleaf, and not just increases in overall

plant population, cause severe soybean yield losses (ca. 70 to 25% of the weed-free control). This reduction in soybean growth is most apparent in flowering node losses. These losses occur throughout the soybean reproductive cycle.

Soybean reporductivity changes are due to the interaction of both the presence of velvetleaf, and to changes in population. Velvetleaf reproductivity does not change, or is slightly increased, with changes in both the presence of soybeans, and population. Velvetleaf has the potential for future replacement of itself, at the expense of soybean.

ACKNOWLEDGEMENTS

I am indebted to many people who made this small piece of research come to harvest:

To Dr. Bill Meggitt for providing a rich and fertile environment in which to do the work,

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To Dr. Don Penner for the insights that helped me reap all that I had sown.

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INTRODUCTION

Velvetleaf is a common and widespread annual broadleaf weed throughout much of the soybean production areas of North America. Its importance to agriculture is primarily due to inadequate control by available soil applied herbicides (19, 20). Enough velvetleaf plants remain to interfere with soybean productivity and to return large quantities of seed to the soil weed seed pool. Typical infestations in Michigan soybean fields range from ca. 2 to 40 plants/m^2 (appendix A). Typical soybean field populations (0.77m row spacings) are 13 to 25 soybean plants/m^2 (49,50,69). These populations result in possible mixtures of 25 to 93% soybean-75 to 7% velvetleaf; with more typical mixtures ranging from 42 to 83% soybean-58-17% velvetleaf. Because of the extensive distribution of velvetleaf, and the failure of soil applied herbicides to control it, there is a need for an extensive evaluation of the effect of velvetleaf on soybean productivity. The present study can be visualized in Figure 1, a conceptual model of possible factors influencing productivity in the soybean-velvetleaf community. This model is not intended as a complete, systematic model of all possible interactions and factors. It is only intended to serve as a heuristic device for visualizing the present study.

Based on this situation the objectives of this work are:

Population Mortality

1 - to determine when, and to what extent, each species dies through the growing season

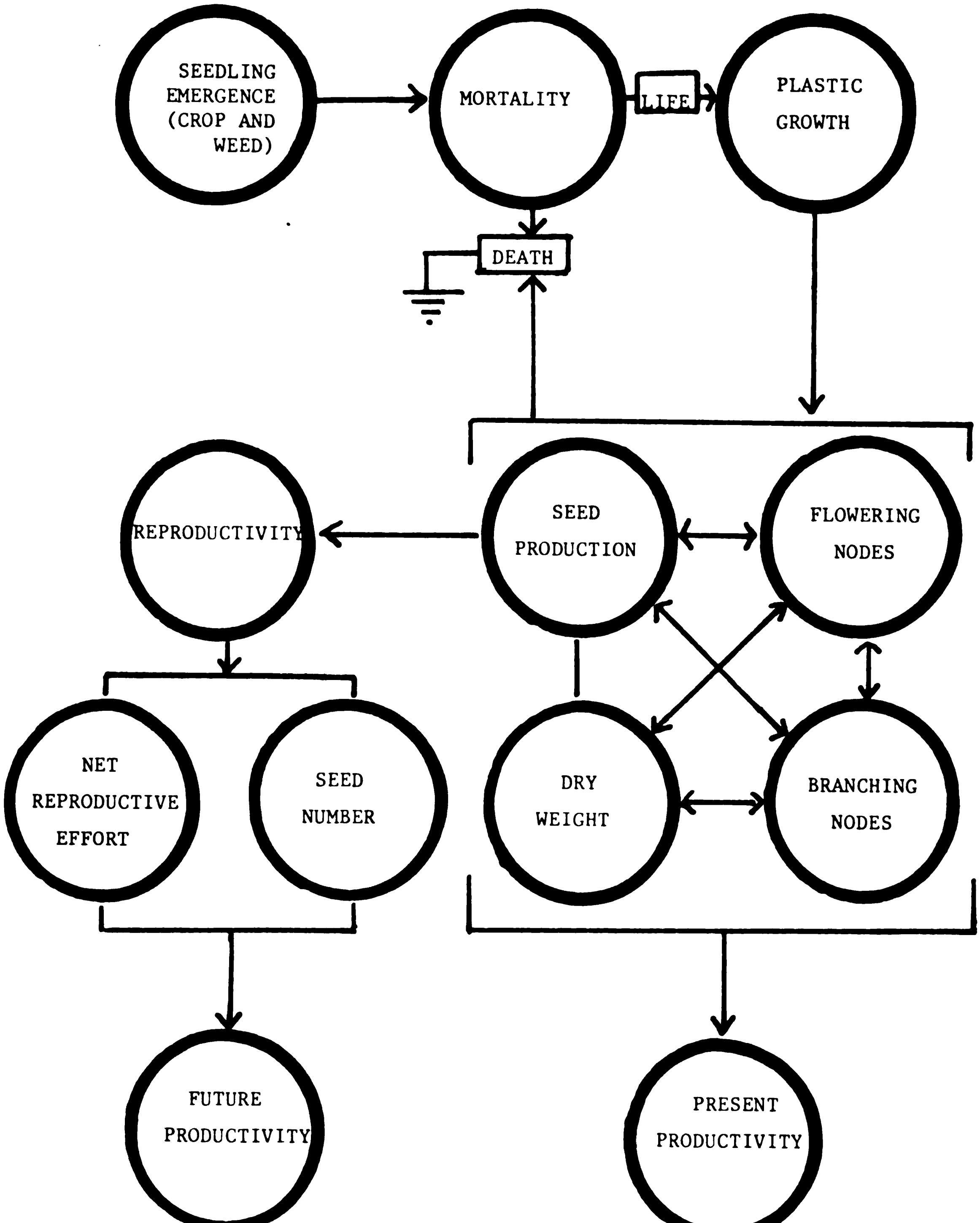


Figure 1. Conceptual model of possible factors influencing productivity in the soybean-velvetleaf community.

2 - to determine if a species mortality is affected by the presence of the other species

3 - to determine if there are any implications in each species' mortality for subsequent growth and development

Plastic Growth

4 - to determine if either species affects the growth and development of the other; and if so, to what extent

5 - to determine whether the observed growth changes are due to changes in plant population, the presence of the other species, or a combination of both factors

6 - to determine which growth parameters most reflect any observed interference

Reproductivity

7 - to determine whether either species affect the seed number production of the other species; and, if so, to what extent

8 - to determine the future replacement potential of both species together, and whether one is favored in this future replacement

9 - to determine whether either species alters the amount of effort devoted to reproductive parts, relative to total biomass accumulation, with changes in plant population and the presence of the other species; and, if so, to what extent.

To fulfill these objectives past research has been reviewed, methodological approaches presented, and research initiated to obtain answers to what was unknown.

The significance of this study can be categorized in four areas. First, an accurate determination of soybean yield losses due to the presence of velvetleaf will enable producers to weigh the costs and benefits of using more intensive weed control programs. Secondly, methodological approaches presented, and the evidence they provide, will help in the development of predictive modeling and systems analysis of crop and weed growth. These future models will hopefully lead to a more complete understanding of biological phenomena, and new, realistic programs of weed control. Thirdly, an understanding of weed and crop seed number production can lead to an understanding of the potential of a species to remain vigorous and live to, among other things, develop herbicide resistance. Finally, survival mechanisms absent in soybean can be projected to plant breeders who may wish to reintroduce them to obtain more vigorous varieties.

REVIEW OF LITERATURE

Velvetleaf-Soybean Interference

An analysis of the literature dealing with velvetleaf interference on soybean reveals an incomplete, and often conflicting, picture. What it does reveal is categorized as data on population mortality, plastic growth changes, and evidence indicating an allelopathic interaction between soybean and velvetleaf. No information exists on factors controlling either species reproductivity.

Population Mortality

There is scant data on population mortality for either species, alone or in mixed communities, through the growing season. One study (86) found that velvetleaf experienced no mortality at 20 velvetleaf/m^2.

Plastic Growth Changes

Dry weight accumulation

Soybean dry weight/plant decreased with increased population (14,22,53). Whereas favorable weather increased velvetleaf dry matter accumulation and decreased soybean seed yields when soybean was infested with velvetleaf (95). The presence of velvetleaf reduced soybean dry matter accumulation (17). The time of velvetleaf emergence was critical to this interference. Dry matter accumulation by velvetleaf decreased when it emerged 10 days after soybean emergence (28). For interference to occur, velvetleaf must emerge soon after soybean. Studies on early growth rates of the two species were inconsistent. In one, if each is grown alone, soybean seedling growth rates exceeded those of velvetleaf seedlings in the first 28 to 40 days (32). In another study (83), velvetleaf growth rates for the first 28 days exceeded those of soybean. Grown alone in the field, the dry matter/m^2 accumulated by soybean per day increased rapidly from 0 to 9 weeks after emerging (79). From 9 to 12 weeks after emergence it became less rapid. Low levels of velvetleaf infestation (3.3 velvetleaf/m^2) decreased the soybean growth rate, and the period of rapid growth, to 0 to 7 weeks, with a slower rate of increase from 7 to 12 weeks (79). Once again, data on the effect of velvetleaf on soybean dry matter/m^2 was not readily available.

Branching nodes

A major way in which soybean plants respond to an increase in space, as measured by yield/plant, is by the production of additional branches (11,53). Increases in soybean population decrease the total number of nodes/stem (22,29,53,64). Studies (28) of the effect of velvetleaf on soybean branch production showed that very high velvetleaf infestations (130 to 240 velvetleaf/m^2) decreased the number of nodes/plant (28). No data is available on the effect of velvetleaf on the number of soybean nodes/m^2.

Flowering nodes

Soybean plants regulated the number of pods and seeds filled under existing environmental conditions by physiological abortion during flowering and early ovule development (16,23,53). Typical reproductive organ abortion rates for midwestern U.S. soybean varieties were 40 to 80% (22). Velvetleaf pod abortion was most likely to happen to early season flowers (110). Those aborting did so 1 to 2 days after flower opening (110). Changes in soybean population decreased both the number of initial flowers formed, and the final number of pods/plant (14,22,80). Very high velvetleaf infestations (130 to 240 velvetleaf/m^2) decreased soybean reproductive organ numbers by 53% (28). No data is available on the effect of velvetleaf on soybean flowering nodes/m^2.

Seed weight

Reported soybean seed yield losses associated with velvetleaf infestations were inconsistent (28,79,95). Early workers (95) found no soybean yield losses from velvetleaf infestations of 10 to 20 velvetleaf/m^2. Other researchers (28) found up to 66% soybean yield losses from full season interference from very high velvetleaf infestations of 130 to 240 velvetleaf/m^2. They (28) found that only those velvetleaf plants emerging with, and up to 10 days after soybean emergence, decreased soybean seed yields. Velvetleaf emerging 20 or more days after soybean emergence had no effect on soybean yield (28). Existing vegetation was killed by current cultural seedbed preparation practices and new velvetleaf seeds were stimulated to germinate, resulting in simultaneous emergence of soybean and velvetleaf (28). Therefore, full season interference by velvetleaf was the most probable situation. Recent work (79) has shown that very low velvetleaf populations (1.6 and 3.3 velvetleaf/m^2) resulted in 13% and 27% soybean yield losses, respectively, from mid-May planting; and 24% and 9% soybean yield losses from late June planting. The delay in soybean planting from mid-May until late June resulted in 25% soybean seed yield losses in the weed-free control (79). Only 9% losses were incurred in the 3.3 velvetleaf/m^2 treatment by delaying planting from mid-May until June (79). The effect of allowing velvetleaf growth in soybean was more profound in infested fields than the effect from a delay in planting.

A clear picture of exact soybean yield losses expected from velvetleaf infestations is not apparent from these studies. There seems to be a variable pattern of yield losses associated with velvetleaf in soybeans.

Allelopathic Interactions

The possibility that the nature of interference by velvetleaf on soybean could include chemical interactions has been suggested (86). Population mortality of weeds neighboring velvetleaf occurred at the germination stage, and not after the other seedlings got established. It (86) was suggested that this mortality could be due to chemical inhibition at the germination and seedling establishment stage. Retig et al. (89) found that diffusible materials out of germinating velvetleaf seeds caused abnormalities to tomato and cabbage roots germinating with the weed seed. The roots were larger due to increases in the number and size of parenchyma cells in the root cortex. The authors (89) felt that these anatomical changes to the crop roots could alter normal functions such as nutrient and water uptake. They then studied (87) the effects of these diffusible substances on cabbage proteins. They found that the substances from the velvetleaf seed increased, and changed the composition of and the peroxidase isozyme levels in the crop seedlings (87). Increases in concentration of the suspected allelopathic compound resulted in increased peroxidase activity (87). Increased peroxidase levels could mean increased oxidative reactions in the crop roots. These oxidative reactions could lead to breakdown of normal cell formation in cortex roots, causing the observed cell normalities. The same workers found (88) velvetleaf seedlings grown with lettuce, cabbage and tomato seedlings inhibited the uptake of ^{14}C urea, hydroxyatrazine and phenylalanine.

Gressel et al. (35) found water-soluble extracts of velvetleaf seed to be selectively inhibitory to alfalfa, radish and turnip germination. The seed extracts were found to be species and variety specific. The alfalfa seedlings affected had a swollen appearance, similar to 2,4-D and coumarin injury. The possibility of microbial interactions being involved in the inhibition were lessened when the inhibitory effects were identical in sterile and non-sterile soil. Intact velvetleaf seed germination inhibited radish and tomato seed germination and radicle development. This inhibition was also demonstrated in the field by diffusible substances from velvetleaf seed. Velvetleaf leaf tissue extracts were also found to contain inhibitory compounds, but not necessarily the same ones. Competition for water, and probably mineral nutrition and light, were ruled out. Light did not play a role in the inhibition. Neither velvetleaf seed germination nor growth was inhibited by these compounds. The inhibitors were found in the highest quantity in the seed embryo and endosperm, less so in the seed coat. Chromatographically isolated amino acid compounds showed identical inhibitory responses as the first compound. More than one of these blastocholines were implicated. The inhibitors were found to be amphoteric, heat stable to 100^{o}C, and ether insoluble.

The authors felt it was conceivable from their results that a steady release of amino acid inhibitors occurred from the velvetleaf seeds and trash after the spring thaw which inhibited other species from germinating (35).

Coulton et al. (17) found velvetleaf plant residues did not inhibit soybean seedling growth for 0-28 days, but did decrease soybean root nodulation. Soybean seedling growth was inhibited by water-soluble velvetleaf leaf extracts; a rate response was observed (17). Three phenolic compounds were paper chromatographically isolated from the velvetleaf leaf tissue water soluble extracts. The isolated eluates of two of the phenolic compounds inhibited radish germination, and their allelopathic potential was confirmed. Soybean growth was reduced by the extracts, as was leaf turgor. The older, lower leaves were chlorotic and mottled. The primary root died and treated roots had an increased number of secondary roots which were shorter and thicker. The velvetleaf extracts increased soybean leaf diffusive resistance and decreased the leaf water potential. Therefore, the treated plants suffered from water stress and had less leaf water content. Additionally, the extracts reduced soybean seedling chlorophylls "a" and "b", and total chlorophyll. This decrease in plant chlorophyll could cause decreased photosynthesis, and result in the observed decrease in dry matter accumulation (17).

These studies indicate that there is a high probability of allelopathic interactions playing a significant role in the interference of velvetleaf on soybean. This chemical interaction could be due to interference on soybean plant water relations.

Analytical and Mathematical Methods To Define Crop and Weed Interference

Introduction

> "Hence as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species, or with the physical conditions of life."
>
> Charles Darwin, 1859

This insight expressed by Darwin (18) over 120 years ago generally depicts the "struggle for existence"(33) between crops and weeds in modern agroecosystems. There exists in these relationships a struggle within species (intra-specific interference) and between species (inter-specific interference). These struggles are related together in the struggle for the "physical conditions of life" (growth requisites such as mineral nutrition, water, light, CO_2, etc.) (111). In addition, biotic contributions, such as exudation of toxins (allelopathy), may mediate interference. Understanding the components of these struggles is a problem that faces agriculturists desiring to know whom will win the battle between crops and weeds. Methodology in weed science is incomplete in these regards (117).

An unnecessary dichotomy exists between the way agronomists and ecologists look at interference (40). Agriculturists usually consider only competition, and look upon it as a difference in a plant's efficiency in securing requisites necessary for growth and reproduction (40). As a consequence, they study the shortages of growth requisites (mineral nutrition, water, CO_2, light, etc.). That approach is directed toward patterning of weeds in crops (the effect of row spacing); effects on yield components (flowers and pods, nodes, etc.); phenology and duration of competition.

The other side of this dichotomy is the ecologist's viewpoint. They look upon interference as the sum of the forces that determine the composition of plant stand we see (levels and extent of weed infestations in the crop). They see interference as all those forces by which one species succeeds at the expense of another, not just as the efficiency by which plants acquire growth requisites. These forces include, among others, the effects of diseases, insects, climate, and the potential of the crop or weed for allelopathy. They look upon this as a long-term process. The forces that lead to the composition of a weed community in a crop field have been at work for a long time. Many agronomists tend to take a short-term look at these processes (40). Rarely are they observed beyond, at most, the duration of one rotational cycle.

An understanding of the long-term equilibria between crops and weeds is important also because of the plasticity or adaptive ability weeds possess. The tremendous seed bank in the soil creates a homoeostatic (2, 65) force upon which single year's practices have little impact. Current problem weeds have evolved and survived under the changing conditions we have imposed by our crop management or mismangement practices (38). Because of this, weeds are innately buffered against our short-term attempts at elimination. Additionally, this pool of weed seed tends to increase when the land is cultivated (43, 75).

These long-term forces are often at odds with present cultural practices. To use herbicides effectively, one must understand the forces behind the wheel. If we ignore them, the long-term result could be increased metabolic resistance to herbicides (38) and increased spread of weed problems due to herbicidal elimination of former weed competitors. By understanding the role of the weed in an agro-ecological sense, one will be prepared to avoid these difficulties.

Objectives

If weed-crop interactions (mortality, plasticity of growth, and reproductivity) in the agro-ecosystem can be better defined, it will serve several functions to us as weed scientists. Properly developed methodologies will facilitate a more complete representation of plant interactions in crop-weed predictive models. These will lead to true, and realistic, integrated pest management strategies. These strategies will facilitate more effective use of the chemical tools we now have.

There is a need to continue traditional examinations of interference, but to this must be added basic research methodologies to increase our awareness of the role of weeds. The objective of this paper is to review the methodologies previously developed for studies of plant interference. Although other reviews have focused on the allelopathic (85) component of interference, this review considers research techniques to quantitatively elucidate and describe interference.

Productivity and fitness

To describe the role of interference in determining the abundance of a weed, and the course of its success and failure in association with a crop, three different criteria must be considered (39,40):

1. factors which determine the density of the weed in the crop,
2. factors which determine the growth, or size, of the weed,
3. factors involved in the reproductive capacity of the weed.

The first two criteria are whether the plant responds by mortality (death through the season), or by a plastic growth response. The latter implies that the crop or weed will continue to live, but at a reduced or increased functional level. Some (92) have warned, though, of the mistake in equating competitive ability entirely with productivity. "Productivity" is assessed on a crop's or weed's growth on a unit area basis (yield per unit area). A crop's or weed's "fitness", on the other hand, is calculated on an individual plant basis (yield per plant). Therefore, both mortality and plastic growth responses in any methodology should consider both ways of looking at a plant's competitive ability: productivity and fitness.

The third factor, the reproductive capacity of a weed, must be assessed because of the yearly contributions it makes to the soil seed pool, or through perennial plant structures. These contributions maintain the buffering, or homoeostatic, forces that continue the survival of the weed.

The assessment of these three criteria have been limited in the experimental designs that have been traditionally used.

Additive and substitutive designs

Weed researchers have traditionally studied competition with additive designs. Additive designs assess the interspecies effects of neighbors by the use of a crop as the indicator species. Mixture responses are produced by the addition of weed plants to a constant density crop stand. This procedure makes possible the measurement and ranking of relative weed aggressiveness (9,10,46,82,107). Examples of this are seen in Figure 2. Because these designs vary both in density and proportion, with resultant confounding of effects, interpretation of either is limited (46). But, because of its relevance to actual field situations in which a weed invades the area occupied by the crop, and because it permits the assessment of effects on yield and cost to the farmer, its use is widespread and appropriate. But, there exists a need to take the analysis further. Most of these problems are eliminated by the use of substitutive designs (46). The main characteristic of a substitutive design is that the proportions of a crop and a weed species, "C" and "W", in a mix are proportionately varied while their overall density (plants per unit area) remains constant (46). Therefore, substitutive designs avoid density-proportion confounding effects, and allow a precise comparison of neighbor effects at one constant density (102). The number of species to be tested has to be small to keep the experimental size reasonable. Perhaps the most useful substitutive design is the replacement series, as seen schematically in Figure 3. The mechanical diallel, directly analogous to and adapted from the genetic diallel analysis, enables the replacement series responses to be assessed in several weed-crop

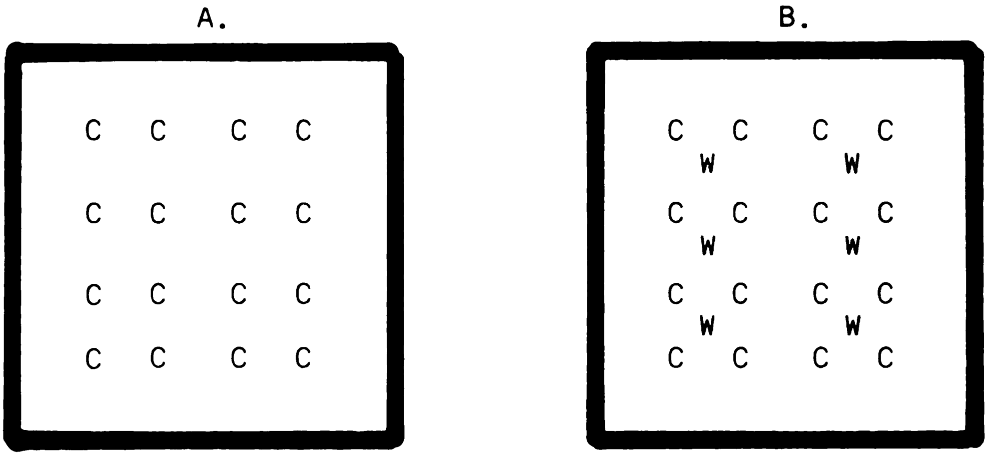


Figure 2. Schematic representation of the additive design plot layout. Each block represents one meter^2. A: Crop plants (C) at 16 plants per meter^2; B: Crop plants (C) at 16 plants per meter^2 plus weed plants at 6 plants per meter^2, the overall density is 22 plants per meter^2.

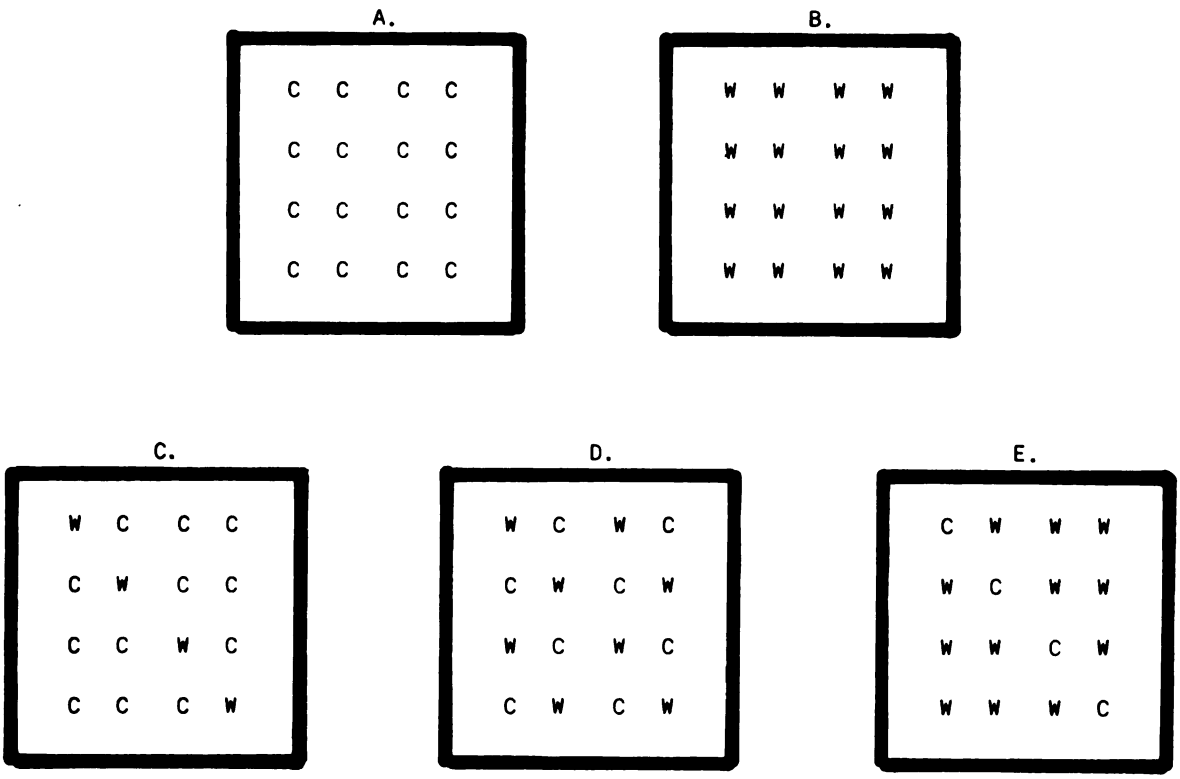


Figure 3. Schematic representation of the replacement series plot layout. Crop plants (C) and weed plants (W) at one constant density of 16 plants per meter^2. Each block represents one meter^2. A: Crop monoculture; B: Weed monoculture; C: 75% crop-25% weed; D: 50% crop-50% weed; E: 25% crop-75% weed.

mixtures. This type of analysis permits the measurement of ecological combining abilities of groups of species. A number of species are grown in several proportions, and their yields in monoculture and mixtures are compared, to derive the ecological equivalent of dominance, recessiveness, overdominance, etc. interactions. Some form of analysis of variance and/or covariance is used to discover the plant interactions (46). This type of analysis has a very good potential for looking at complex association of weeds in a crop. Because it separates and eliminates the problems of confounding of density and proportion, more can be learned of crop-weed relationships than from the additive models. The scope of this complex analysis is broader than most researchers desire, and because the aim of this review is to provide relatively simple and readily available analytic tools, further inquiry into this analysis is left to the researcher through the bibliography (1,27,34,47,48,59,60,70,71,72,77,78,90,101, 104,106,109).

The severity of weed-crop interference can be determined by comparing the response of both species in pure stands to that when both are grown together. The quantitative and qualitative differences revealed in this comparison will indicate the ways in which the crop and weed interfere with each other. The methodologies to enable this discovery process to occur deal with population dynamics, plastic growth responses (productivity and fitness), and reproductive strategies. Within each of these categories, the response of the plant due to density and proportion will be considered.

Population dynamics:
Mortal responses

> "Look at the most vigorous species; by as much as it swarms in numbers, so much will it tend to increase still further."
>
> Charles Darwin 1859 (18)

The first way in which crop or weed survival is determined is by the numbers, or population, it establishes (44). Mortality responses to density and proportion will determine whether it will survive to reproduce. The mortal response of a plant can occur anytime from before it germinates (enforced dormancy) until after the growing season. Once the plant germinates, the chance of it dying remains the same through the growing season (44,99,100), barring environmental catastrophies. This response to death is startingly linear. Elimination is a steady process, and not necessarily due to occasional periods of stress. Yoda (116) saw this too in defining the observed linear -3/2 power function to be discussed in a subsequent section. The risk of mortality remained through the plant's life, and the plant community was continuously changing its numbers in relation to the size of the plant members. Density induced stress in a population exaggerates differences between individuals and encourages a hierarchy of exploitation. This results in decreasing numbers of large plants, and increasing numbers of small individuals, with increasing density (58,63). It is the weaker, smaller members that stand the largest chance of death through the growing season. In pure stands, given sufficient time, the mortality suffered in high density will cause the population to converge toward a common density level (62,93,94,115). This density will be converged upon despite initial densities, and will always be lower on fertile ground (98).

To understand the crop-weed interaction in terms of mortal responses, it is necessary to study the differences in reaction to pure and mixed stands of crops and weeds. A convenient way of thinking of this is differences in alien- and self-thinning (42,116). "Self-thinning", or "self-decimation" (67), is that reduction in the chance of plant's survival brought about by increases in density of its own species. "Alien-thinning" is the reduction in survival due to increased density of an associated species. For two species to form a stable association or to co-exist requires that self-thinning exceed alien-thinning. If this does not occur, one species will replace the other. This phenomenon has implications for whether a crop and weed can naturally co-exist, or whether mortality responses will tend to eliminate one or the other. Mortality can be induced by changes in density, or changes in proportion.

Density and proportion induced mortality

Plotting the function of density versus the chance of an emerged seedling surviving the growing season can reveal density induced death due to alien- and self-thinning (42) (Figure 4).

$$\text{\% chance of survival through the season} = \frac{\text{\# of plants at harvest}}{\text{\# of plants at emergence}} \times 100$$

The effects of proportion can also be represented graphically, and construction of this type of figure with replacement series data proves extremely useful (Figure 5). Interpretation of both types of responses

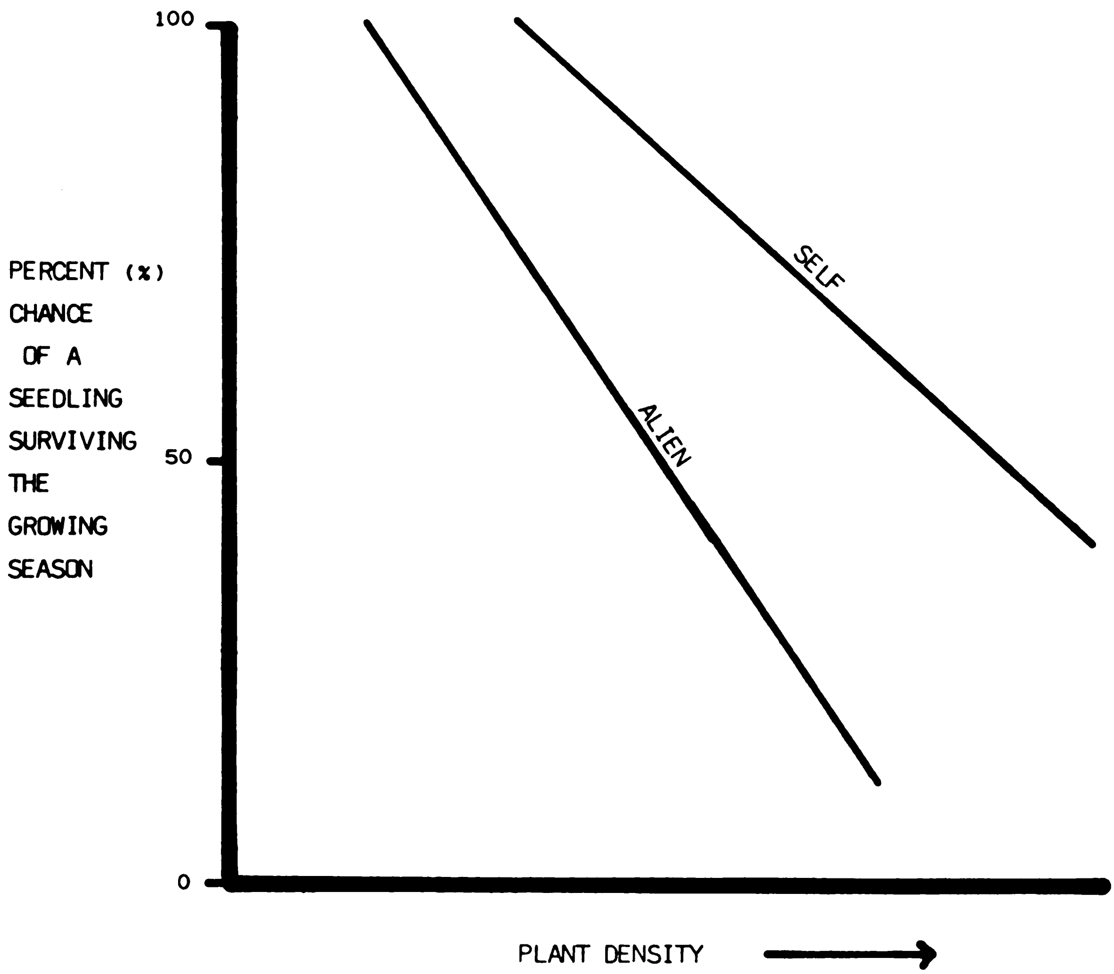


Figure 4. Percent (%) chance of seedling surviving the growing season in response to changes in the plant density of itself (self) and an associated (alien) species.

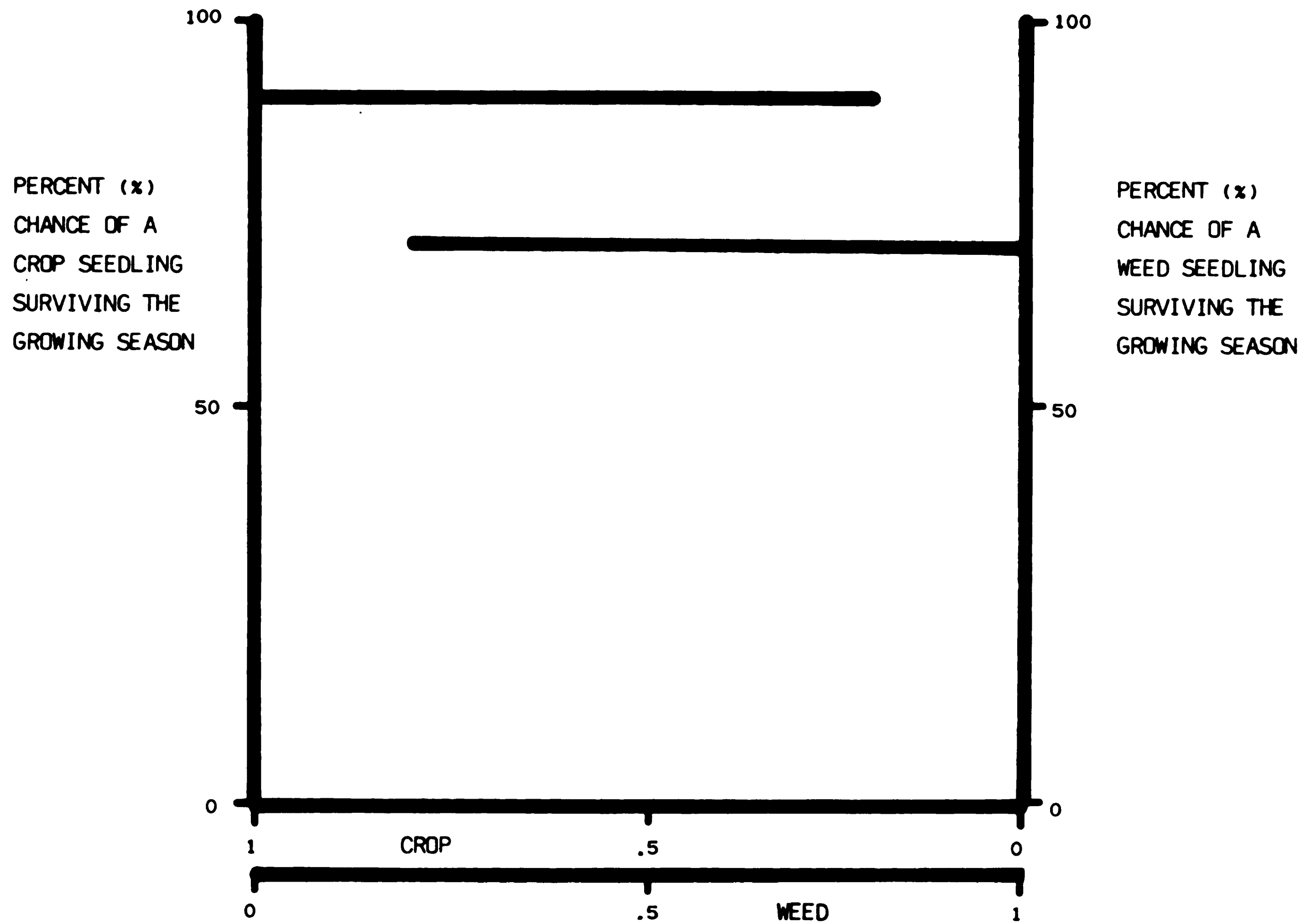


Figure 5. Percent (%) chance of a crop or weed seedling surviving the growing season in response to changes in the proportion of itself and an associated species.

is similar. When mortality of both species remains the same for changes in proportion or density, the make-up of the weed-crop stand will be determined by other factors. This type of response would indicate the species are very similar in growth, and in the time of growth. If one species shows greater survival under mixed stand changes in density and proportion, it will dominate the population of the stand, and eventually eliminate the other species. This can have positive agronomic effects if the crop is dominant. If the mortality response of both species increases when grown together under changing density and proportion conditions, this could be indirect evidence of an allelopathic interaction.

Plastic growth response

The second factor to be considered in crop-weed interactions is the changes in plant size induced by changes in density and proportion. Typical changes incurred are those of dry matter accumulation, seed yield, node or branch number, etc. (41). Increases or decreases in these growth parameters can have decisive effects on the plant's ability to compete. The assessment of the plant's competitive ability in experimental designs can take the form of evaluation of a species' "productivity" (yield per unit area), or its "fitness" (individual plant yield).

Additive designs are useful to assess a crop's or weed's changing responses to density and proportion. But because they confound these two factors, an experimental design is needed that separates them. The "replacement series" does just this function. Its principle usefulness is in assessing a plant's competitive ability in terms of yield per unit area (productivity). Its usefulness as an indication of "fitness" will also be assessed in a subsequent discussion.

Replacement series

Replacement series experimental designs are usually performed with two species, e.g. a crop and a weed. They are relatively easy to establish in the field or greenhouse, and the amount of information that can be obtained from them is immense. This elegant type of analysis was presented first by de Wit (111,112). Several others have utilized his methodology in their research (3,4,5,6,7,13,21,25,36,37, 52,101,102,103,104,105,113,114). De Wit's concept was to look at "space" relations between plants, alone and in mixtures, and express those relationships in a mathematical way. He did this by measuring how plants "crowd for the same space," at one spacing or density. Plants probably do not literally seize, or "crowd", but each plant possesses characteristics which allow it to differentially assume growth factors, grow and occupy space at a specific rate of speed. Therefore, de Wit uses the term space in the sense of all those requisites, like water, minerals, light, and a time factor. The time factor reveals whether interfering species utilize these growth factors at the same time, or at different times (111). "Space" is the exhaustible supply factors of the environment (112). "Space" has also been defined as biological space, a composite of all growth factors and resources (36). The de Wit analysis is based on the simple assumption that the yield of each species in a mixture is proportional to the share of the environmental resources it can acquire. If this sharing is unequal, then the aggressor will acquire more, and the weaker species less (103).

The mathematical model is based on two species: crop "C" and weed "W". The density, D, or number of plants per unit area is kept constant:

$$C + W = D$$

Both species are grown in monocultures and in mixtures of varying proportions of the crop and weed. Monoculture responses can be compared to varying ratios in the mixture to discern the mutual changes brought about. The differences between the monoculture and mixture responses reveal several qualitative interrelationships. The simplest level of interpretation can be discerned from the replacement series diagram (Figure 6). The actual yield parameter measured can be one of several quantitative factors: seed yield, dry matter, tiller number, reproductive organ number, leaf weight, etc. For the purposes of "productivity" evaluation here, the yield is expressed as yield per unit area. "Fitness" determinations of yield per individual plant will be discussed in subsequent sections.

The horizontal axis represents the relative proportions of each species' contribution to the mixture. They range from none to 100%, and the corresponding proportions of the other species from 100% to none.

Perhaps the best interpretation of these diagrams is presented by Hill and Shimamoto (51). Figure 7A represents the case where the response of the mixture, and its individual species components, can

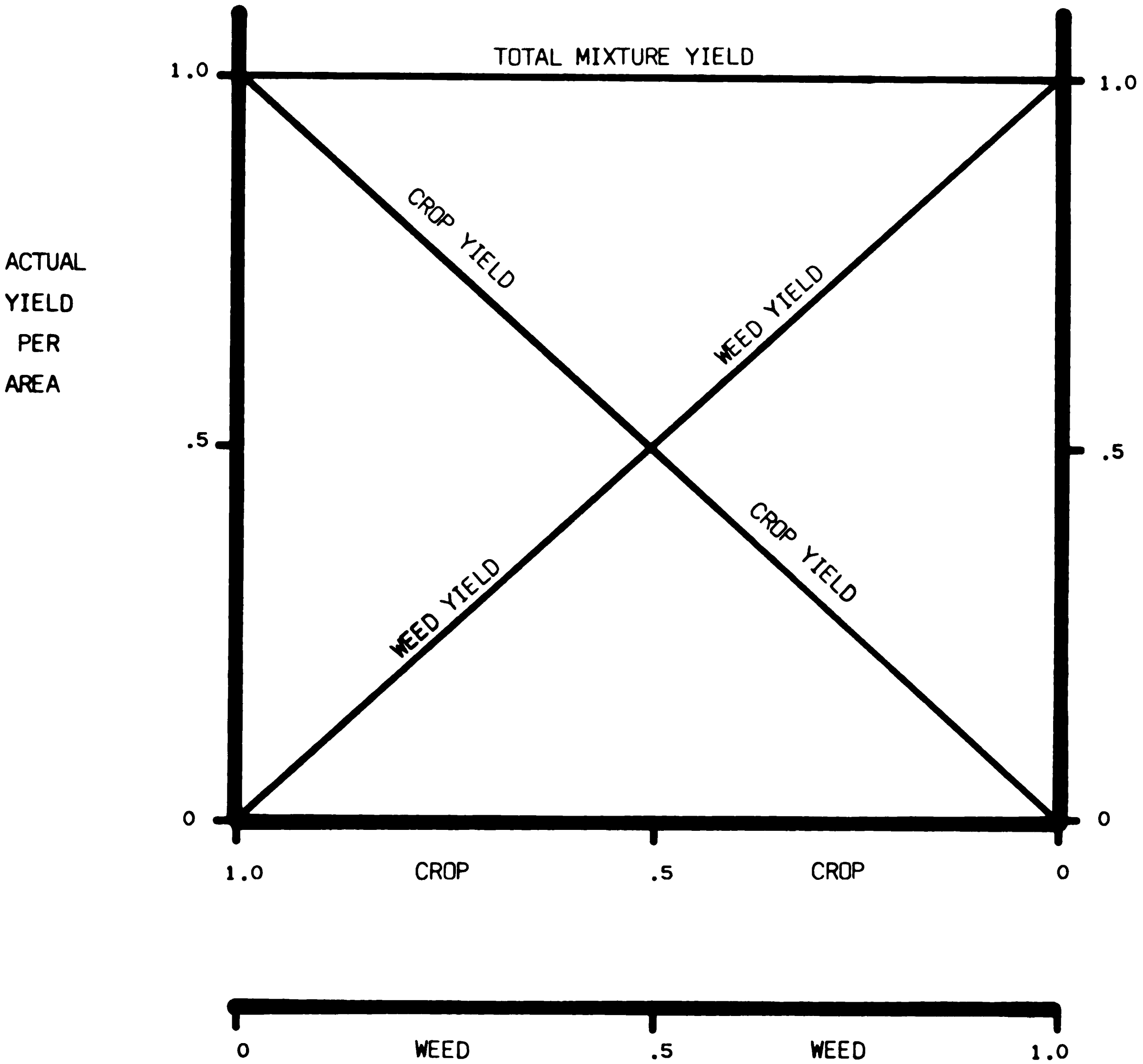


Figure 6. The replacement series diagram: actual yield per area versus crop and weed mixture proportion.

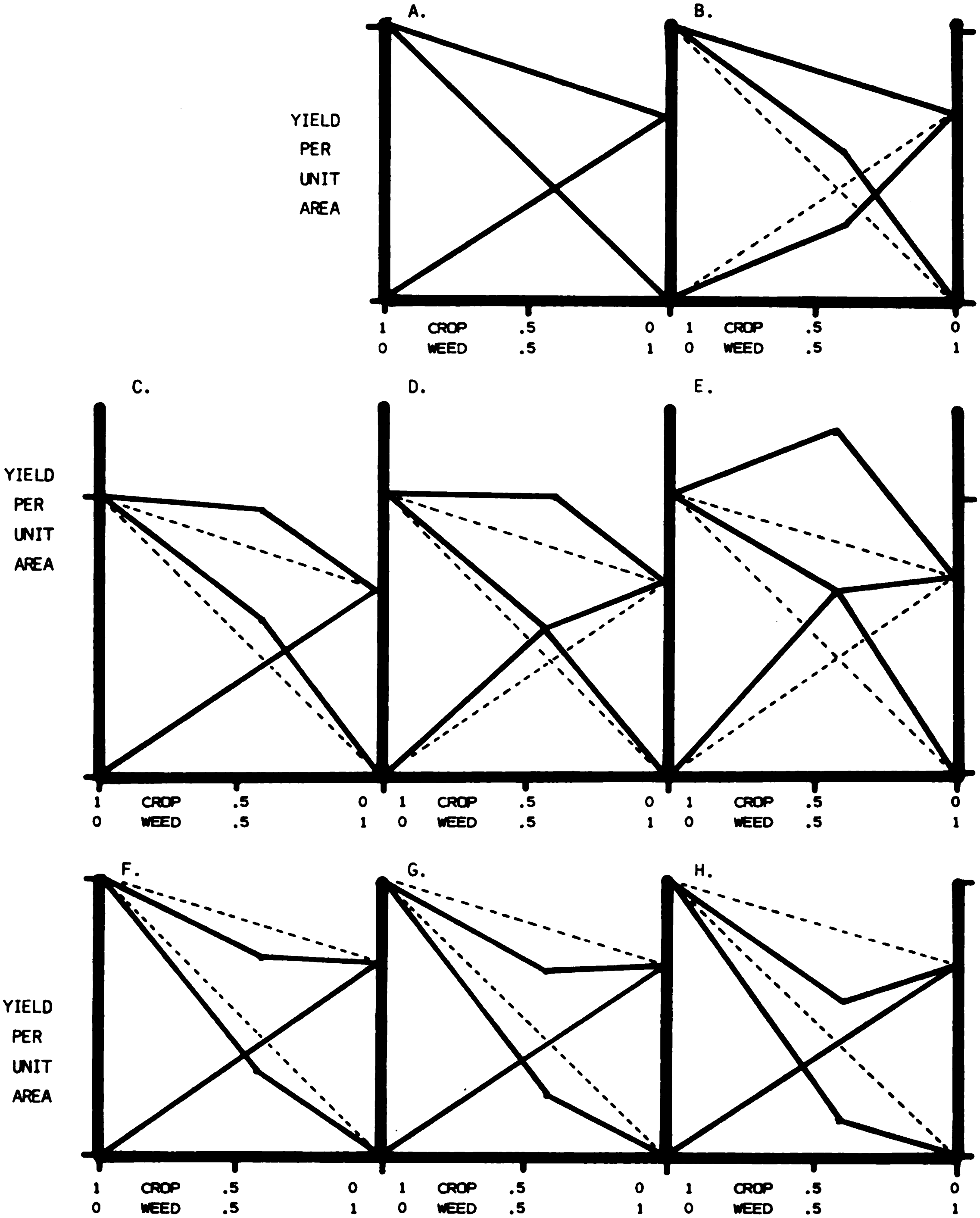


Figure 7. Replacement series diagrams: Models of possible crop-weed interactions. A: Mutual exclusion; B: Compensation; C: Partial positive complementation; D: Complete positive complementation; E: Positive overcomplementation; F: Partial negative complementation; G: Complete negative complementation; H: Negative overcomplementation.

be predicted from two monoculture responses. This relationship arises when either: 1. the crop and weed do not interfere with each other, or 2. both species' ability to interfere with the growth of the other is equivalent. The effect of each on the other is the same. The actual yields of the two do not have to be equal; although they make equivalent demands on the environment, they convert those factors to yield with different efficiencies. This is the relationship that de Wit (111,112) termed "mutually exclusive".

Figure 7B represents a compensatory interaction between crop and weed. One species gains in the mixture at the expense of the other. These gains and losses by each species counterbalance so the total mixture cannot be predicted from monocultural responses. The crop and weed make different demands on growth requisites; or the efficiency with which they acquire these requisites are different.

Complementary interactions occur when the gains and losses of the crop and weed do not counterbalance. Therefore, neither the total mixture yield nor the crop and weed mixture components can be predicted from the monoculture responses. Positive complementation (Figure 7C, 7D, 7E) occurs when the mixture performance exceeds the average of the constituent monocultures. This occurs when the species escape, to some degree their mutual competition. Both species fail to suffer as much as would be expected from the monoculture responses. This interaction could arise from: 1. a symbiotic relationship whereby one or both of the species aided the other (e.g. grass - legume association); or 2. the growth periods of the species did not coincide in the growing season. Negative complementation (Figure 7F, 7G, 7H) occurs when mixture performance falls below that of the monoculture average. This situation occurs when one, or both, of the species does not contribute its share to the total yield. The interaction could arise if: 1. a species produced a toxin that reduced the growth of the other species, or of both species; 2. a mutually stimulatory effect of individuals in pure stands is destroyed by mixing.

Complementation between the crop and weed can be partially, completely or overcompensating. Partial complementation occurs when the mixture performance is less than the better monoculture (positive), or more than the lesser monoculture (negative). Complete complementation occurs when the mixture performance is equal to the better monoculture (positive), or the lesser monoculture (negative). Overcomplementation occurs when the mixture performance is greater than the better monoculture (positive), or less than the lesser monoculture (negative). Positive over-complementation can also be described as a cooperative interaction. Negative over-complementation is mutual inhibition (perhaps allelopathy).

The relative degree of a species' aggressiveness can be ascertained from the component yield curves in the replacement series diagrams. Curves that are convex are from the relatively more aggressive species than are the concave curves (42).

Hill and Shimamoto (51) developed a scaling test that provides tests of significance for some apsects of the replacement series diagrams. They aid in assigning responses to the appropriate interaction. Three indices, "A", "B" and "C", first must be obtained for the weed and the crop:

A = 2(Mean of the 75% crop - 25% weed mix) - (Mean of the 50% crop - 50% weed mix + Mean of the crop monoculture)

B = 2(Mean of the 25% crop - 75% weed mix) - (Mean of the 50% crop - 50% weed mix + Mean of the weed monoculture)

C = 2(Mean of the 50% crop - 50% weed mix) - (Mean of the crop monoculture + Mean of the weed monoculture)

If all the tests (A, B and C) are equal to zero, within the limits of experimental error, the crop-weed interaction is "mutually exclusive" or of a compensatory type. If "C" is significant, the interaction is complementary. The "A" and "B" tests detect those 75%-25% mixtures whose components interact in a way not anticipated from the response of the monoculture and the 50%-50% mixtures. The use of a statistical confidence statement (e.g. 95% confidence limits about the observed mixture mean) can also be used in this regard.

Relative yield

It is difficult to compare the performance of different species in terms of absolute yields: a kilogram of velvetleaf seed is something completely different than a kilogram of soybean seed. These difficulties can be overcome by the comparison of pure stand and mixture yields in terms of relative yield of each species:

$$\text{Relative Yield} = \frac{\text{Yield in Mixture}}{\text{Yield in Pure Stand}}$$

and:

$$\text{Relative Yield Total} = \text{Relative yield of crop} + \text{Relative yield of weed}$$

The relative yields of both the crop and the weed can be calculated and summed, to give the "relative yield totals" (RYT). The RYT can be used to describe the mutual interaction that occurs between the species:

1) RYT = 1: This situation implies each species is making the same demands for "space" as the other. They are "mutually exclusive" (Figure 7A) or complementary (Figure 7B).
2) RYT > 1: This situation suggests one or both of the species are less affected by interspecific interactions than could be predicted from their monoculture responses. It suggests that they are: a) making different demands on the same resources; b) occupy different niches in time or space; or c) exhibit some sort of symbiotic relationship.
3) RYT < 1: This situation occurs when one or both species are more affected by interspecific competition than would be expected from their pure stand responses, mutual antagonism. Possible mechanisms that could explain this interaction are: a) the action of phytotoxins produced by one or both species; or b) pure stand stimulatory effect is lost in the mixture.

These interpretations of the RYT reveal the mutual interaction between the plant pairs at several proportions.

Relative replacement
rate (RRR)

Data derived from this type of analysis can also be used to give a representation of the long-term shift in favor of one species of another. This is particularly important for prediction purposes in perennial cropping systems. If one species produces more relative to the other over time, the lesser species will be excluded. The long term, dynamic, equilibrium forces on the crop and weed can be determined by this line of inquiry. De Wit originally used the RRR for seed numbers of each species. It can be argued that the use of other yield parameters (e.g. seed yield, dry weight, etc.) to indicate long term equilibria, and subsequent "replacement" of one species for another, is not appropriate. Although the connection here may be immediately abstruse, this line of analysis can reveal the pressure on the equilibria each yield component exerts. In this way, the effect of dry matter per unit area of one species on another can be compared. The dominance of any factor could be decisive in these long term equilibria "replacement" shifts, and not just propagule numbers alone.

The relative replacement rate (RRR) of the crop (C) species in reference to the weed (W) (RRR_{CW}) can be obtained by (3,6,7,105,111, 112,113,114):

$$RRR_{CW} = \frac{\text{Crop yield in Mix} \div \text{Crop proportion (\%) in the Mix}}{\text{Weed yield in Mix} \div \text{Weed proportion (\%) in the Mix}}$$

The following interpretations for the significance of this are:

1) $RRR_{CW} = 1$: This situation implies that both species are competing for the same "space" in the same way (i.e., mutually exclusive). If this situation exists at all mixture proportions, then the species will tend to form a stable community. They are replacing each

other on a 1 to 1 basis, and their proportionate composition will not change.

2) $RRR_{CW} > 1$: With this situation, the crop (C) is replacing itself relative to the weed (W) at a greater rate. The crop is replacing the weed in the mixture. If the situation maintains itself in all mixture proportions, then the weed will be replaced over subsequent generations.

3) $RRR_{CW} < 1$: This situation is the converse of the last situation ($RRR_{CW} > 1$). The weed is replacing the crop. The relative replacement rate is favoring the weed. If this situation is true for all mixture proportions, subsequent generations will see the crop eliminated.

The RRR characterizes the mutual interference of both species. It provides a key to the long term equilibrium interactions of the crop and the weed. It provides us with information about which species is the better competitor. The implications for perennial cropping systems are not as immediately obvious. The RRR gives us the key to which species may replace the other and at what rate in subsequent years. The implication of the equilibrium is found in the intensity with which the weed replaces itself when associated with a particular crop. If the RRR_{CW} is much less than 1, it is favored over the long-term. It is replacing itself at a high rate. It is increasing the buffering capacity against its extinction by increasing itself in the soil seed pool. This type of equilibrium force is set against the use of herbicides used against it. If the equilibrium is strongly in the weed's favor, then it will undoubtedly survive long enough to develop some resistance or alternate strategy to overcome the herbicide. This phenomenon is already occurring.

Ratio diagram

This analysis of extinction and dynamic weed equilibria can be represented, and understood, with the use of the "Ratio Diagram" (111, 112). Both axes are in terms of a log scale. The horizontal axis is the ratio of the crop area to the weed area occupied (proportion of each in the mix). The vertical axis is the ratio of the actual crop yield to the weed yield. These pairs are plotted and the shape of the defined function reveals much about their interaction (Figure 8). To aid in visualizing, point "C" can be seen as the crop monoculture, and point "W" as the weed monoculture. Although these points are not plotted, they might aid in visualizing the change in mixture proportions from "W" to "C" along the 45^o diagonal line. If the calculated points fall along this line for all mixture proportions, then each increment of increased (or decreased) area is met by an exact 1 to 1 increase (or decrease) in yield. In other words, the species are replacing each other on a 1 to 1 basis ($RRR_{CW} = 1$). This is represented by the diagonal line, and the interaction between the species is mutually exclusive.

Another situation can be visualized where the crop consistently does better than the weed in all mixture proportions. This is the case where $RRR_{CW} > 1$ (Figure 9). Although this function is parallel to the diagonal (RRR = 1), the fact that it is consistently greater

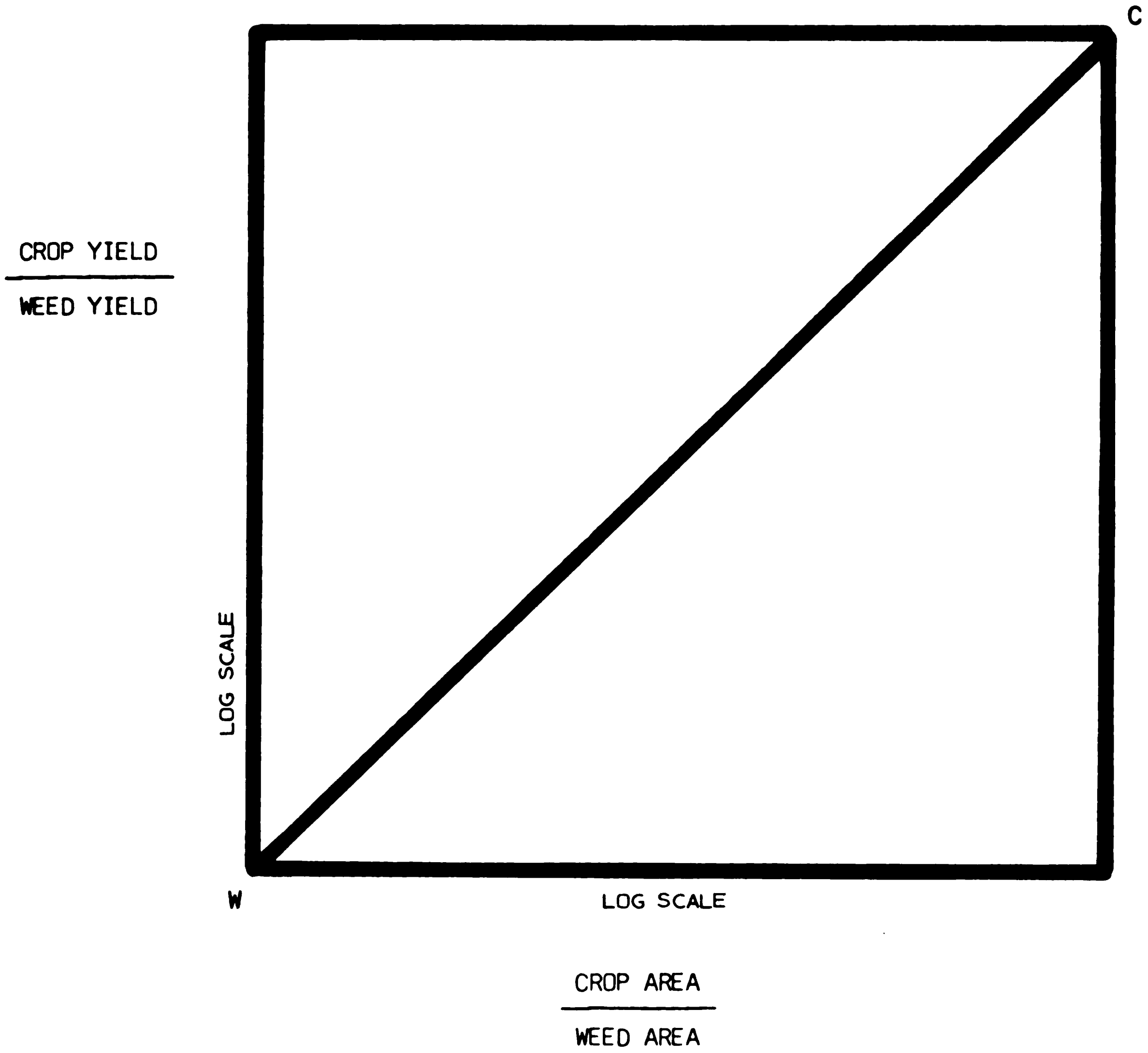


Figure 8. The ratio diagram: The ratio of crop yield to weed yield versus the ratio of crop area to weed area.

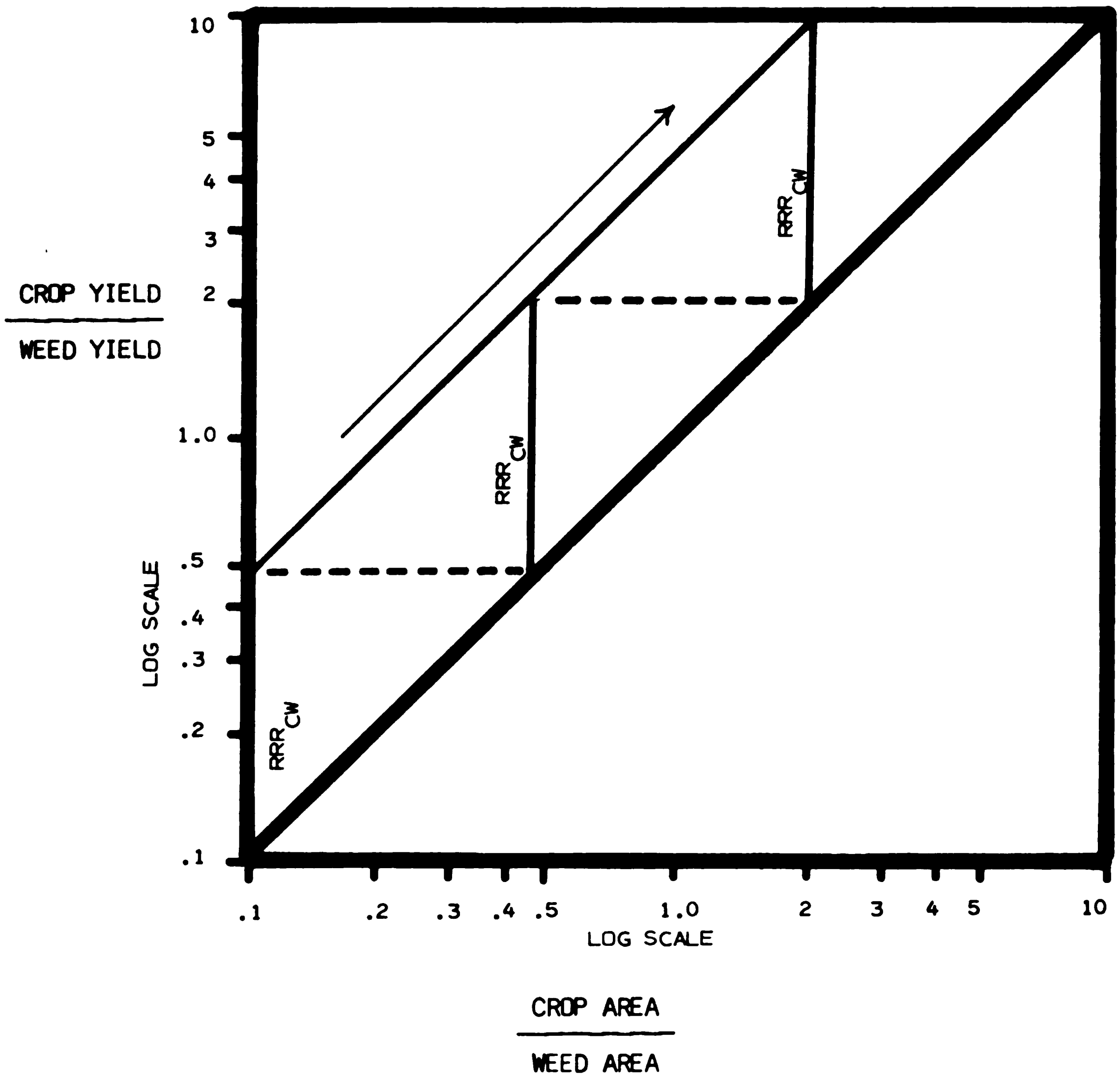


Figure 9. The ratio diagram of the relative reproductive rate of the crop relative to the weed (RRR_{CW}) greater than unity.

than one implies the equilibrium will move in direction of the arrow. Each subsequent generation will let the RRR value move toward the extinction of the weed. In the case represented in Figure 9, it will take three generations (3 RRR shifts along dotted line) for the weed to be eliminated (assuming no dormancy). The converse situation can also be visualized in Figure 10. Because the weed is replacing itself at a relatively higher rate than the crop is (RRR < 1), the long-term shift in the population favors the weed, and will lead (in this example) to the extinction of the crop in three generations. Admittedly, this is an unrealistic situation. Firstly, because we do not let most crops re-seed themselves, but re-establish a high density crop stand each year. Secondly, because as subsequent generations move the mixture proportion in favor of the dominant species, the RRR is bound to change. These frequency dependent competitive interactions are common, and will be discussed later in this section. Despite these limitations, they do reveal a dynamic equilibria force that will enable the weed to succeed with continued cropping and indicate a need for a rotational crop that severely reduces weed reproductive ability. An increase in the seed bank along with the adaptive capacity favors the development of herbicide resistance of other evolving strategy, etc.

Frequency dependent interactions are revealed by two other possible calculated functions on the ratio diagram. These proportion dependent interactions show species affecting each other in other ways than just competing for the same space. The first is the case where the slope of the function is not parallel to the diagonal, and

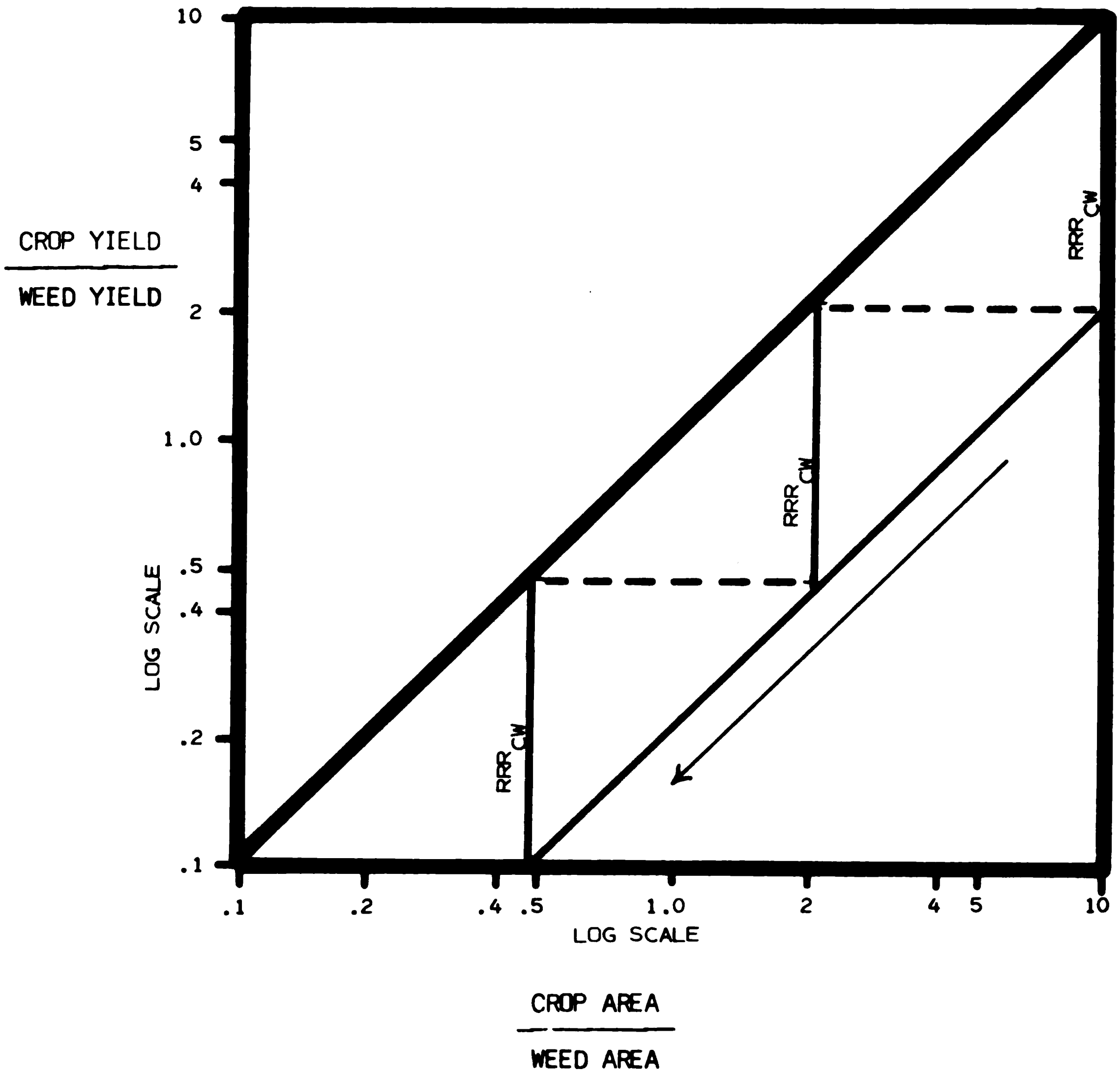


Figure 10. The ratio diagram of the relative reproductive rate of the crop relative to the weed (RRR_{CW}) less than unity.

is less than a 45^{o} slope (Figure 11). This type of interaction leads to an equilibrium, or stable, mixture (81) at the intersection of the calculated function and the diagonal. For mixture proportions to the left of the diagonal ($RRR_{CW} > 1$), the increase in the replacement potential favors the crop so it moves along the arrow by rapid replacement to the intersection point. At those ratios, the crop is the minority component and it is favored. At points on the calculated function to the right of the diagonal, the minority component, the weed, is replacing itself relatively more rapidly than the crop. Therefore, the weed replaces the crop until it meets the intersection with the diagonal. Therefore, the equilibrium forces in this situation favor the minority component and the mixture moves itself to a stable equilibrium proportional mixture at the diagonal intersection point. At that point, the $RRR_{CW} = 1$ and it tends to a stable proportionate mixture there. With this interaction is the implication that both species are crowding for "space" that is not completely the same for both. An example would be: 1) the case where one species develops early in the season, the other developing later in the season; or 2) one species profits by the presence of the other (e.g. legume-grass association).

The converse situation exists where the calculated function is frequency dependent, and the slope is greater than 45^{o} (Figure 12). The situation is where the crop and weed not only crowd for the same "space", but some other, active process is involved. An example would be one species producing a toxin that restricted the growth of one or both members of the mixture. For mixture proportions to the left of the

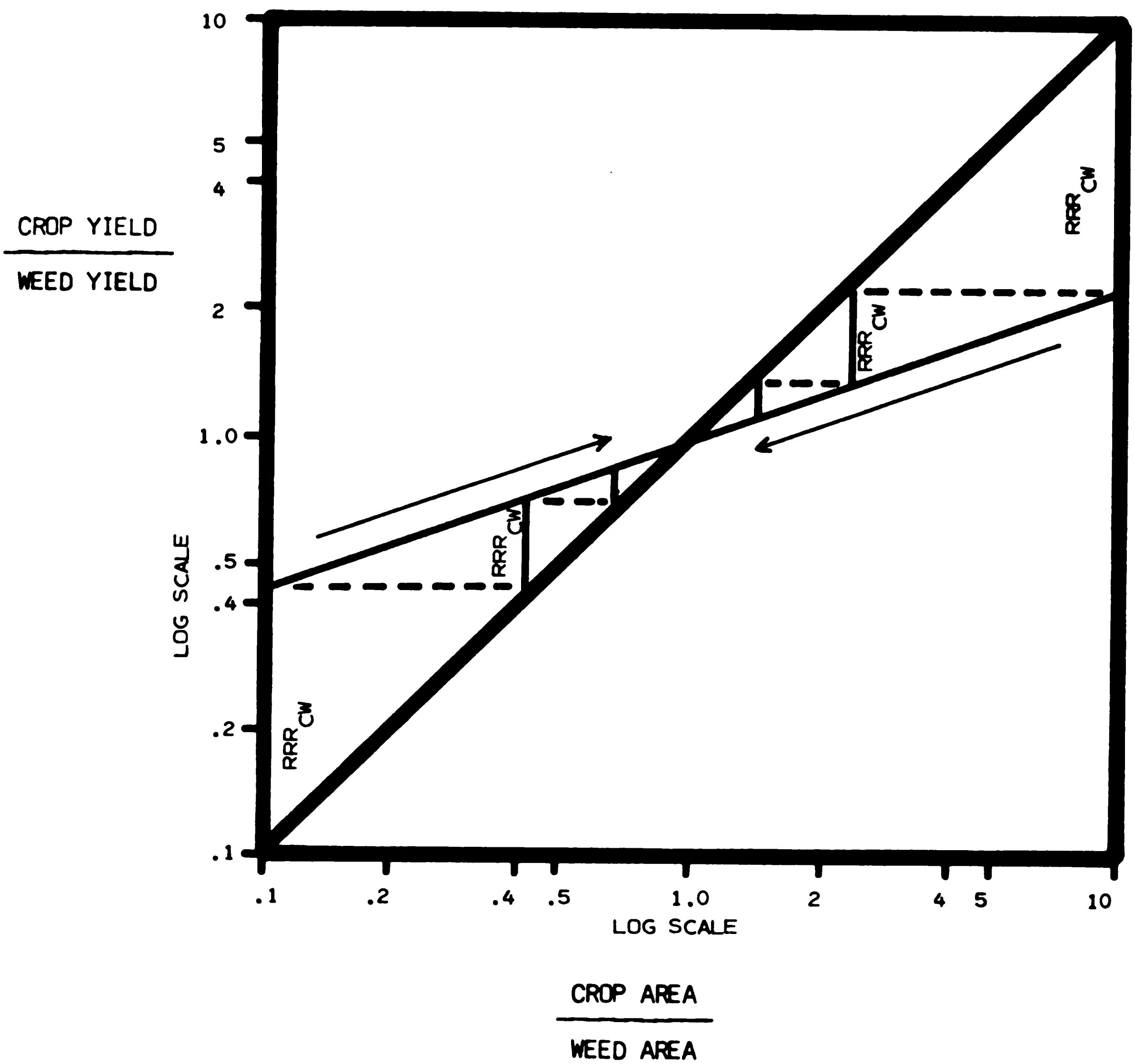


Figure 11. The ratio diagram of mixture proportion dependent responses: Slope less than 45°

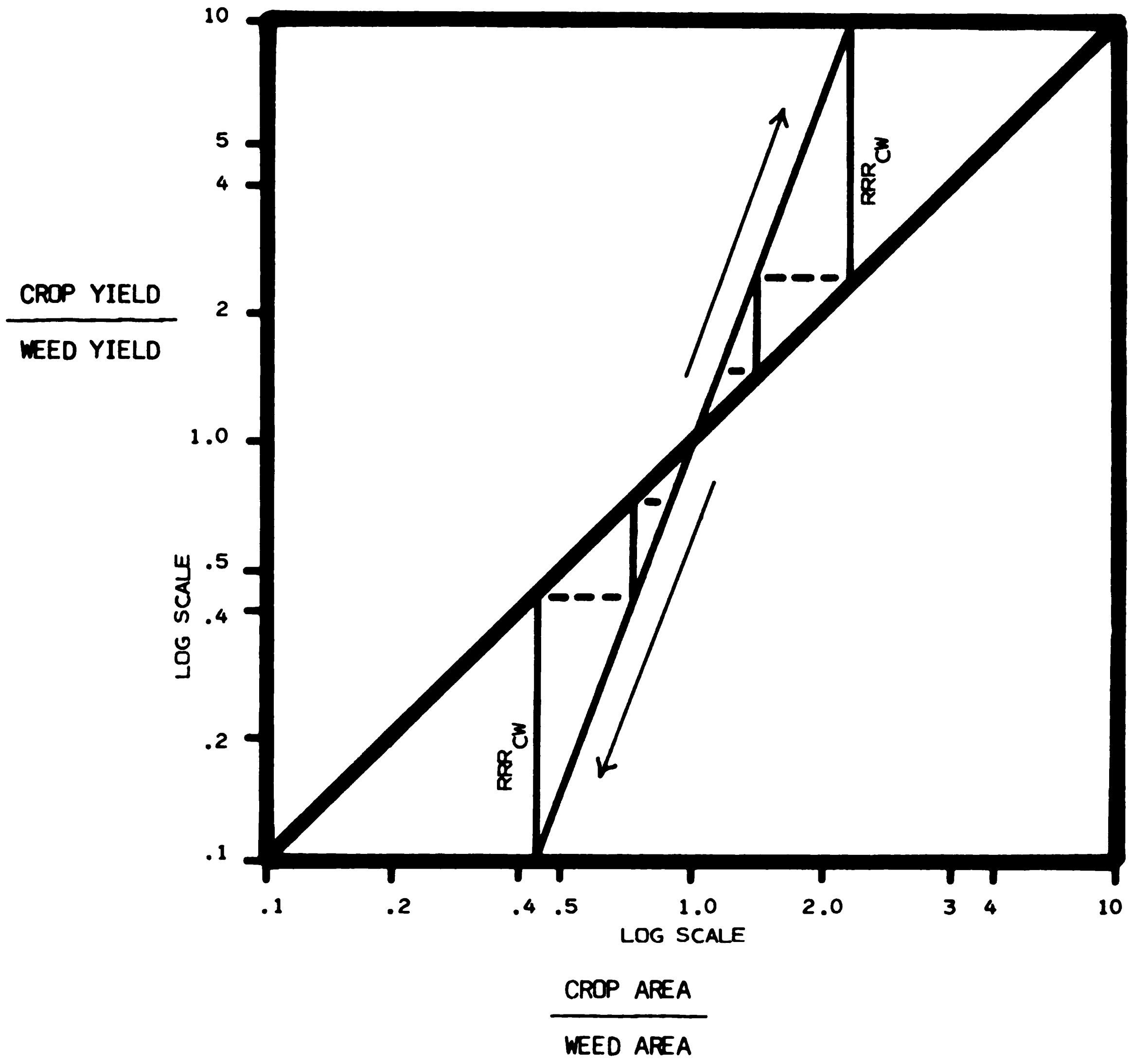


Figure 12. The ratio diagram of mixture proportion dependent responses: Slope greater than 45°.

diagonal ($RRR_{CW} > 1$) the relative replacement rate favors the increase of the crop over time, with exclusion of the weed. The equilibria goes in the direction away from the diagonal. This leads to an unstable condition. The mixture proportions to the right of the diagonal ($RRR_{CW} < 1$) tend to the exclusion of the crop over time. The mixture at the intersection in this case is not at equilibrium, in fact replacement forces acting at this point go away from it in both directions. The tendency favors one species to be dominant, and for the replacement of the other over time. The location of this intersection point will ultimately determine which species will succeed. The species in the proportional majority of the mixture at the intersection point will dominate over the other. Because the equilibrium forces go away from the intersection point, the most numerous species will eliminate the other over time.

Regression of individual mean on associate mean

Another revealing way to express the manner by which associate species condition the response of another species is by regressing the individual mean against the associate mean of the species in a mixture (52). For a given mixture proportion, the mean yield of one species is regressed against the monoculture yield times the proportion it appears in the mixture as (e.g. for the 50% crop - 50% weed mix the regression pairs are: 1) associate mean is the yield of the 50% crop component of the mixture; and 2) the individual mean is 50% of the crop monoculture mean.) When a regression function is defined by these pairs, the relative aggressiveness of the two species can be determined.

Weak competitors will be characterized by a high individual mean performance and a low associate effect (i.e., a steeper slope) (Figure 13). The implication of this is that the more aggressive species in the mixture is able to obtain a disproportionately higher share of the "space" at the expense of the weaker species. Additionally, if the regression line fit is good, the implication is that the species is able to compete aggressively over a wide range of mixture proportions. In other words, they have "general competitive ability". Conversely, some species display weaker or stronger competitive responses depending on the proportions of the mix. In other words, they have "frequency dependent competitive ability".

Individual fitness responses

The second index of whether one species will eventually dominate another associate species is "fitness", or competitive ability, of the individual (yield/plant). The replacement series analysis lends itself to this evaluation by substitution on the vertical axis of the mean weight per plant for the yield per unit area. This will give an estimate of an individual plant's ability to "crowd out" an associate species individual. But, more insight is gained by the application of mathematical models first elucidated by Mitscherlich (73) and refined by several Japanese researchers (8,12,23,26,55,57,58,61,62, 63,68,74,84,93,94,108,115,116). Historically, this analysis followed Mitscherlich with the statement of the "C-D effect" and the "Y-D effect" (93,94) and finally the "- 3/2 power law" of Yoda et al. (116). The original analysis was done in terms of intra-specific interference,

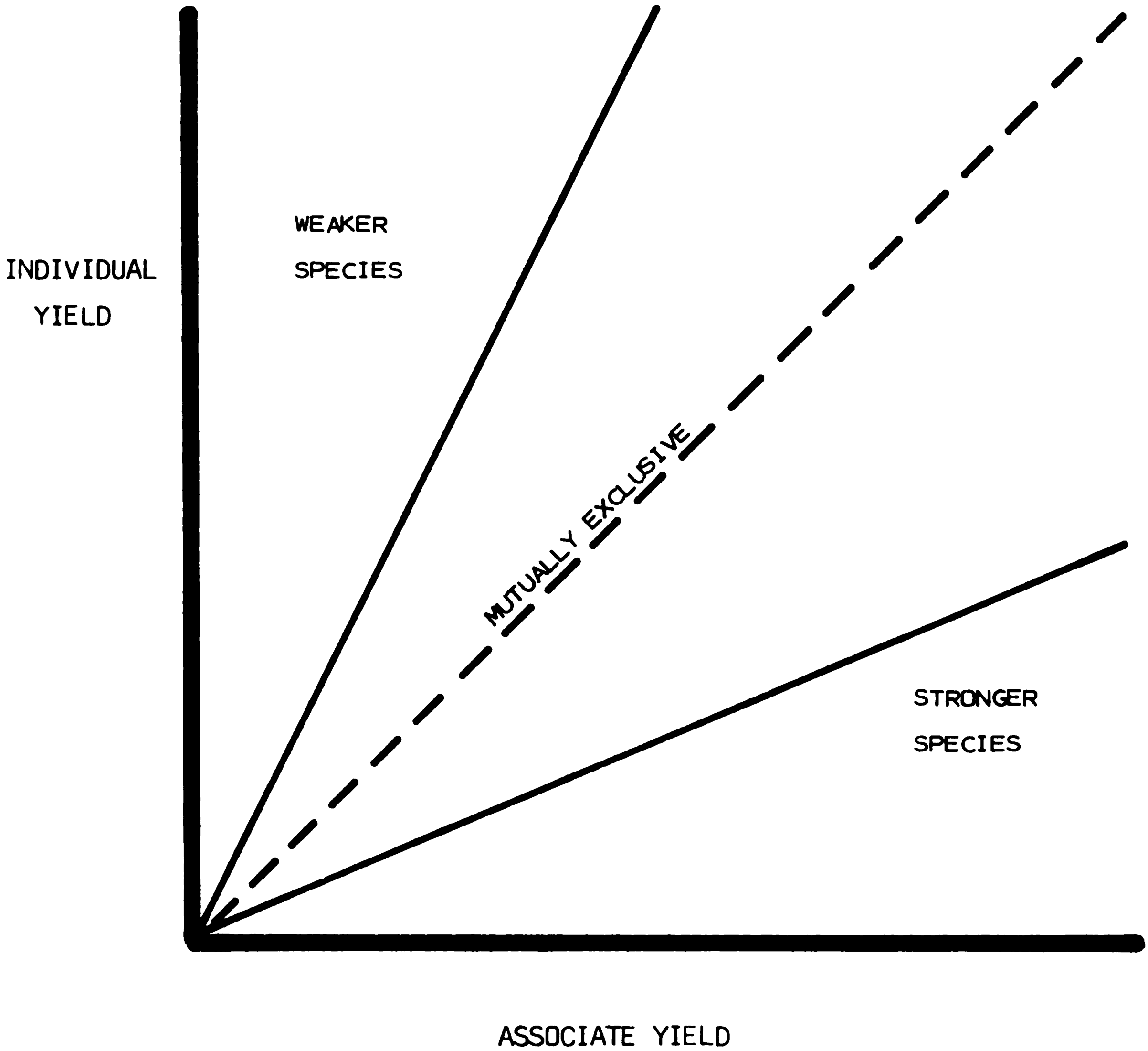


Figure 13: Regression of individual yield on associate yield for the determination of a species relative interference ability.

but comparison of intra- to inter-specific effects reveal much of the interactions of crops and weeds.

The "Y-D" and "C-D" effects

The "Y-D effect" or yield-density effect (56,62,63), briefly stated, says that in pure stands of a species the total yield per area becomes constant with the passage of time, and independent of density (Figure 14), $yd^{a-1} = K$ where:

y = yield per unit area

d = plant density

k = constant

a = index that increases with time: a = 0 at time (+) zero

a = 1 at time (+) ∞

The "Y-D" effect is a corollary to the "C-D" effect, or "competition-density effect". It states that the product of the mean weight per plant and the density are constant when sufficient time has passed (Figure 15). $wd^{a} = K$ where:

w = mean weight per plant

d = plant density

"K" and "a" are constants

a = gradient of C-D function that increases with time:

a = 0 at time (+) zero

a = 1 at time (+) ∞

As time passes, the minus slope increases to about a -1 slope, or more. These relationships hold for total plant weight, and for constituent weights: leaf, stem, root, and seed weights. The final slope, though,

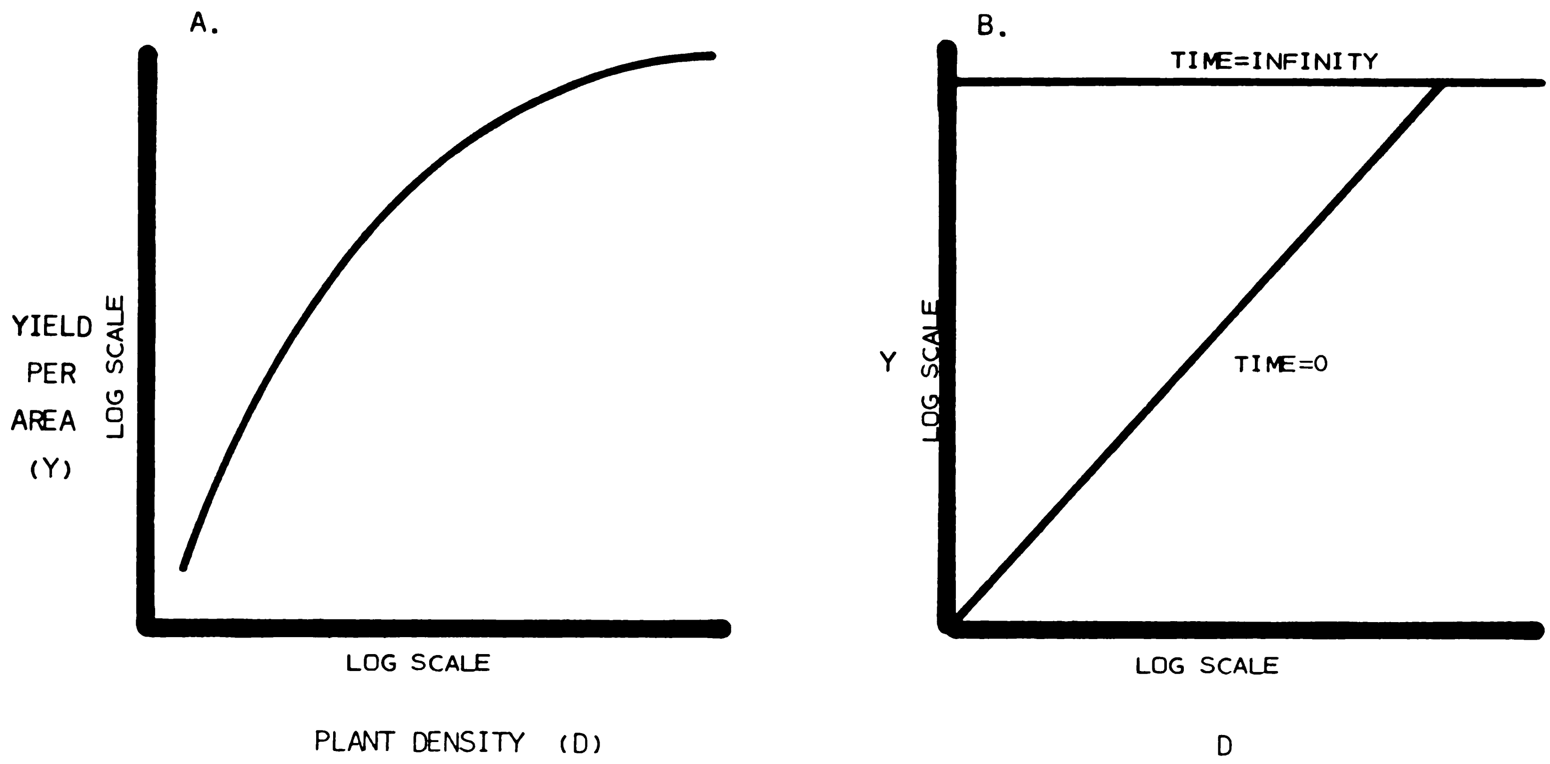


Figure 14. Graphical representation of the "Y-D" effect: Yield per unit area (Y) versus plant density (D). A: Response measured at maximum plant growth; B: Response measured at T=0, and at T=Infinity.

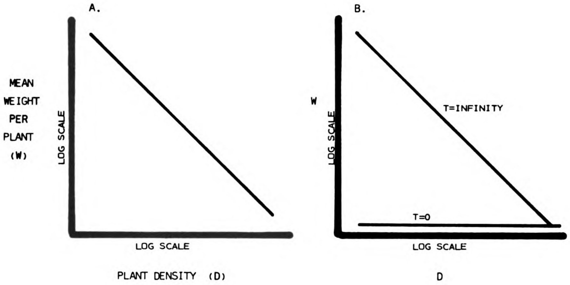


Figure 15. Graphical representation of the "C-D" effect: Mean weight per plant (W) versus plant density (D). A: Response measured at maximum plant growth; B: Response measured at Time=0, and Time=Infinity.

is not always -1.

- 3/2 power law of
self thinning

Subsequent to the definition of the "C-D" and "Y-D" effects, Yoda _et al_. (116) investigated overcrowded natural stands of redroot pigweed (_Amaranthus retroflexus_ L.), common ragweed (_Ambrosia artemisiifolia_ L.), lambsquarters (_Chenopodium album_ L.), and horseweed (_Erigeron canadensis_ L.) and found a slightly different relationship. What they found was:

$w = cd^{-3/2}$ where:

w = mean weight per plant

d = plant density

c = a constant characteristic of the individual species

They found that the slope of the mean plant weight versus the plant density, on log-log scales, was -3/2 (Figure 16). This says that mean weight per plant is always at the maximum for what the land can support at a given density in overcrowded stands. The applicability of this has been confirmed by several other researchers (8,12,26,55,61,68,84,108). The authors (116) found wide-spread applicability of this law, but still only said its use as a model "could be accepted as a crude approximation". Its usefulness in determining interactions between crops and weeds is not diminished by this. The relationship looks at interference to both changes in plant number (mortality) and individual plant size (plasticity). Both of these factors are revealed in intra-specific density dependent growth. This "normal" pattern can be compared with the growth patterns revealed in the mixture responses.

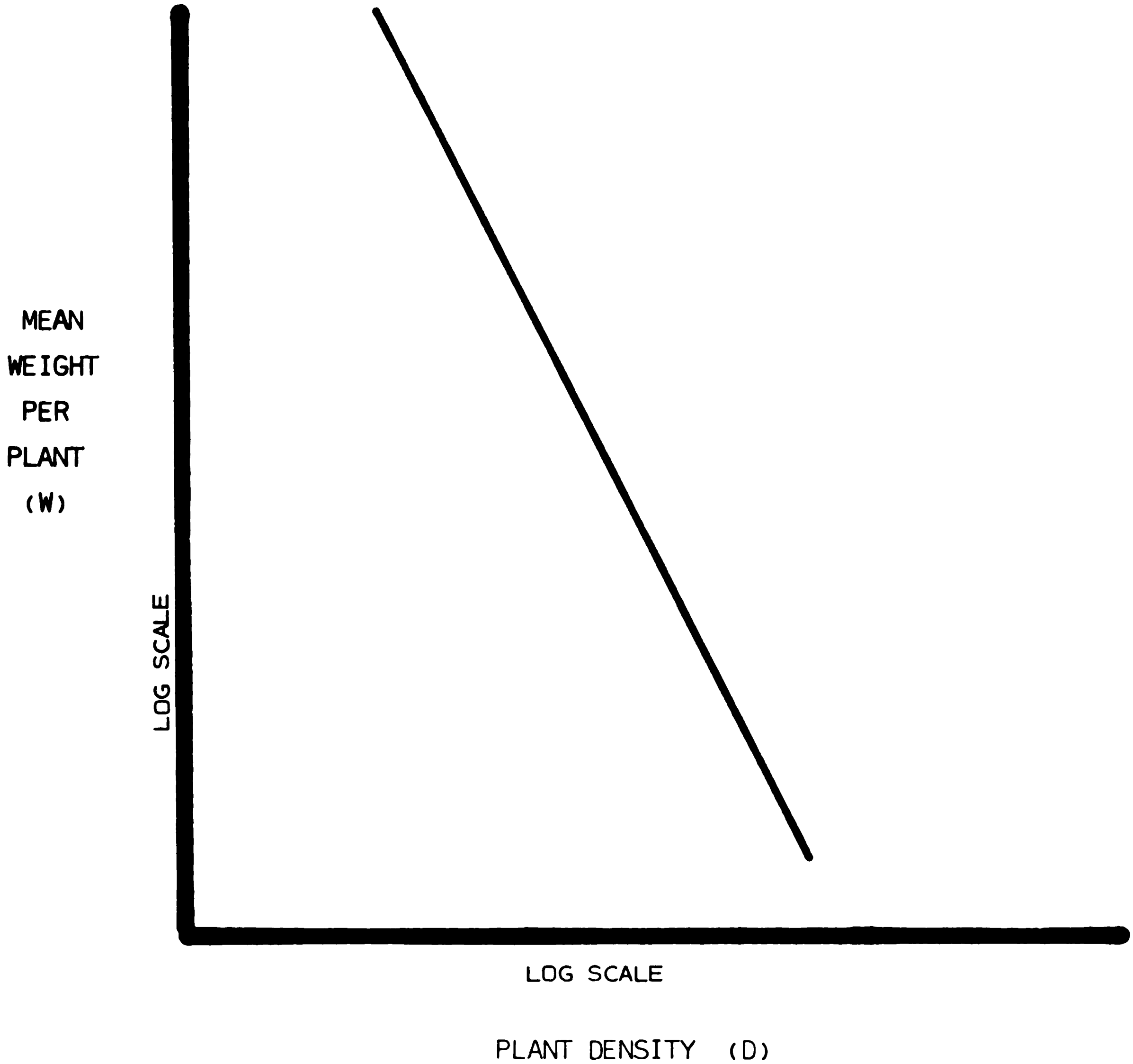


Figure 16. Graphical representation of the -3/2 power law of self-thinning: Mean weight per plant versus plant density.

Hirano and Kira (54) did an analysis of a "normal" plant (persimmon) and compared it to a species with known autotoxicity from root exudation (peach). They did not grow the species together, but only compared the growth, and deviations from the C-D function, of the two grown in pure cultures. The comparison of these intraspecific responses to mixture responses could reveal selective allelopathic responses if the scope of the analysis is extended. The basic premise of their analysis is that log-log plotting of plant density versus the reciprocal of the mean plant weight can reveal two types of growth patterns (Figures 17A and 17B). Both say the same thing. The assumption of this analysis is that linear functions are normal competitive responses, and curvilinear functions are indicated by the allelopathic responses. The decrease in weight per plant at the higher densities indicates a growth reduction due to some factor besides the normal density-dependent growth response defined by the -3/2 power law. There is the possibility of other interpretations, but there is a strong inference of allelopathic growth reduction. As with all allelopathy determinations, this type of analysis needs to be coupled with other types of analysis for confirmation of the phenomenon.

Mixed stand analysis requires that confounding due to changes in proportion and density must be avoided. Because of this, intraspecific responses must only be compared to total mixture responses at the same density. The components of the mixture cannot be directly compared to their respective monocultures, as the monoculture and species component of the mix are at two different densities.

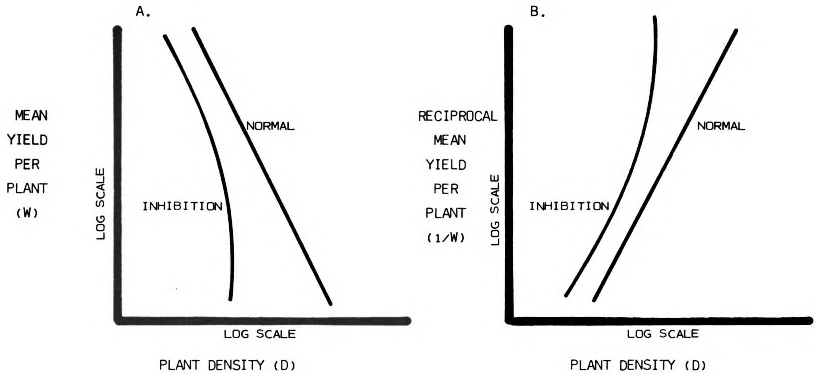


Figure 17. Normal and inhibited growth patterns revealed by alternate graphical presentations of: A) The mean yield per plant versus plant density; B) Reciprocal mean yield per plant versus density.

"Sakai test"

Sakai (90,91,92) proposed a test that can be modified slightly to allow the analysis of the replacement series data for "fitness" (Figure 18). The mean yield per plant of the crop and weed are plotted on the vertical axis. The replacement series is the horizontal axis. Comparison of the species response in pure stands to that in various mixture proportions will reveal the species' individual fitness, or competitive ability:

Figure 18A - This graph indicates both species respond the same in pure stands as they do in mixtures. Their relative fitness is unchanged by being in the mixture.

Figure 18B - In this situation, the individual crop plant fitness is decreased, and the weed fitness increased, by their mutual association.

Figure 18C - Both crop and weed fitness are reduced by their association in a mixture. This could be a response due to a non-selective allelopathic compound produced by either species.

Figure 18D - In this situation, both crop and weed benefit by their mutual association. They are not competing for exactly the same "space", therefore their individual fitness is increased.

In all these cases, there is the possibility of a frequency dependent fitness. At any particular proportion, one or the other species could dominate, while at other proportions the situation could change.

The foregoing discussion concerned itself with the plastic responses a species makes when confronted with changes in density and

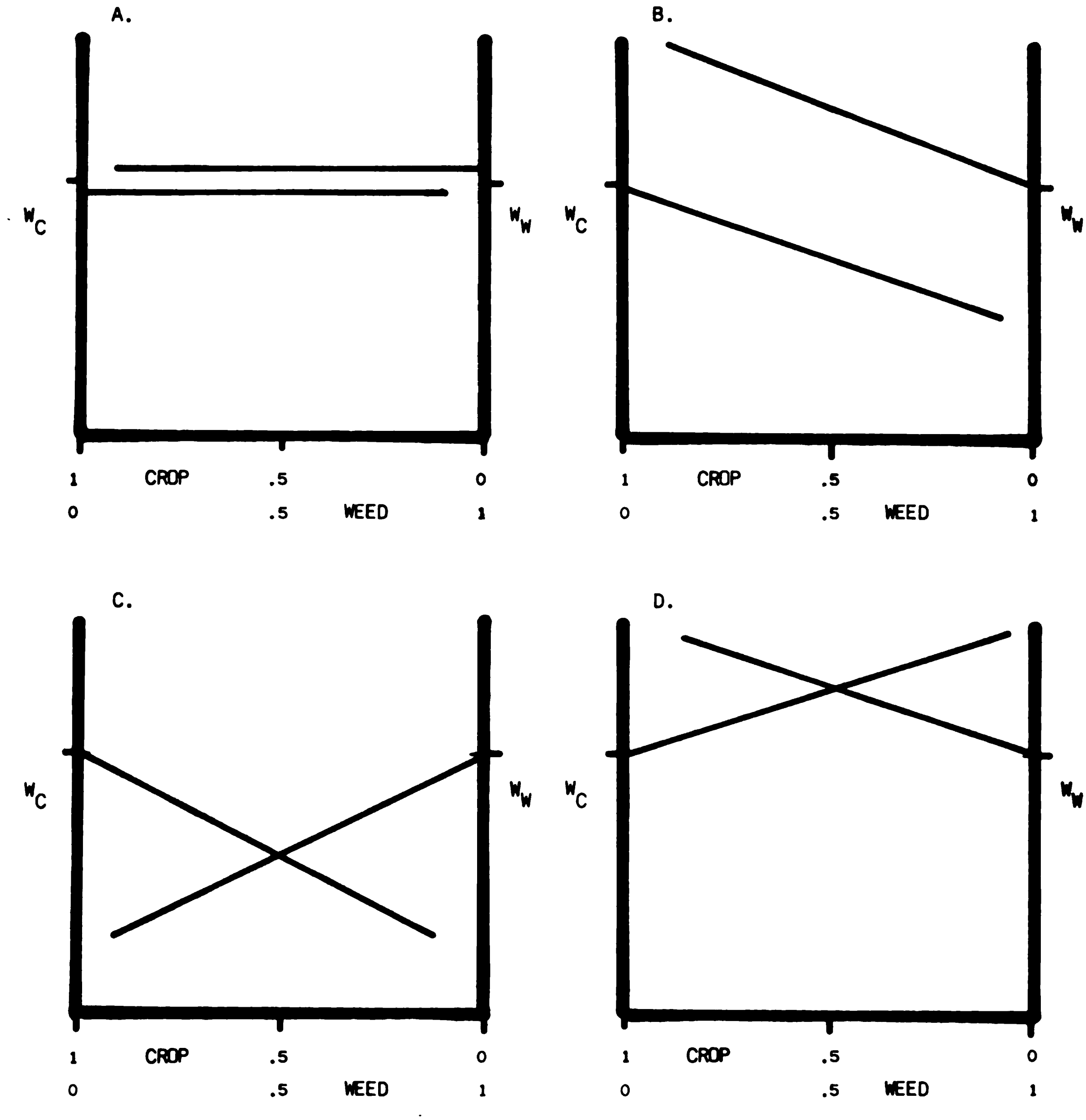


Figure 18. The replacement series diagram as an indicator of plant fitness: The Sakai test. A) Mutually exclusive; B) Compensation; C) Mutual inhibition; D) Positive complementation. W_C: Mean weight per crop plant; W_W: Mean weight per weed plant.

proportion from itself, and other associated species. The dynamic equilibria developed between the species will determine its ultimate fate: "When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportionate numbers and kinds to what we call chance...But how false a view this is!" Charles Darwin, 1859 (18).

Reproductive strategies

The third way in which plants determine whether they, or their associates, will survive into the future is their reproductive strategy. Every change in allocation, or partitioning, of assimilatory products between vegetative or reproductive plant parts represents a reproductive strategy (16). The amount of effort spent on a particular vegetative or reproductive organ, relative to the total energy available for work, can be an index of the relative value which natural selection has placed upon that function or structure (45). This index has been defined as the net reproductive effort:

$$\text{Net reproductive effort} = \frac{\text{Total energy as propagules}}{\text{Total energy as starting capital + net production}}$$

If there is relatively little loss of leaves, etc., at harvest, then the net production can be approximated by biomass at harvest. Starting capital, or initial seed weight, can be discounted as insignificantly small for plants reproducing by seed. Perennial plants reproducing by vegetative organs must be accounted for. Their starting capital is significant.

$$\text{Estimate of net reproductive effort} = \frac{\text{Total weight of propagules}}{\text{Total biomass weight at maturity}}$$

In practice, biomass at maturity will underestimate total plant production due to senescence losses. This index is similar to the "harvest index" (24,76,97). Comparisons of the net reproductive effort (NRE) between crop and weed has some inherent dangers. The energy required to form various plant organs and structures requires widely different caloric inputs: a gram of high oil soybean is not equal to a gram of velvetleaf stem. Comparison then between species can be inherently erroneous. Comparisons within the species to the effects of changes in density, proportion and both are possible. Because the NRE is not stated in terms of yield per plant or area, these considerations are obviated. The NRE of a crop or weed can be expressed in terms of the comparison of pure and mixed stands (Figure 19). Changes in the NRE response to changes in density and proportion will reveal possible long-term changes to the contribution a weed (or possibly a crop) will make to the soil seed pool. This can have long-term consequences for its survival, and ability to resist agronomic control practices.

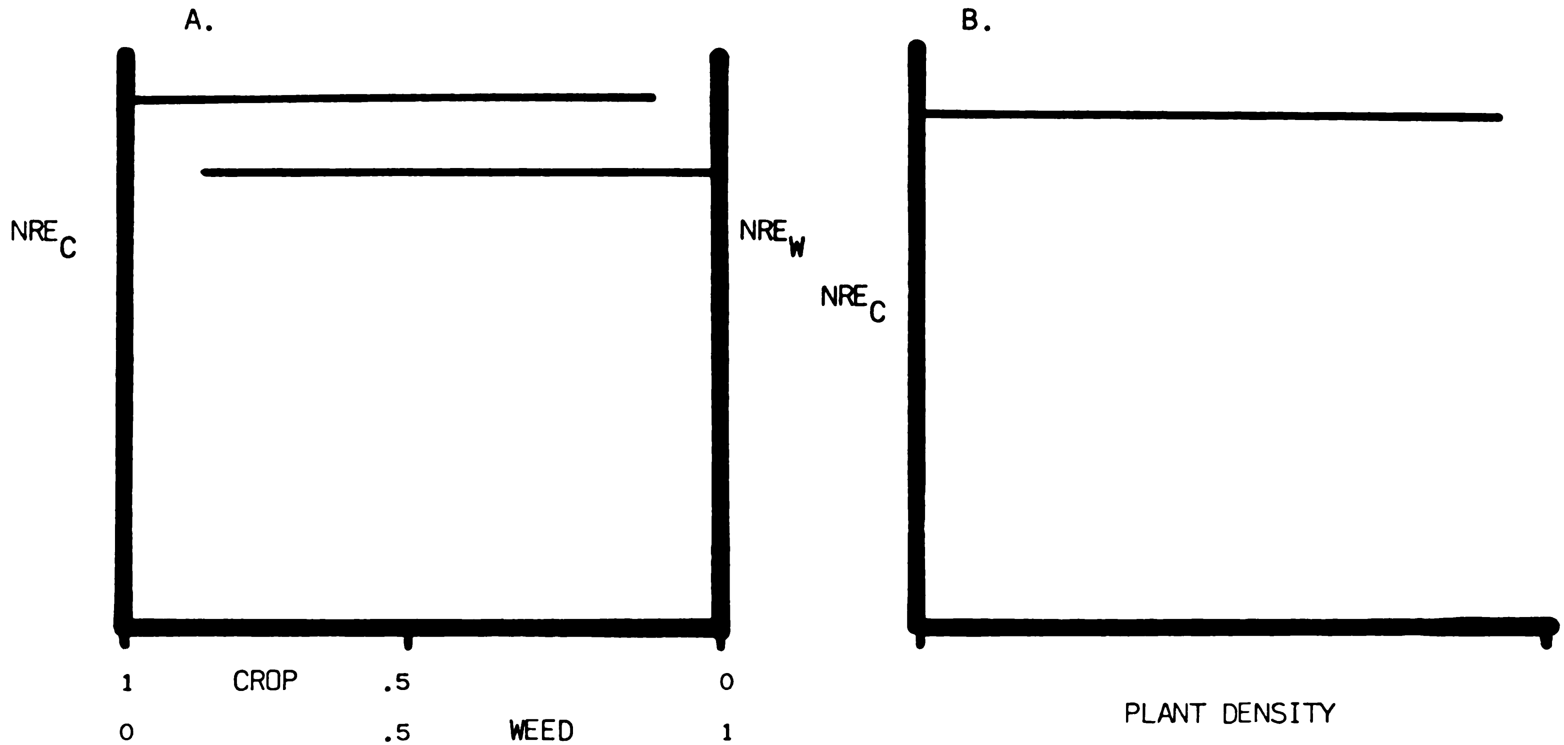


Figure 19. Graphical representations of the net reproductive effort (NRE). A: Changes in crop (NRE_C) and weed (NRE_W) net reproductive effort in response to changes in proportion; B: Changes in the net reproductive effort in response to changes in plant density.

SUMMARY

Traditional additive experimental designs serve a key function in providing information on overall effects due to weed infestations. Hopefully, the designs presented here will allow the separation of observed responses due to changes in density and proportion. It is also hoped these designs will enable a truly representative predictive modeling of the agroecosystem.

Methods and Materials

Occurrence and Periodicity Experiments

Experiments were conducted at Hillsdale County, and at Gratiot County, Michigan in 1978. In 1979, they were conducted at Gratiot County, Monroe County, and at Ingham County, Michigan. Table 1 shows location, planting date, soybean variety, and soil texture and organic matter content. All locations had high density (greater than 200 velvetleaf seedlings/m^2 in early season) velvetleaf infestations. Individual plots were 3.1m by 8m, with four 0.77m wide soybean rows. The plots were subdivided into 6/m^2 subplots. The experiments were designed as a randomized complete block design, with four replications. The weedy control treatments in 1978 and 1979 provided the no-herbicide data. Pre-plant incorporated herbicide treatments included pendimethalin (1.7 kg/ha), trifluralin (1.1 kg/ha), chloramben (3.4 kg/ha), metribuzin (0.6 kg/ha), and the combination of chloramben (3.4 kg/ha) plus metribuzin (0.6 kg/ha) plus pendimethalin (1.7 kg/ha). The herbicide treated plots

Table 1. Location, year, planting date, soybean variety, and soil texture and percent organic matter (% O.M.) of the soil for occurrence and periodicity experiments conducted in 1978-1979.

Location and year	Planting date	Soybean variety	Soil texture	Soil % O.M.
Hillsdale Co.-1978	May 19	Corsoy	Sandy clay loam	3.0
Gratiot Co.-1978	May 30	Corsoy	Clay loam	5.4
Gratiot Co.-1979	May 30	Evans	Clay loam	5.4
Monroe Co.-1979	June 15	Corsoy	Sandy loam	4.0
Ingham Co.-1979	May 21	Evans	Sandy clay loam	3.3

were only performed in 1979. The data collected included the numbers of velvetleaf seedlings emerging every 2 weeks, and the depths in the soil of that emergence, through the growing season. Every 2 weeks, starting with 2 weeks after planting, the number of velvetleaf appearing were counted. Using a soil sampling probe, the seedlings were excavated and the depth of emergence was measured by the distance from the soil surface to the appearance of the first lateral root hairs (30). Soybean emergence averaged 5 days after planting. Therefore, the first sample date represented velvetleaf seedling emergence within the first 10 days of soybean emergence. After each data collection, velvetleaf and soybeans in all six subplots were removed with a contact herbicide, paraquat, or by razor-blade. In all cases care was taken not to disturb the soil surface of adjacent plots. Each $1m^2$ subplot was used only once. The data presented represents the velvetleaf emerging in the sampled 2 week period only, with no cumulative numbers being evaluated. Emergence depth data was averaged for each subplot. Figures and tables presented were averaged over replications, years and locations. Herbicide treated plots were analyzed as randomized complete blocks, and 5% L.S.D.'s calculated (15,66,96). Data on typical velvetleaf infestations in Michigan soybean production areas were taken at midseason, late July through early August of 1979. Because velvetleaf typically appears in soybean fields as patches, and not as entire field infestations, data was collected, and calculated, for those infestations in spots. Only velvetleaf infestations visible above the soybean canopy were used. Data presented represents 13 locations, 4 counties of lower Michigan, .47-1m row spacings, and soils ranging from organic, clay loam, loam, to sandy loams.

Plastic Growth, Population Mortality and Reproductive Strategy Experiments

Experiments conducted for plastic growth, population dynamics and reproductive strategy responses include the additive design, field density replacement series, varied density replacement series, and empirical observations of natural velvetleaf infestation population mortality.

Figure 20 shows the layout of individual plots in both the additive design and the field density replacement series (Figure 20A), and in the varied density replacement series (Figure 20B), experiments. In all three experiments the outside two soybean rows served as "guard" rows; as did the 0.62m buffer areas at the ends of the plot, and between subplots. Each subplot consisted of two rows of soybeans. Two subplots were used so that midseason dry matter accumulation determinations drawn from one would not prevent subsequent data collection for the other parameters. The soybean rows were oriented east-west in 1978, and north-south in 1979. All three experiments were located near the intersection of Beaumont and Forest Roads, Michigan State University Agricultural Experiment Station, East Lansing. All three experiments were laid out in a randomized complete block design. The additive design, and the field density replacement series, experiments consisted of four replications in both 1978 and 1979. The varied density replacement series experiment was conducted in 1979 only, with three replications. Table 2 shows planting dates, seed varieties, and the dates of branching

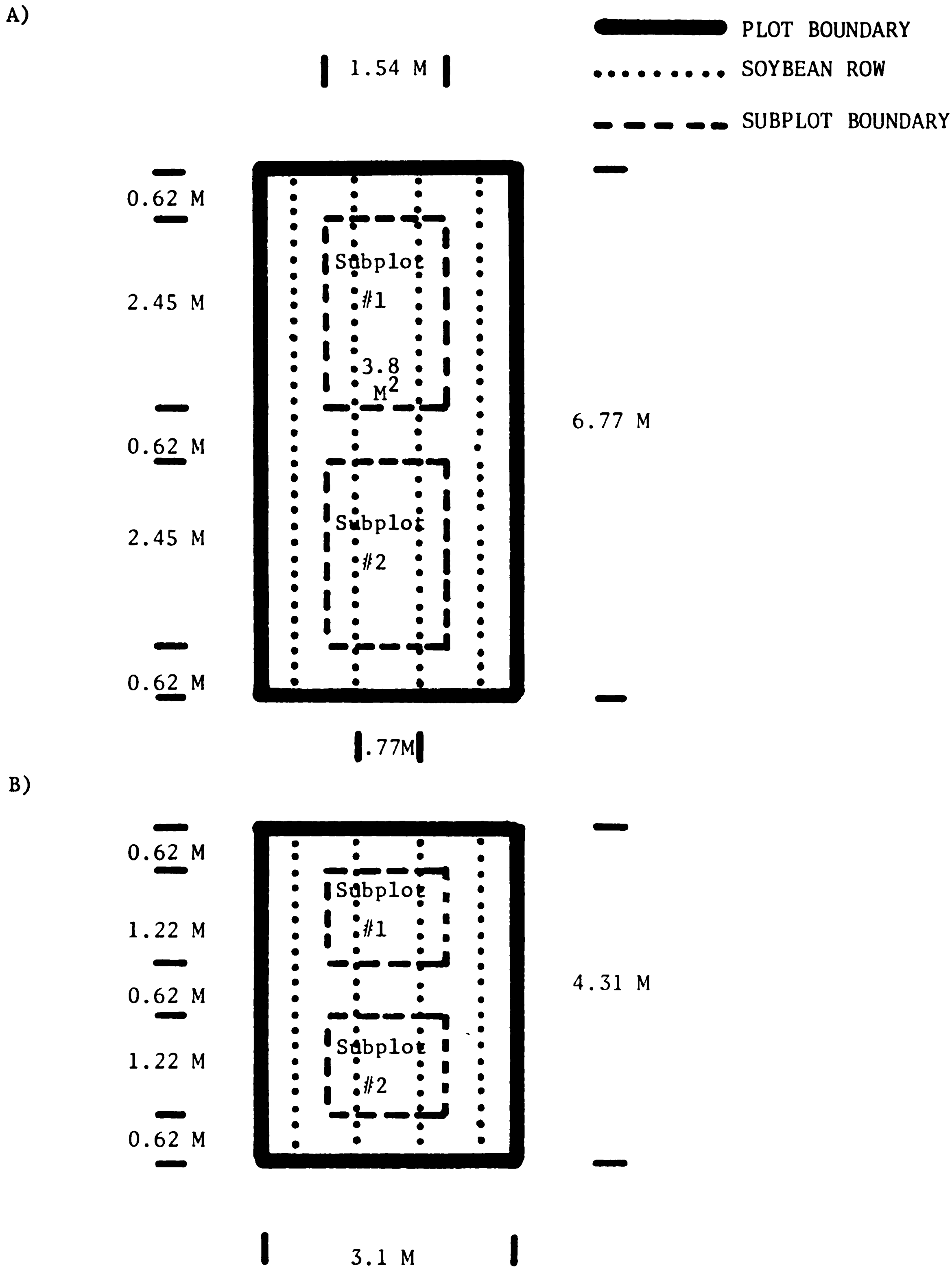


Figure 20. Individual plot layouts and dimensions for the additive design and field density replacement series experiments (A), and for the varied density replacement series (B).

Table 2. Planting dates, seed variety, and harvest dates for dry weight, seed weight and flowering and branching node determinations in 1978-1979 for the plastic growth, population mortality, and reproductive strategy experiments.

Year	Planting date	Soybean seed variety	Velvetleaf seed variety
1978	June 1	Corsoy	Pennsylvania 1977
1979	May 16	Hark	Pennsylvania 1977

Year	Flowering node and branching node determinations	Dry weight	Soybean seed weight
1978	August 7	August 14	October 7
1979	August 7	August 20	October 10

node, flowering node, dry weight and seed weight harvests. The experiments were blocked by the varying soil types. They all had 3.97% organic matter content, with a pH of 7.2. The texture ranged from a Brookstone sandy clay to a clay loam (Argiaquoll and Haplaquoll). The field had no apparent history of velvetleaf prior to 1978. Grassy weed control was accomplished with 0.6 kg/ha of trifluralin applied preplant incorporated in both 1978 and 1979. The soybeans were planted with a two row plate-type planter. The velvetleaf were planted with a PLANET JR. into the soybean row, and thinned to the desired densities and proportions ten days after planting. Between the soybean rows were kept totally weed-free through the growing season, and all but velvetleaf were removed in the soybean row. The velvetleaf and soybean data collected in all three experiments included midseason dry weight accumulation per m^2, and per plant; branching nodes per m^2, and per plant; flowering nodes per m^2, and per plant, at midseason and at harvest (soybeans only); percent immature soybean pods (1979 only); seed weight per m^2, and per plant; seed number per m^2, and per plant; weight per weed; percent velvetleaf germination; and the plant populations at various times in the growing season. Velvetleaf and soybean data collected only in the field density replacement series, and in 1979 only, included leaf tissue for analysis of nitrogen, phosphorus, potassium, calcium, magnesium, sodium, manganese, copper, boron, zinc, aluminum and iron. Soybean data collected only in the additive design experiment, and only in 1979, included soybean stem diameter and soybean height to the first node.

Dry weight accumulation data was collected at midseason (August), the peak of vegetative growth, for the best estimate of maximum vegetation biomass. Plants were cut at the soil surface from the entire 3.8 m^2 subplot, bagged, dried and weighed.

Ten representative plants of each species, from each subplot, were sampled for numbers of branching nodes. The numbers of branches were counted, excluding petiolar and peduncular stems. Data was averaged over each subplot for further analysis.

One hundred grams of new, fully expanded leaves of both species were collected in early August of 1979 for macro- and micronutrient leaf analysis. Subplot samples were dried and analyzed by the Plant Analysis Laboratory, Ohio Agricultural Research and Development Center, Department of Agronomy, University of Ohio, Wooster.

Ten representative plants of each species, from each subplot, were sampled for midseason flowering node numbers. Visible reproductive parts, pods and flowers, of each species were counted, and averaged over each subplot. In 1979 only, soybean pods were counted from the entire 3.8m^2 subplot as part of hand cleaning operations on soybean seed. The counts were separated into mature pods and immature pods (pods without seeds, or with seeds weighing less than 200 mg/seed). After harvest in 1979 only, 10 representative soybean plants were sampled for stem diameter, and height from the soil surface to the first node, determinations. Data was averaged over each plot for further analysis. Stem diameters were measured with a micrometer just below the first node.

Mature, field dried, soybean plants were harvested from each 3.8 M^2 subplot in early October of 1978 and 1979. All pods were counted as discussed previously, and soybean seed was hand separated from the pods. Seed weight, seed number and weight per seed data were assembled at that time. Velvetleaf seed pods were collected in the field from live plants throughout the weeds indeterminate reproductive phase. Mature, entirely blackened, pods were collected before the dehiscent seed fell from the pod. These velvetleaf seed harvesting operations occurred every 2-3 days, from early August until the soybean seed harvest. At soybean seed harvest all mature and immature velvetleaf pods were collected. Velvetleaf pods were hand crushed, winnowed and the seed separated from pod chaff with an air blower seed cleaner. Velvetleaf seed subsamples of 20 seeds per plot were placed in 100 cm plastic petri dishes with 5 ml of distilled water to determine velvetleaf seed viability. Filter paper was used in the petri dishes, which were sealed with parafilm to retain moisture for germination. The petri dishes were dark germinated at 20^{o}C for 5 days. Viability was determined by the appearance of the white radicle from the seed.

Densities and mixture proportions for the additive design, field density replacement series and varied replacement series experiments were determined at various times after the initial, early, thinning operations. Densities and mixture ratios used in data analysis relate to the population conditions at the time of actual data collection for each individual parameter measured (i.e. soybean seed weight data densities and proportions were those that existed in the plot in early October). The soybean population in the additive design experiment was 16.4 soybeans/m^2 in 1978, and 16.6 soybeans/m^2 in 1979. The velvetleaf densities added to the soybean stand in the additive design experiment were 0, 2.5, 4.7 and 9.7 velvetleaf/m^2 in 1978; in 1979 they were

3.7, 7.4, 10.5 and 24.6 velvetleaf/m^2. The densities in the varied density replacement series (1979 only) were 5.8, 22.3 and 83.3 plants/m^2. Within each of these three population densities there was a soybean monoculture, a velvetleaf monoculture, and a 50% soybean - 50% velvetleaf mixture. The overall plant population, within any one of the three densities, was the same in monocultures and mixtures. The overall population density in the field density replacement series experiment was 13.2 plants/m^2 in 1978, and 13.7 plants/m^2 in 1979. All plots, whether monocultures or mixtures, were at this overall density. The mixture proportions used in analyzing the field density replacement series experiment appear in Table 3. The mixture proportions are listed by growth parameter measured, and by year. With every set of mixtures listed were also soybean and velvetleaf monocultures, which were not included in Table 3. All mixture proportions were determined on each plot. Those plots which deviated more than ca. 6-7% in terms of density or proportion were discarded and missing plot calculations were performed. All three experiments were analyzed as randomized complete block designs. The varied density replacement series experiment had 3 blocks; and the additive design and field density replacement series experiments had 4 blocks. The 5% L.S.D. and/or 95% confidence limits were calculated as appropriate to determine mean separation significance. Also calculated was the Net Reproductive Effort (45), the individual plants percent chance of surviving (45) and the regression of the individual mean on the associate mean (52). Because trend analysis revealed a highly linear trend in population mortality through the growing season, regression analysis

Table 3. The typical field density replacement series experiment mixture proportions used for growth data analysis in 1978-1979 (Soy=soybean; Vele=velvetleaf).

Year	Growth Parameter	Mixture Proportions
1978	Seed weight and branching nodes	76% Soy-24% Vele
		51% Soy-49% Vele
		40% Soy-60% Vele
		25% Soy-75% Vele
1978	Flowering nodes	No useable data
1978	Dry weight	76% Soy-24% Vele
		60% Soy-40% Vele
		49% Soy-51% Vele
		25% Soy-75% Vele
1979	Seed weight	66% Soy-34% Vele
		55% Soy-45% Vele
		43% Soy-57% Vele
		35% Soy-65% Vele
1979	Flowering nodes	69% Soy-31% Vele
		64% Soy-36% Vele
		54% Soy-46% Vele
		44% Soy-56% Vele
1979	Branching nodes	65% Soy-35% Vele
		52% Soy-48% Vele
		36% Soy-64% Vele
1979	Dry weight	77% Soy-23% Vele
		53% Soy-47% Vele
		37% Soy-63% Vele

was performed on population data.

Empirical observations of velvetleaf population mortality were made in a soybean field in Monroe County in 1979. Three one m^2 plots were staked out in a heavily infested portion of the field. Guard, or buffer, areas were maintained around the data collection zones. Velvetleaf populations were counted on July 6 and 17, August 2 and 23, September 12 and October 19 of 1979 only. All three plots were carefully hand weeded for all species except velvetleaf.

RESULTS AND DISCUSSION

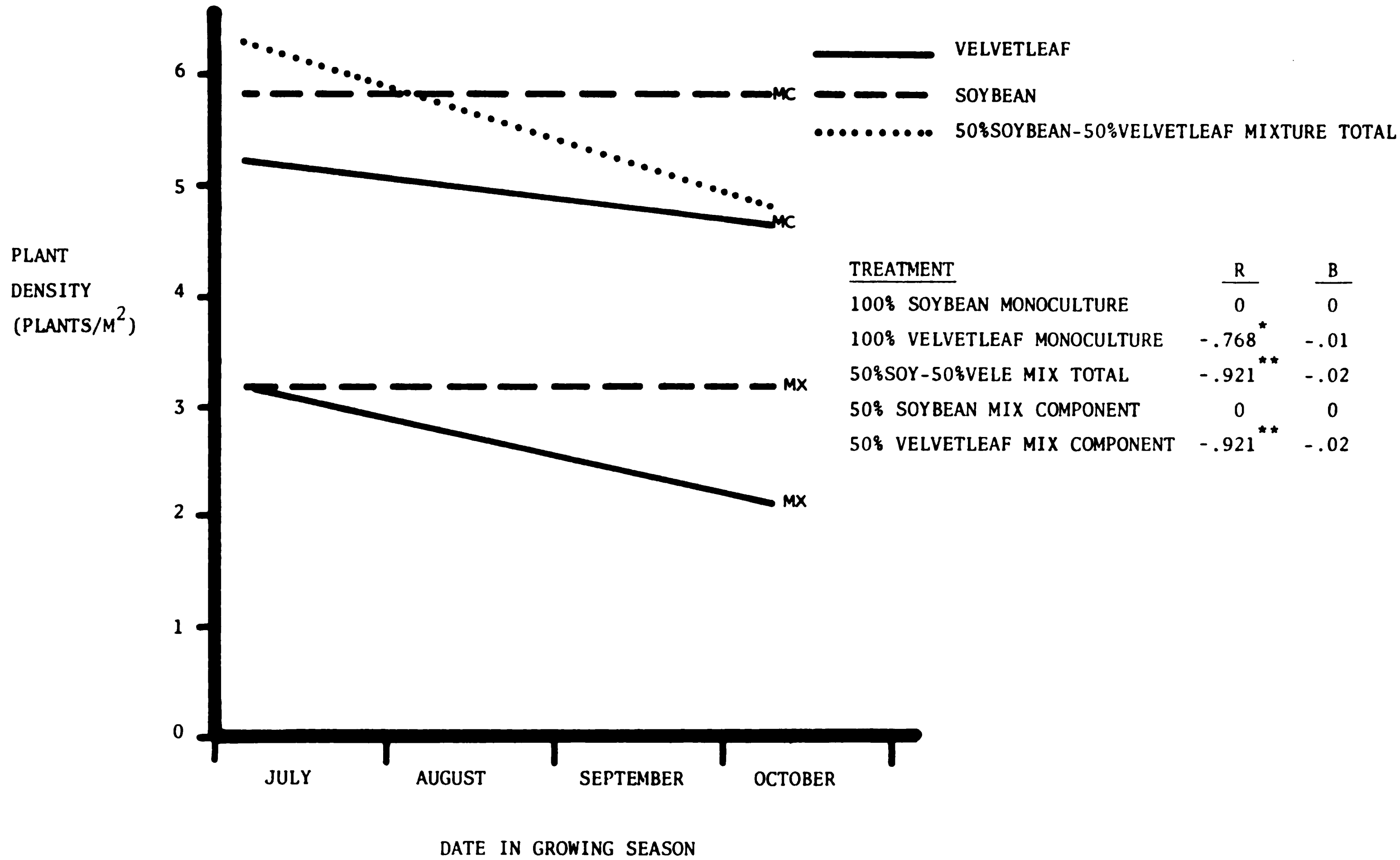
Population Dynamics

Mortality in the community of soybean and velvetleaf plants can be characterized by several events (figure 21). First, the greater the initial population of either species, in monoculture or in 50% soybean - 50% velvetleaf mixtures, the greater the death rate through the growing season. Secondly, the rate of mortality for both species was linear through the growing season. Thirdly, at field populations (ca. 22 plants/m^2) and below velvetleaf mortality was greater than that of soybean. This was true for both species monocultures and the 50% soybean - 50% velvetleaf mixtures. Lastly, unlike mortal responses at higher (ca. 83 plants/m^2) and lower (ca. 6 plants/m^2) populations, velvetleaf mortality at field populations (ca. 22 plants/m^2) in 50% soybean - 50% velvetleaf mixtures was less than that of it monoculture. This is evidence of the weeds ability to adapt and optimize its population at typical soybean field populations. This fact, plus the evidence indicating a greater resistance to death of soybean relative to that of velvetleaf, predispose soybean to smaller (figure 22) less productive (figure 23), plants.

Plastic Growth Responses

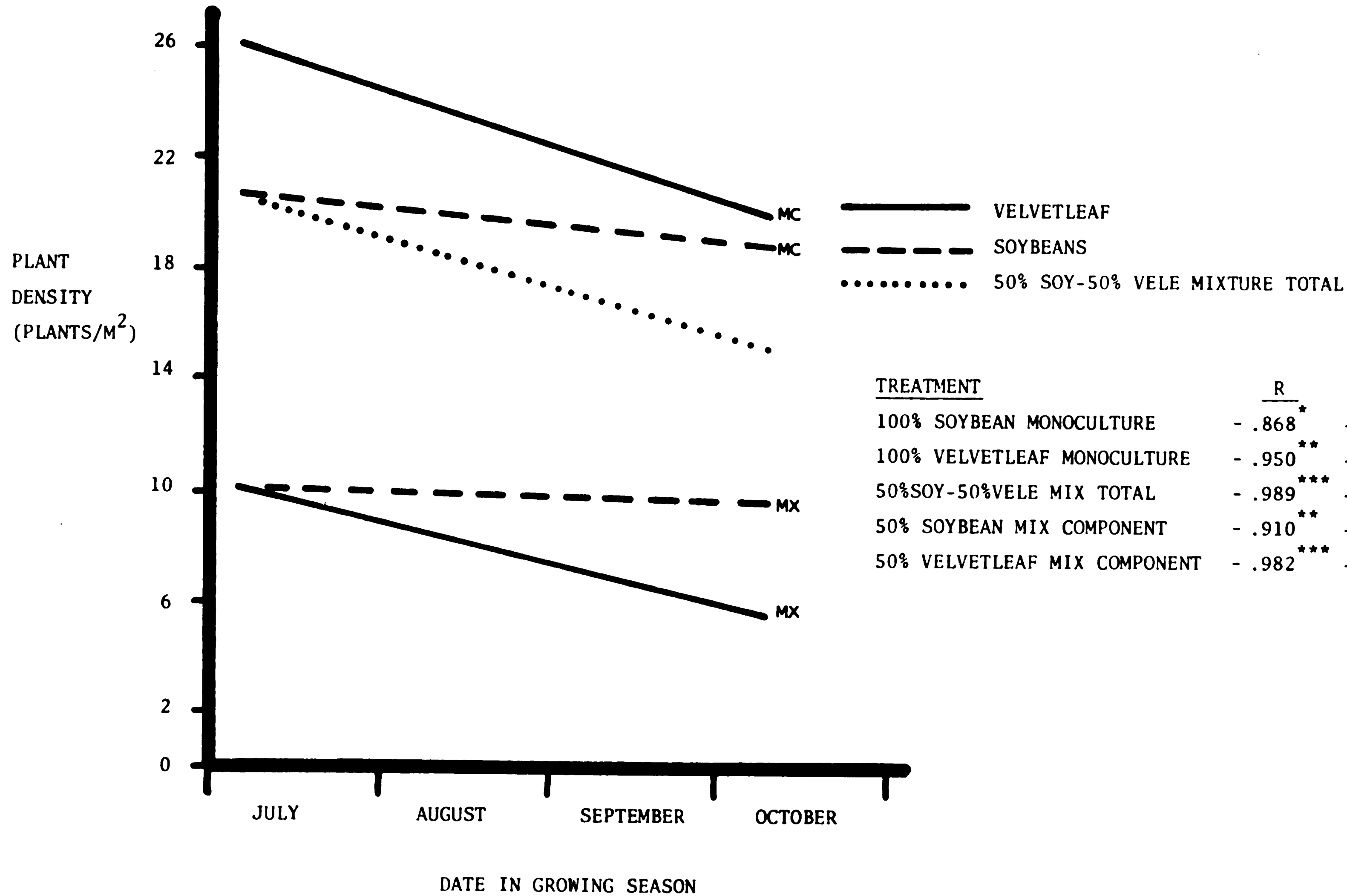
Dry Matter

Soybean dry weight growth responses can be characterized by several events. Soybean dry weight/m^2 decreased with the addition of



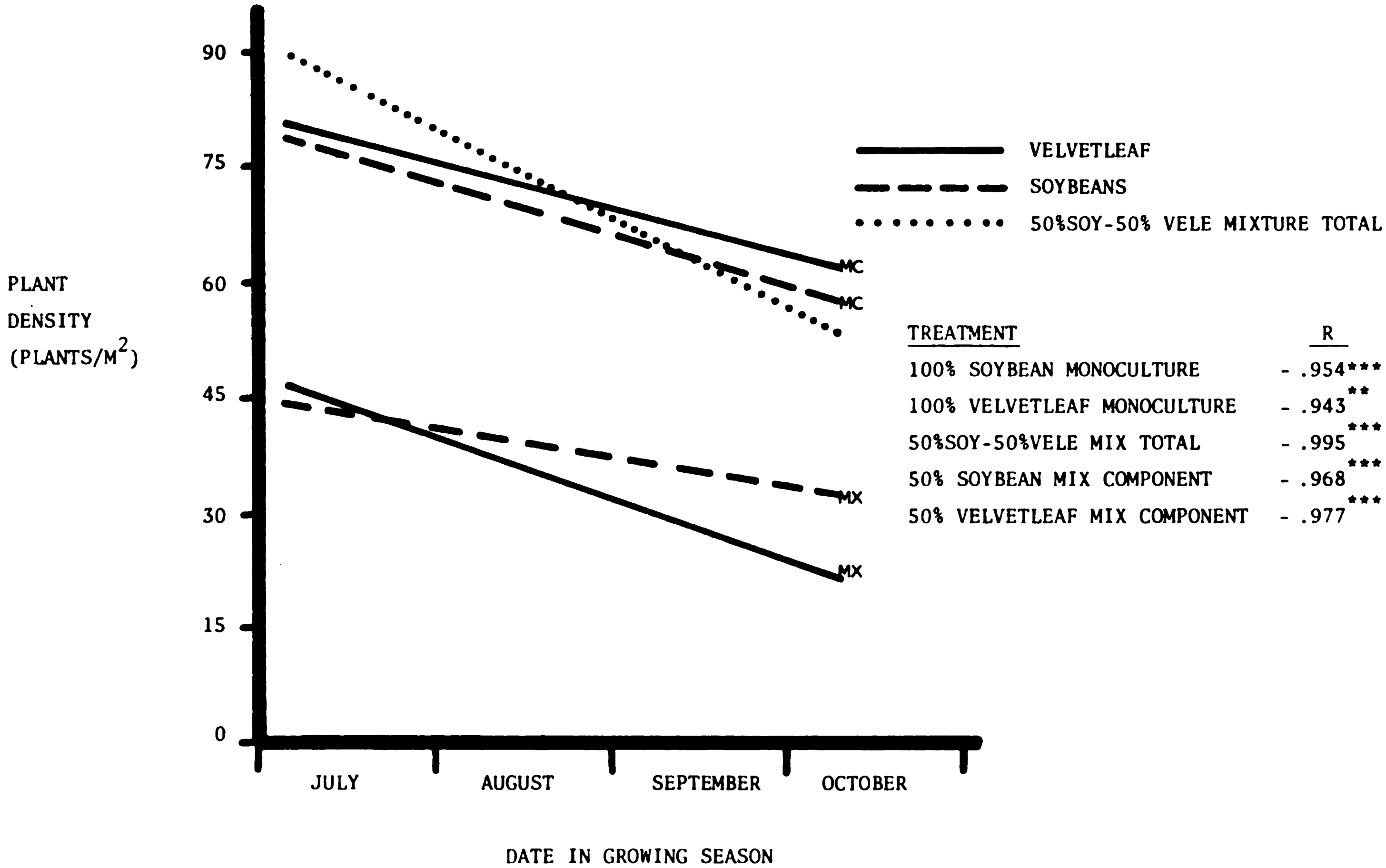
TREATMENT	R	B
100% SOYBEAN MONOCULTURE	0	0
100% VELVETLEAF MONOCULTURE	-.768*	-.01
50%SOY-50%VELE MIX TOTAL	-.921**	-.02
50% SOYBEAN MIX COMPONENT	0	0
50% VELVETLEAF MIX COMPONENT	-.921**	-.02

Figure 21A. Linear regression of plant density (initial density ca. 6 plants/M^2) of soybeans (SOY) and velvetleaf (VELE), in monoculture (MC) and in 50% soybean-50% velvetleaf mixtures (MX), through the growing season (July-October 1979); with associated regression coefficients (R) and slopes (B).



TREATMENT	R	B
100% SOYBEAN MONOCULTURE	- .868*	-.03
100% VELVETLEAF MONOCULTURE	- .950**	-.12
50%SOY-50%VELE MIX TOTAL	- .989***	-.10
50% SOYBEAN MIX COMPONENT	- .910**	-.01
50% VELVETLEAF MIX COMPONENT	- .982***	-.09

Figure 21B. Linear regression of plant density (initial density ca. 22 plants per M^2) of soybeans (SOY) and velvetleaf (VELE), in monoculture (MC) and in 50% soybean-50% velvetleaf mixtures (MX), through the growing season (July-October 1979); with associated regression.



TREATMENT	R	B
100% SOYBEAN MONOCULTURE	- .954***	-.40
100% VELVETLEAF MONOCULTURE	- .943**	-.38
50%SOY-50%VELE MIX TOTAL	- .995***	-.72
50% SOYBEAN MIX COMPONENT	- .968***	-.24
50% VELVETLEAF MIX COMPONENT	- .977***	-.49

Figure 21C. Linear regression of plant density (initial density ca. 83 plants/M^2) of soybeans (SOY) and velvetleaf (VELE), in monoculture (MC) and in 50% soybean-50% velvetleaf mixtures (MX), through the growing season (July-October 1979); with associated regression coefficients (R) and slopes (B).

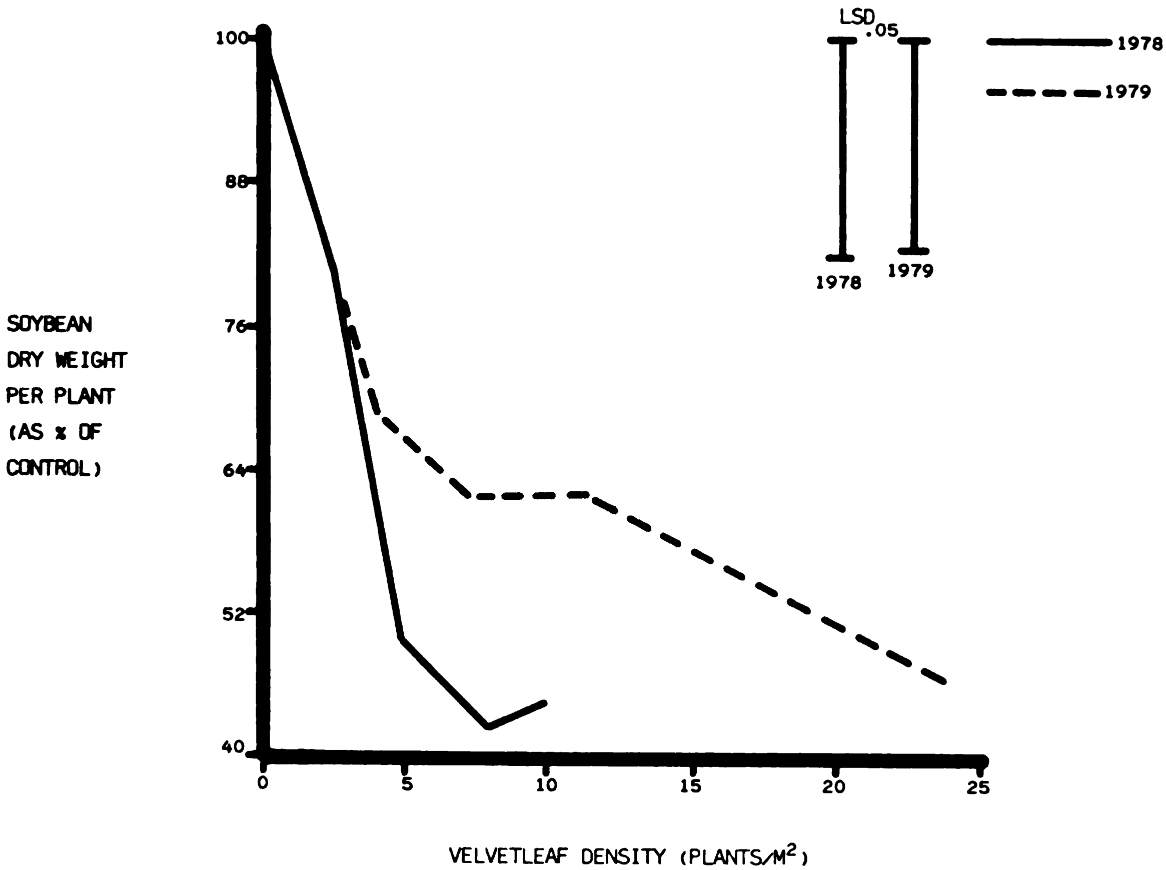


Figure 22. Effect of various densities of velvetleaf on soybean dry weight/plant (expressed as a percent of the weed-free control) in a constant density soybean stand.

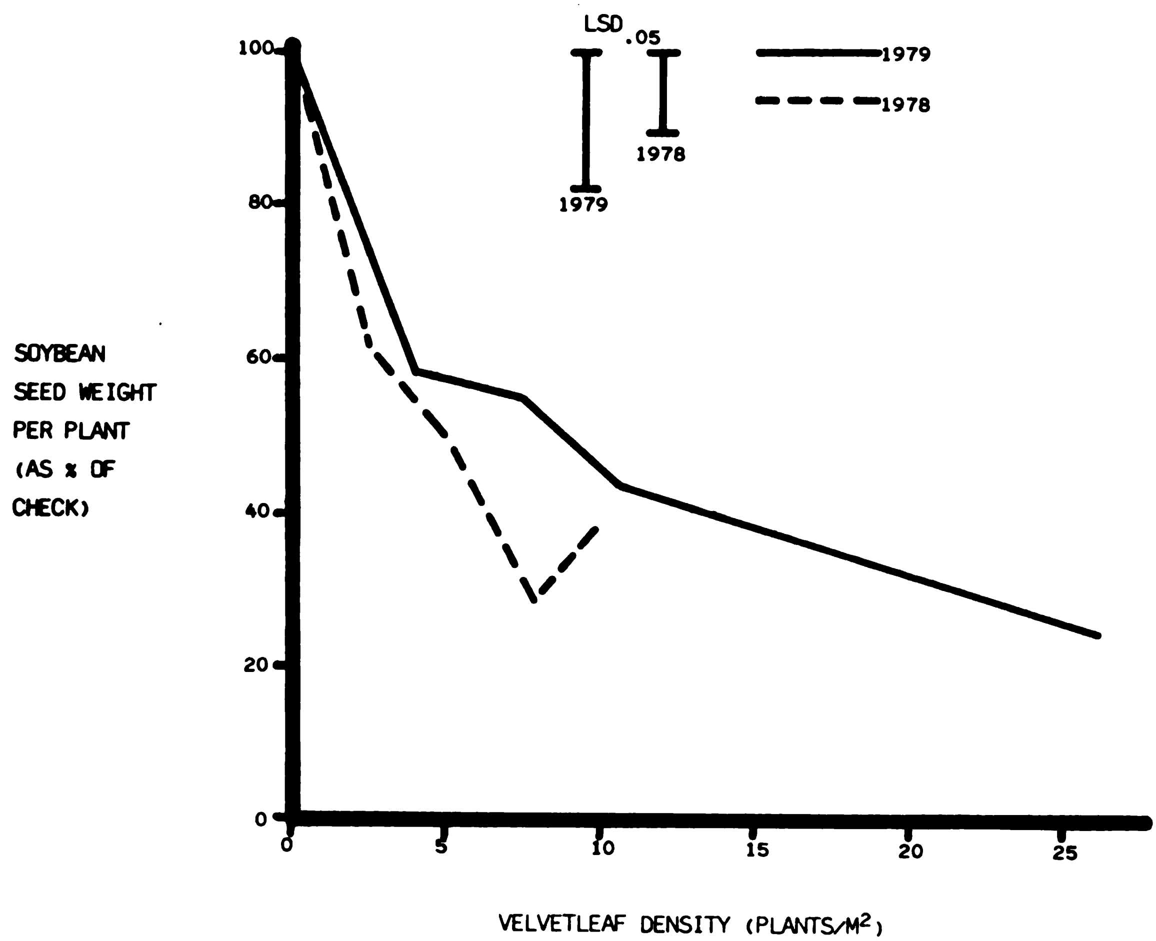


Figure 23. Effect of various velvetleaf densities on soybean seed weight/plant (expressed as a percent of weed-free control) in a constant density soybean stand.

low populations (3.7 velvetleaf/m^2) of velvetleaf (figure 24). Further losses were associated with added velvetleaf plants (up to 23.6 velvetleaf/m^2). The rate of loss became less with added velvetleaf/m^2. The observed soybean dry weight/m^2 losses seen in the additive design (figure 24) were not due to changes in overall plant population. No differences were observed in soybean dry weight/m^2 with changes in plant population from 5.8 to 83.3 plants/m^2 when grown in 50% soybean - 50% velvetleaf mixtures. The observed losses (Figure 24) were due to the presence of velvetleaf (changes in plant proportion), especially in the 70 to 60% soybean - 30 to 40% velvetleaf mixtures (Figure 25). The interactions between soybean and velvetleaf can be characterized by three different, proportion dependent, responses. First, both species were mutually exclusive in mixtures of 37% or less soybean. Secondly, they displayed a compensatory, or complete positive complementation, interaction in the 60 to 49% soybean - 40 to 51% velvetleaf mixtures. Thirdly, they interacted in a complete negative complementation, or negative overcomplementation interaction in 76 to 77% soybean - 24 to 23% velvetleaf mixtures. Soybean losses were most severe in high soybean-low velvetleaf proportioned mixtures. Velvetleaf growth was not reduced, and in some mixtures was stimulated, due to the presence of soybean.

A tissue analysis of new, fully expanded leaves at midseason (early August) showed no differences in soybean of velvetleaf nitrogen, phosphorus, potassium, calcium, magnesium, sodium, manganese, copper, boron, zinc or aluminum content with changes in either plant population or mixture composition (changes is plant proportion). Interference

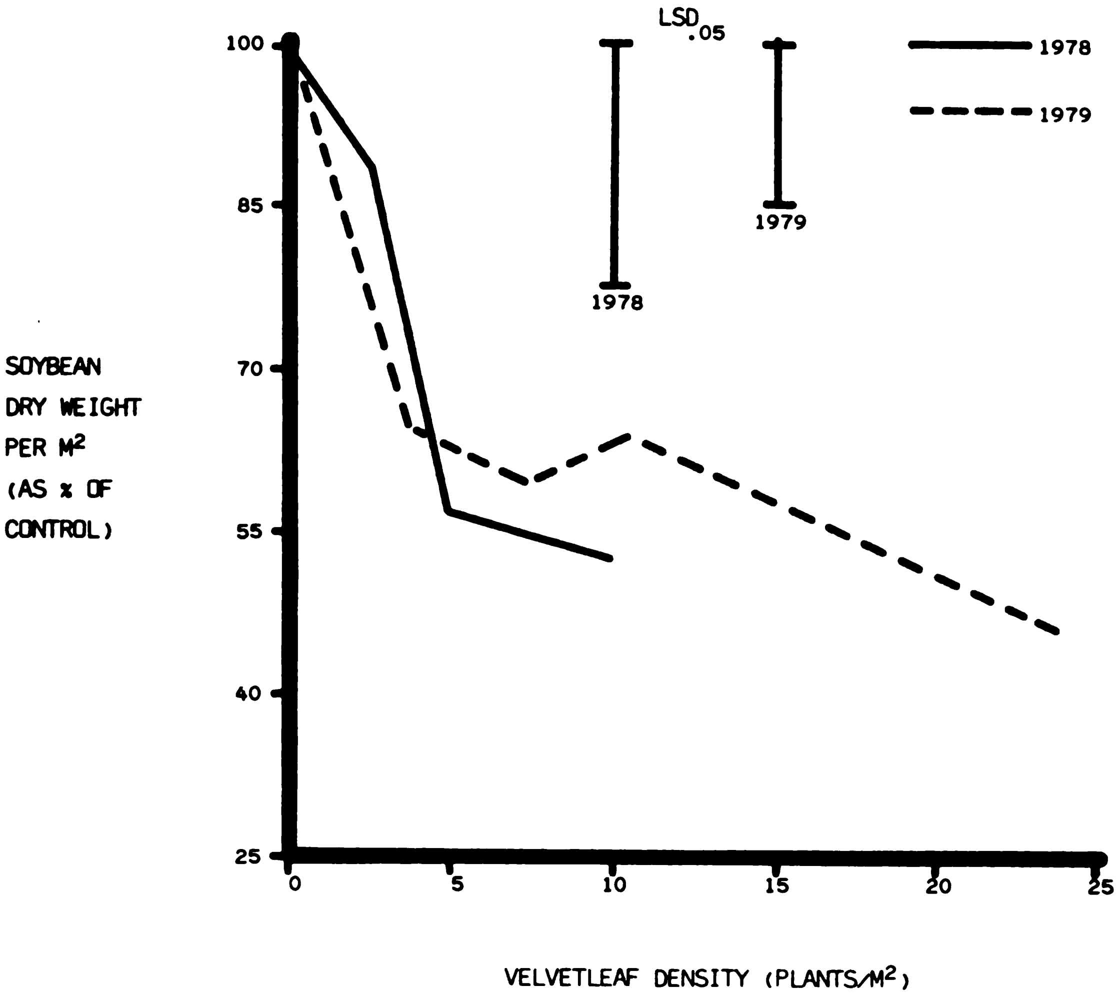


Figure 24. Effect of various densities of velvetleaf on soybean dry weight/M^2 (expressed as a percent of the weed-free control) in a constant density soybean stand.

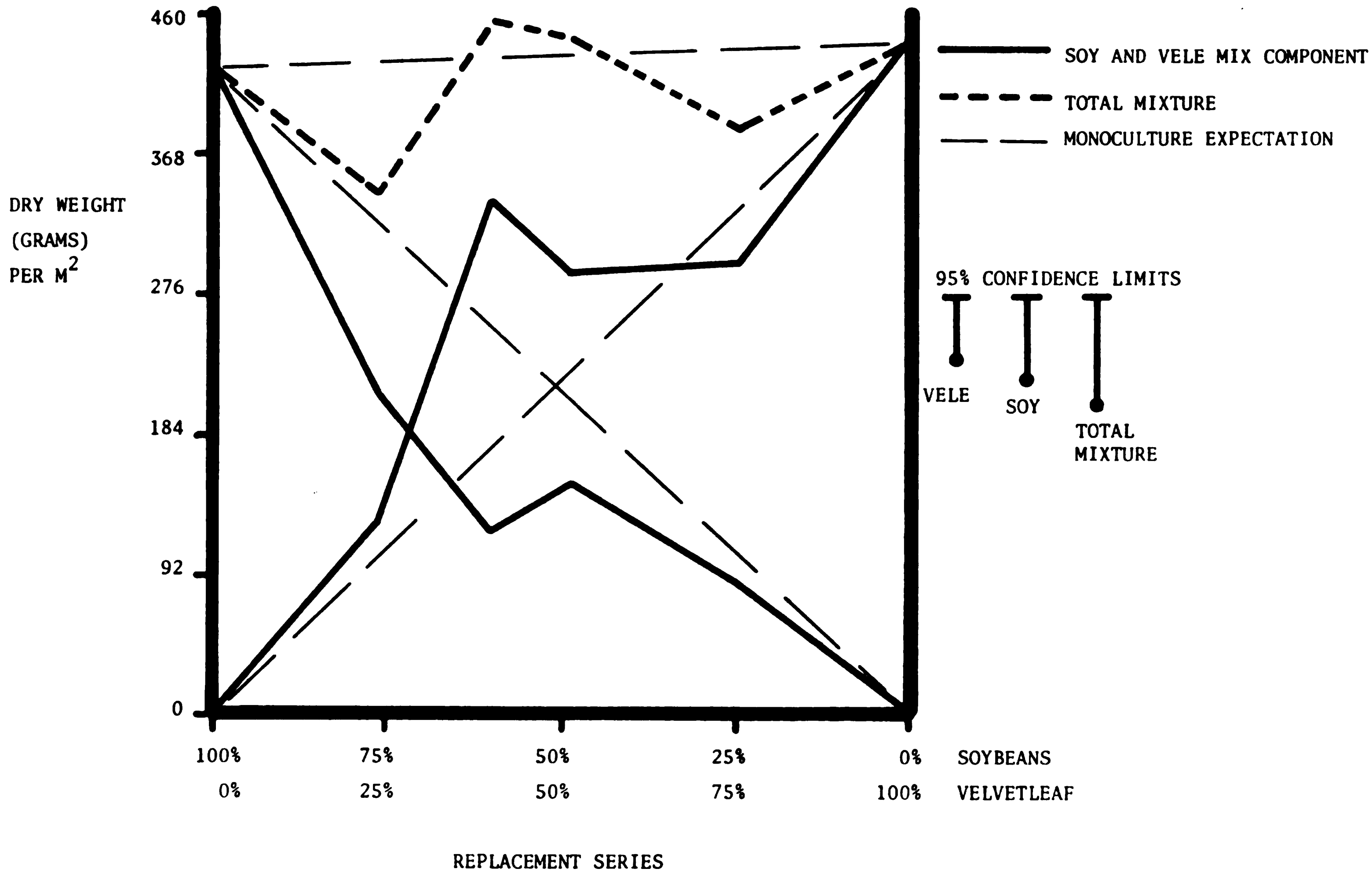


Figure 25A. Replacement series diagram of soybean (SOY) and velvetleaf (VELE) dry weight per M^2 at midseason 1978 at a constant typical soybean field density.

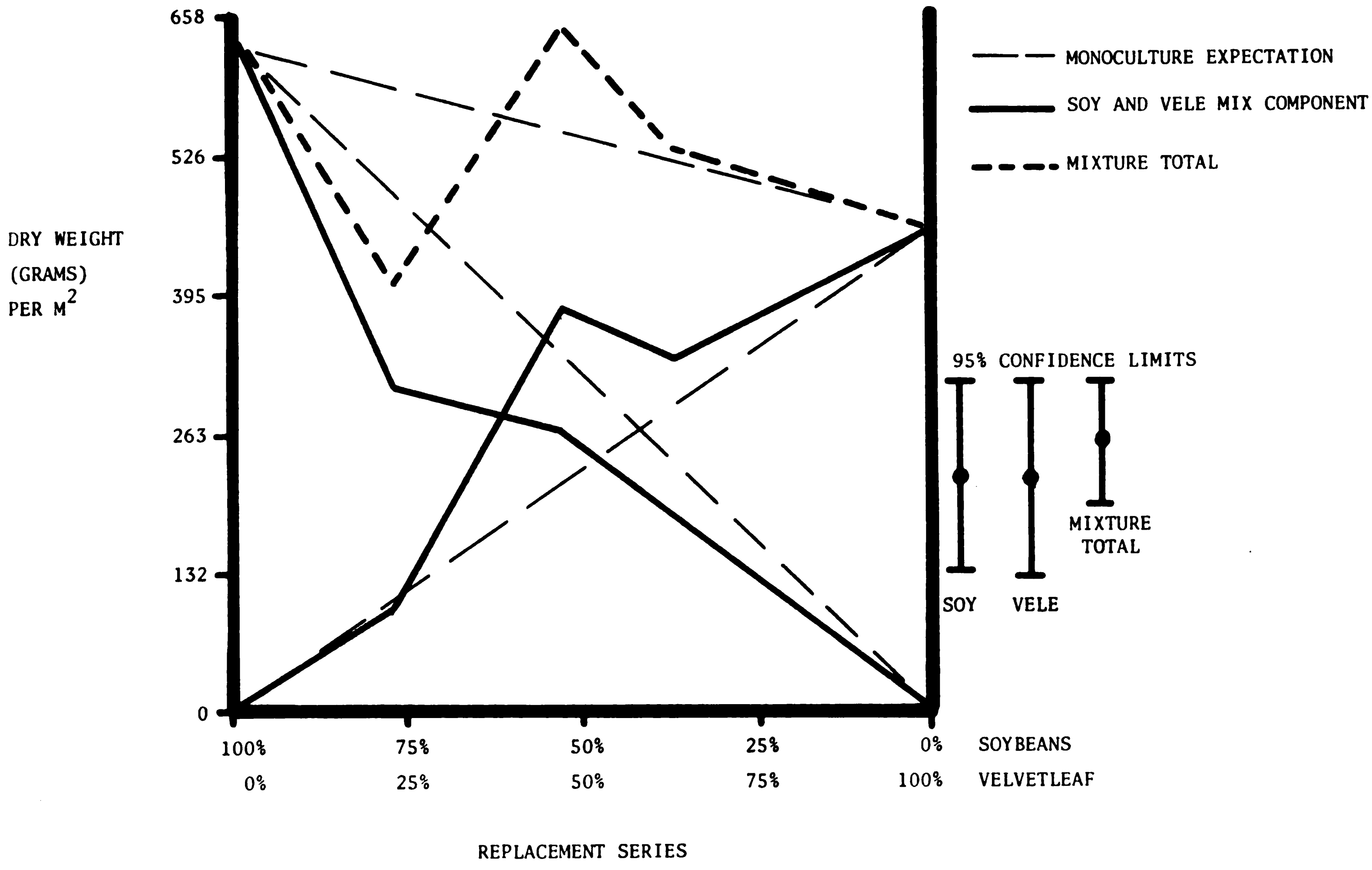


Figure 25B. Replacement series diagram of soybean (SOY) and velvetleaf (VELE) dry weight per M^2 at midseason 1979 at a constant typical soybean field density.

for soil nutrients was not implicated in the observed dry matter/m^2 losses.

Branching nodes

Branching node production was characterized by different responses in different years. In 1979, soybean branching nodes/m^2 decreased with the addition of low populations (3.7 velvetleaf/m^2) of velvetleaf (Figure 26). Further losses were associated with added velvetleaf (up to 23.3 velvetleaf/m^2). The rate of loss became less with added velvetleaf/m^2. In 1978 no differences in soybean branching nodes/m^2 occurred with the addition of up to 9.7 velvetleaf/m^2.

Soybean branching nodes/m^2 either yielded less than expected in certain mixtures (1978), or yielded as expected (1979), from the monoculture yields with changes in species mixture proportion at typical soybean field populations (Figure 27).

Soybean branching node/m^2 accumulation was less in 50% soybean - 50% velvetleaf mixtures than in monocultures with changes in plant population from 5.8 to 83.3 plants/m^2 in 1979 (Figure 28).

The overall effect of velvetleaf on soybean branching nodes/m^2 is obscure. In the one year that there were losses (1979) (Figure 26), the effect was due to changes in plant population (Figure 28).

Flowering nodes

Flowering node production can be expressed by several events. By midseason (early August) soybean flowering nodes/m^2 decreased with the addition of low populations (2.4 velvetleaf/m^2) of velvetleaf

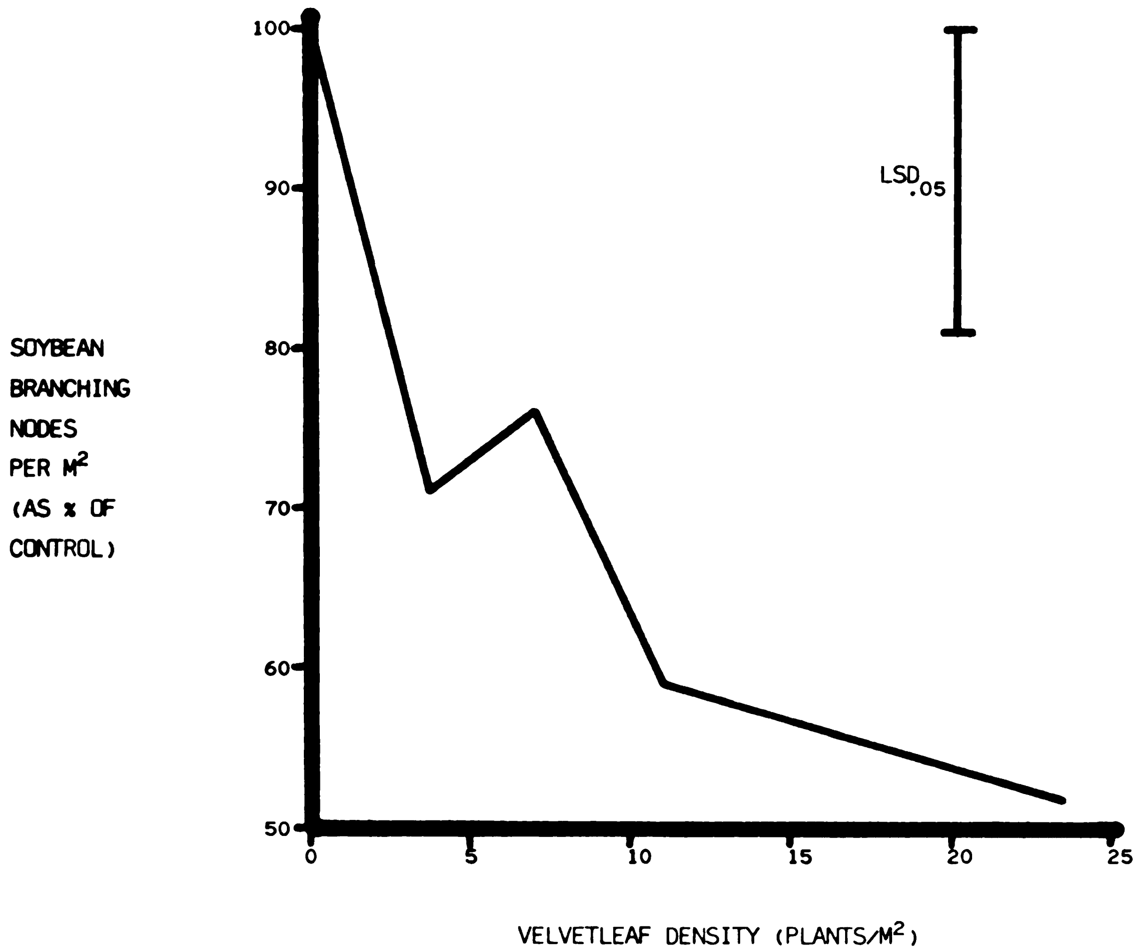


Figure 26. Effect of various velvetleaf densities on soybean branching nodes/M^2 (expressed as a percent of the weed-free control) in a constant density soybean stand (1979).

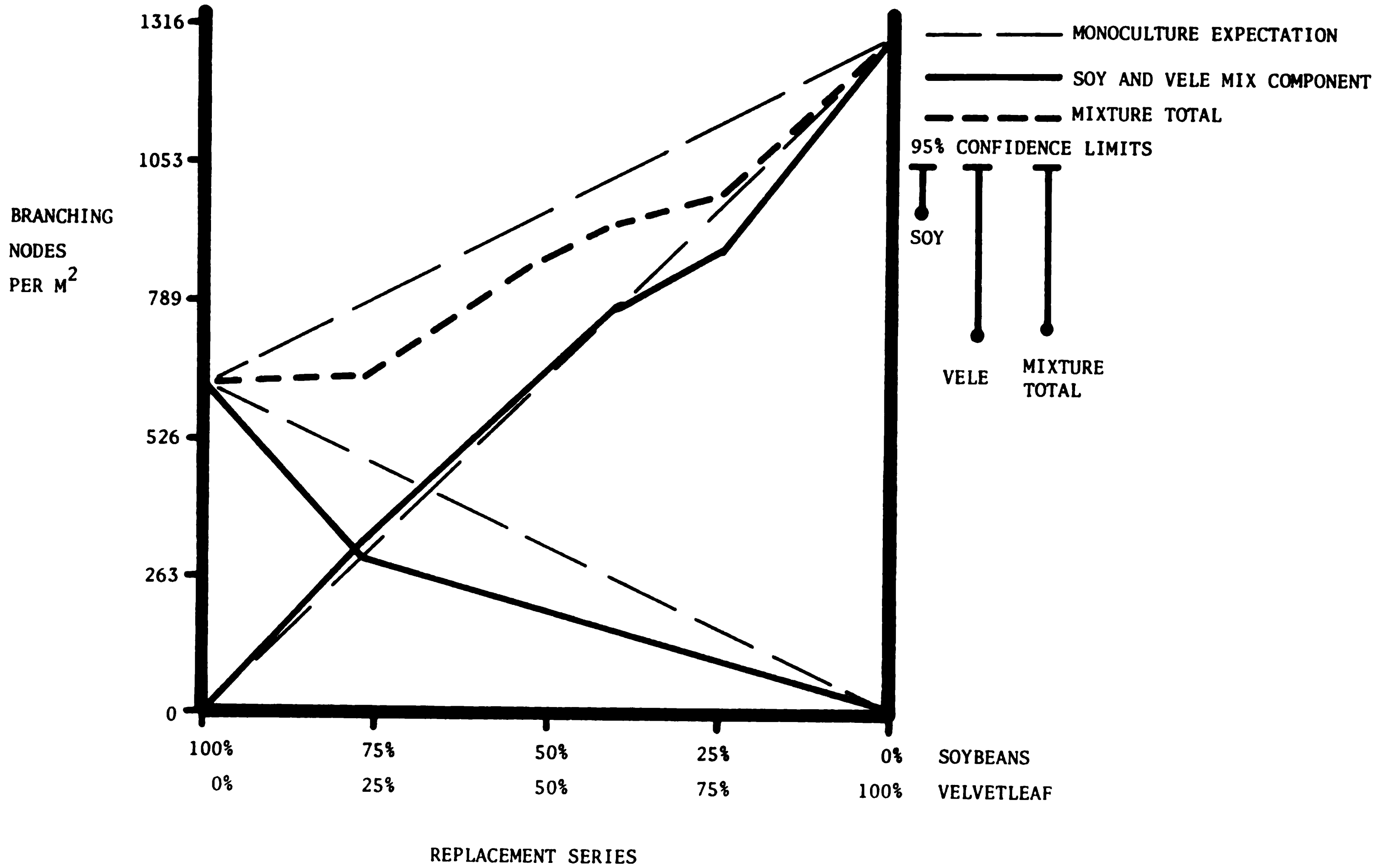


Figure 27A. Replacement series diagram of soybean (SOY) and velvetleaf (VELE) branching nodes per M^2 at midseason 1978 at a constant typical soybean field density.

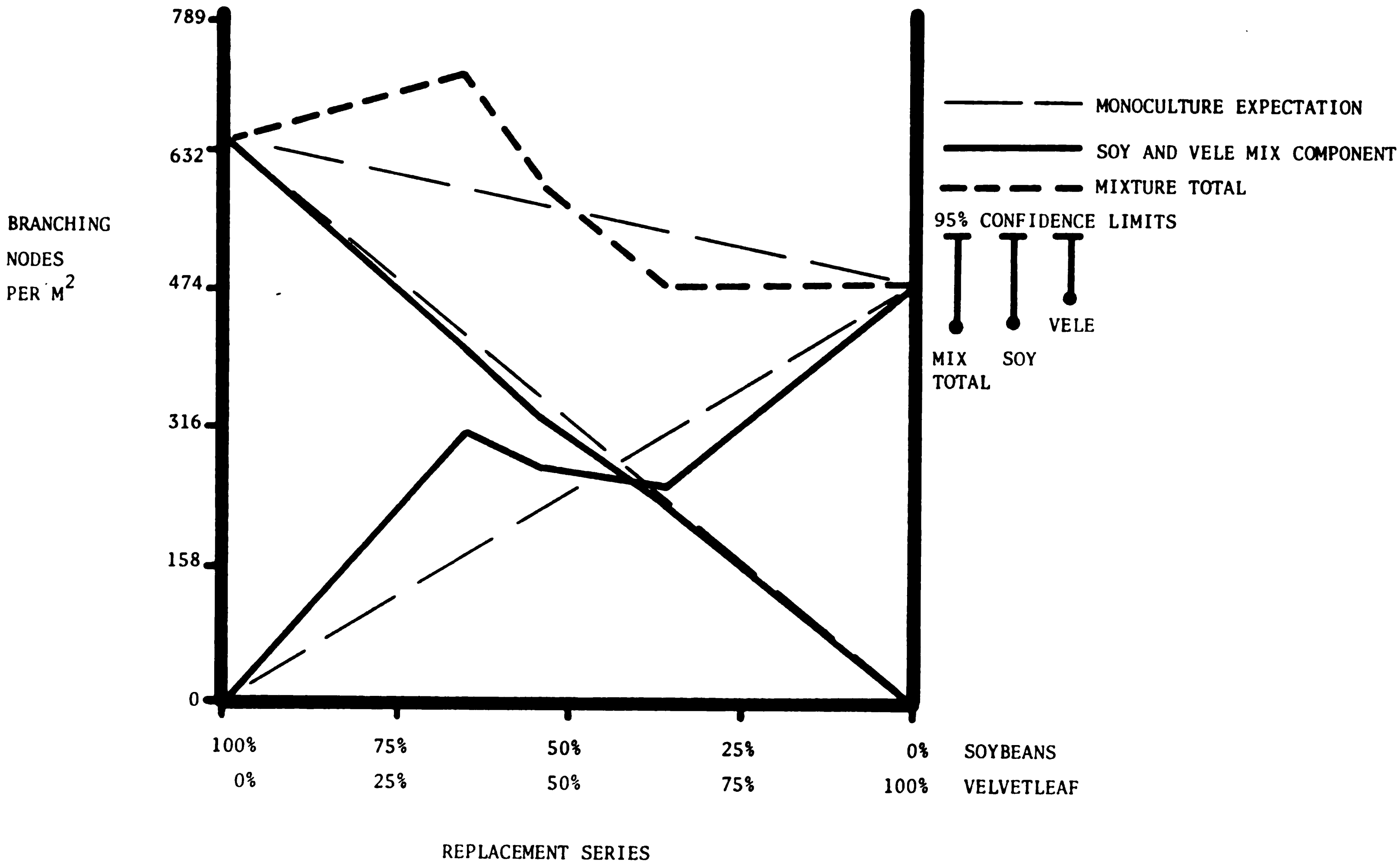


Figure 27B. Replacement series diagram of soybean (SOY) and velvetleaf (VELE) branching nodes per M^2 at midseason 1979 at a constant typical soybean field density.

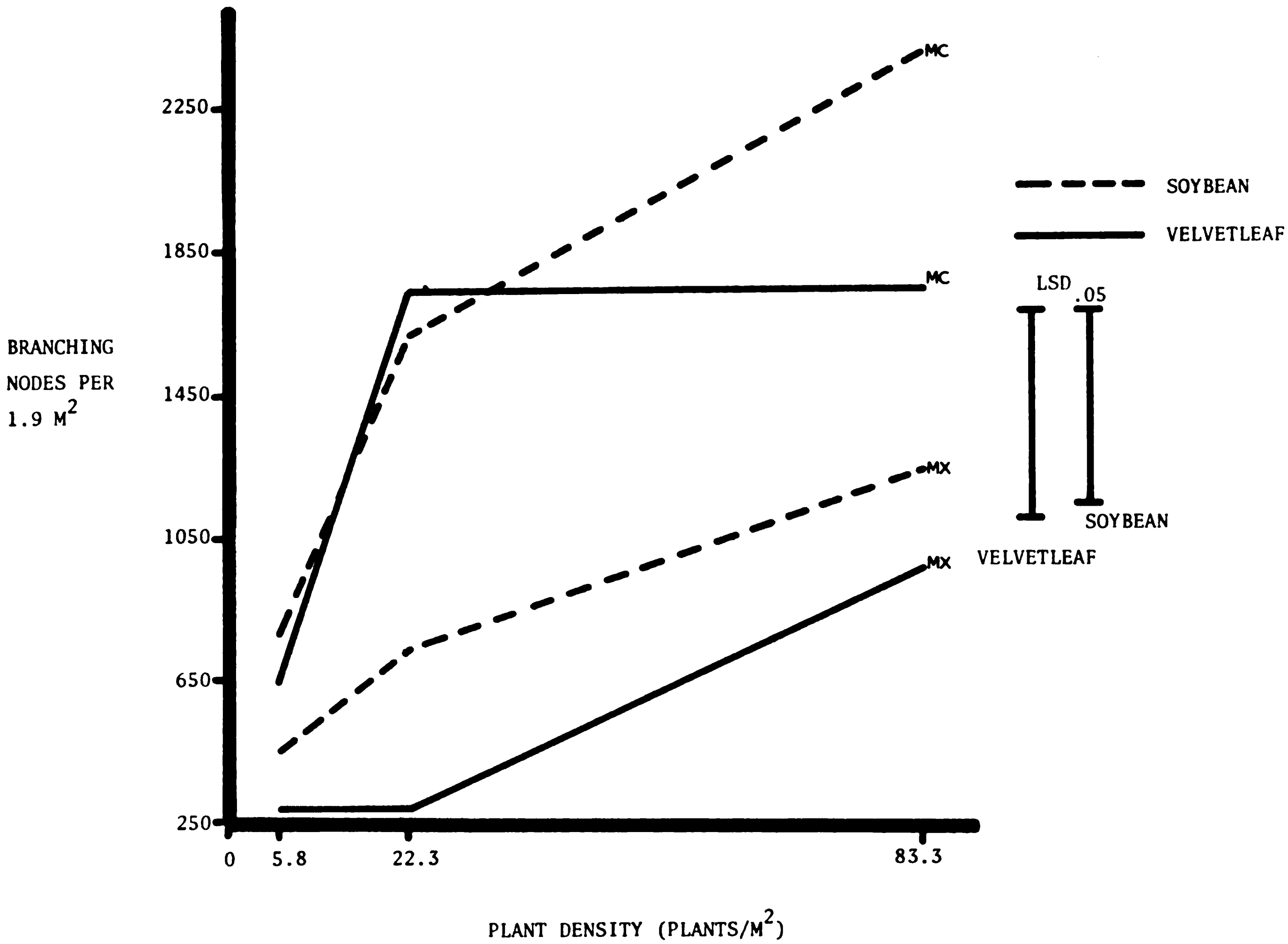


Figure 28. Effect of plant density on the branching nodes per unit area of soybeans and velvetleaf in monoculture (MC) and in 50% soybean-50% velvetleaf mixtures (MX) in 1979.

(Figure 29). The rate of loss either remained relatively constant (1978) or decreased with added velvetleaf/m^2 (1979). Soybean flowering node/m^2 losses were severe from both planting (May) until midseason, and from midseason until harvest (October) (Figure 30). The severe early season soybean flowering node losses provide evidence against interference for light as the main cause of interference. Velvetleaf plants did not overtop the soybean leaf canopy until mid-August.

Soybean flowering nodes/m^2 in 50% soybean - 50% velvetleaf mixtures did not change with changes in plant population near typical soybean field population (5.8 to 22.3 plants/m^2) (Figure 31). With changes in plant population soybean flowering node/m^2 accumulation was less in 50% soybean - 50% velvetleaf mixtures than in monoculture.

Soybean flowering nodes/m^2 were less than expected from the monoculture yield at all mixture proportions tested (Figure 32). The interaction could be described as negative complete complementation. The observed severe (ca. 76 to 40% of the weed-free control) soybean flowering node losses were due to the presence of velvetleaf, and not to changes in plant population. Velvetleaf flowering node production was unaffected by the presence of soybean plants (Figure 32).

Seed weight

Soybean seed weight/m^2 decreased with the addition of low populations (2.4 velvetleaf/m^2) of velvetleaf (Figure 33). The rate of loss decreased with added velvetleaf/m^2. The losses incurred were similar in both years. The losses observed in the data drawn from the additive design (Figure 33) were not due to changes in plant population.

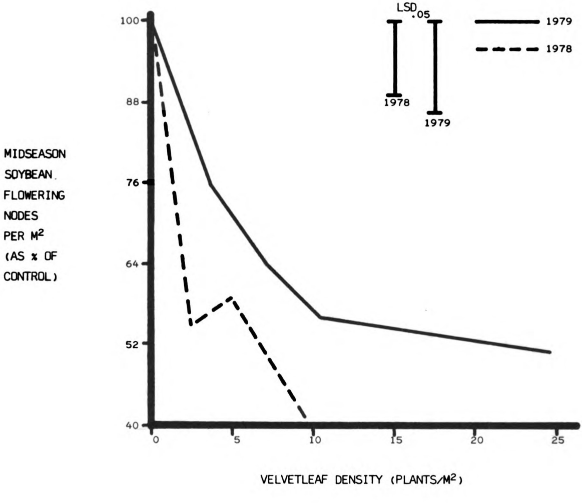


Figure 29. Effect of various velvetleaf densities on soybean flowering nodes/M^2 at midseason (expresses as a percent of the weed-free control) in a constant density soybean stand.

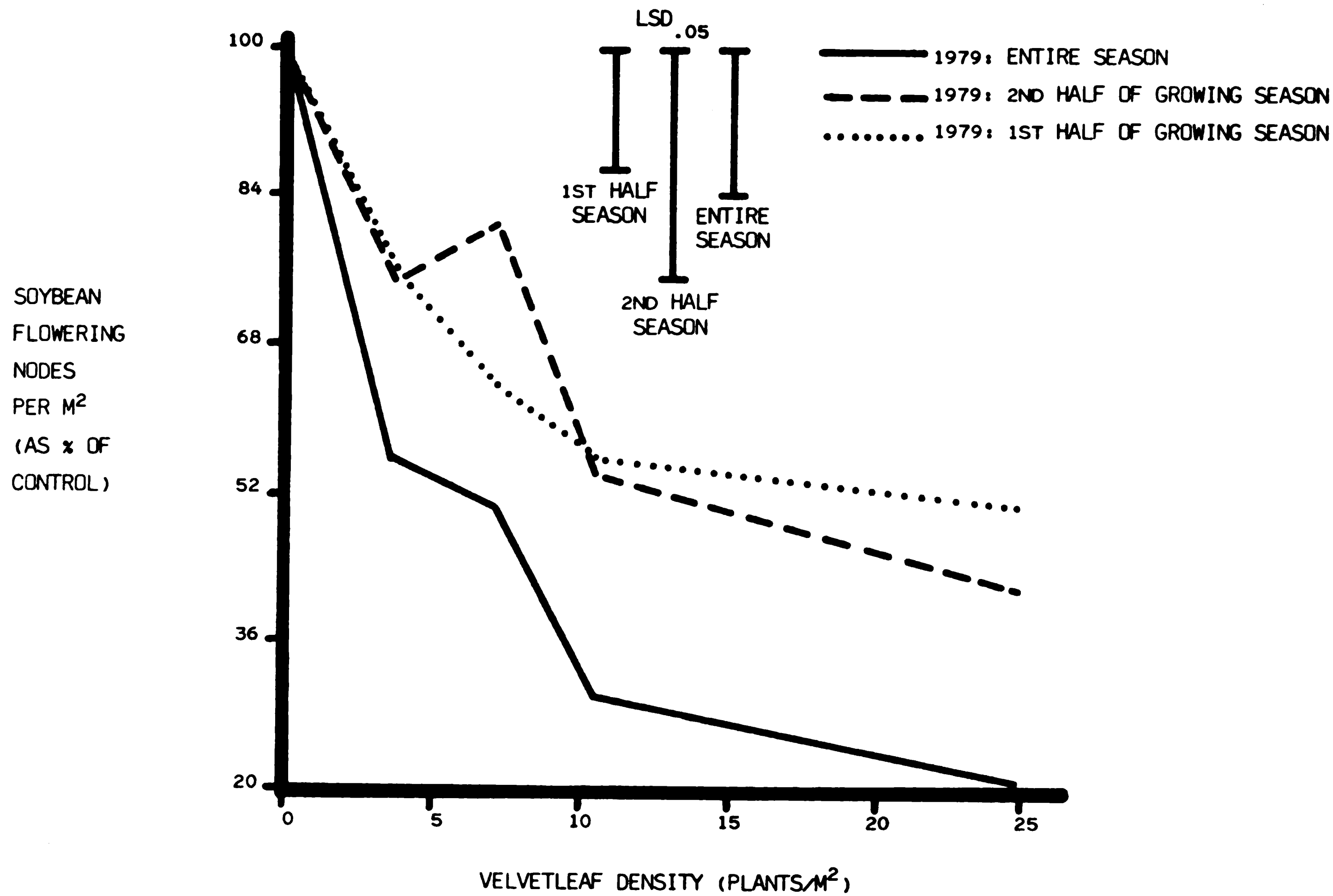


Figure 30. Effect of various velvetleaf densities on soybean flowering nodes/M^2 (expressed as a percent of the weed-free control) in the first half of the growing season (May (1979) or June (1978) through August), second half of the growing season (August through October), or the entire season (May (1979) or June (1978) through October) in a constant density soybean stand.

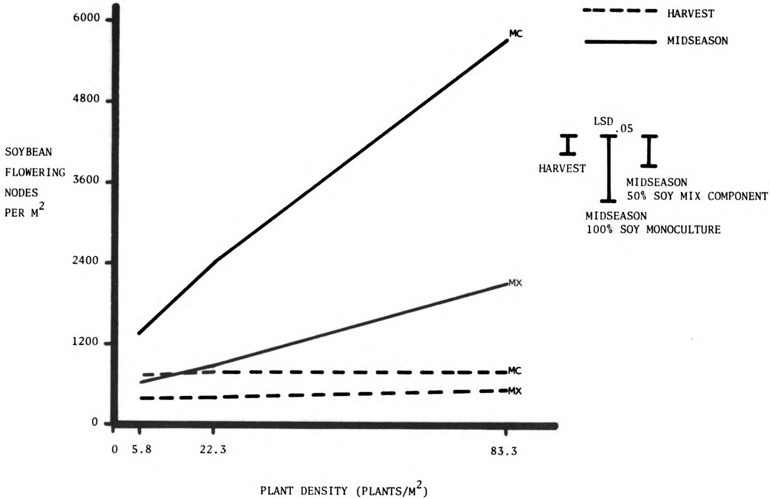


Figure 31. Effect of plant density on flowering nodes per M^2 of soybeans (SOY) at midseason and harvest, in monoculture (MC) or in 50% soybean-50% velvetleaf mixtures in 1979.

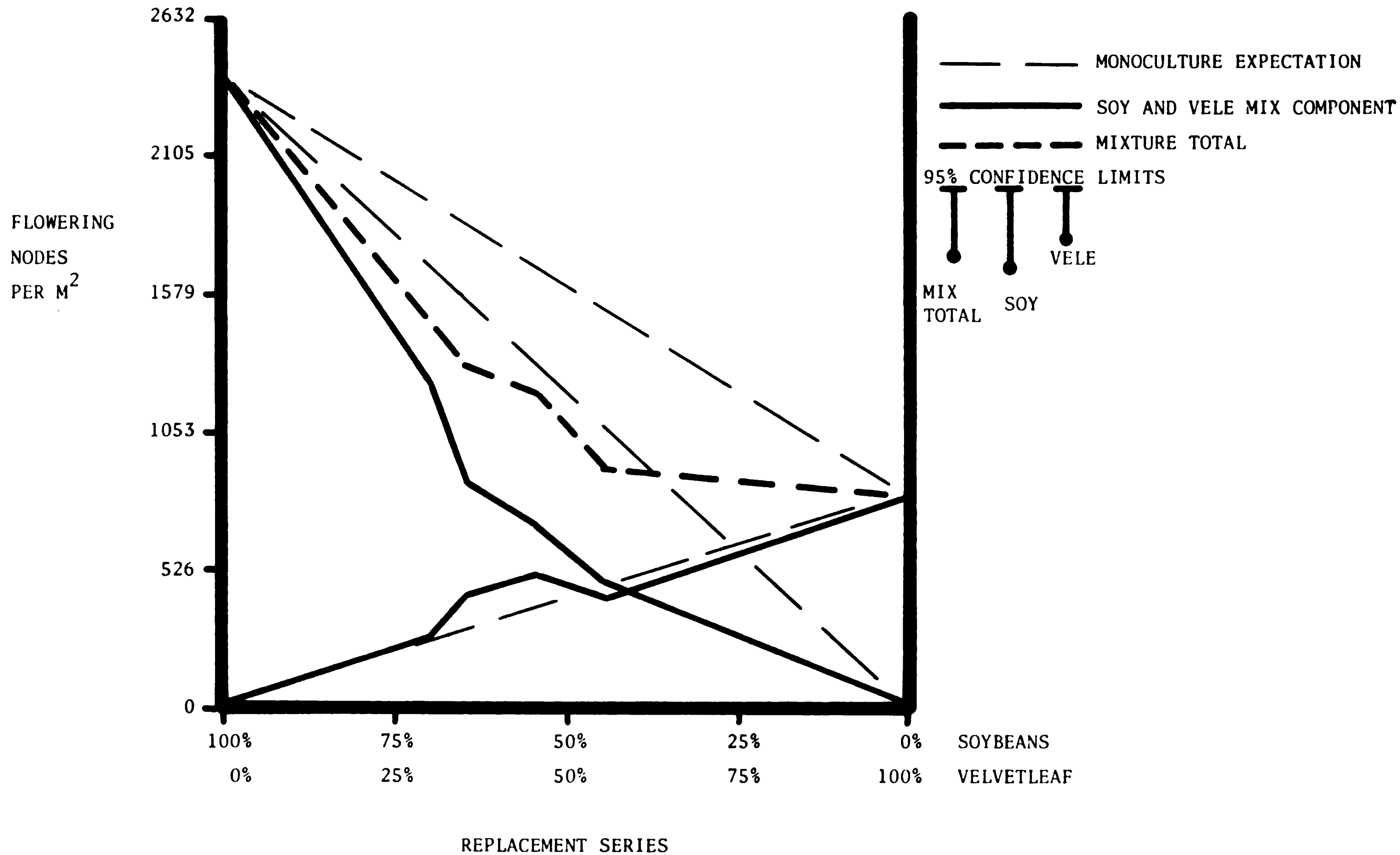


Figure 32. Replacement series diagram of soybean (SOY) and velvetleaf (VELE) flowering nodes per M^2 at midseason 1979 at a constant typical soybean field density.

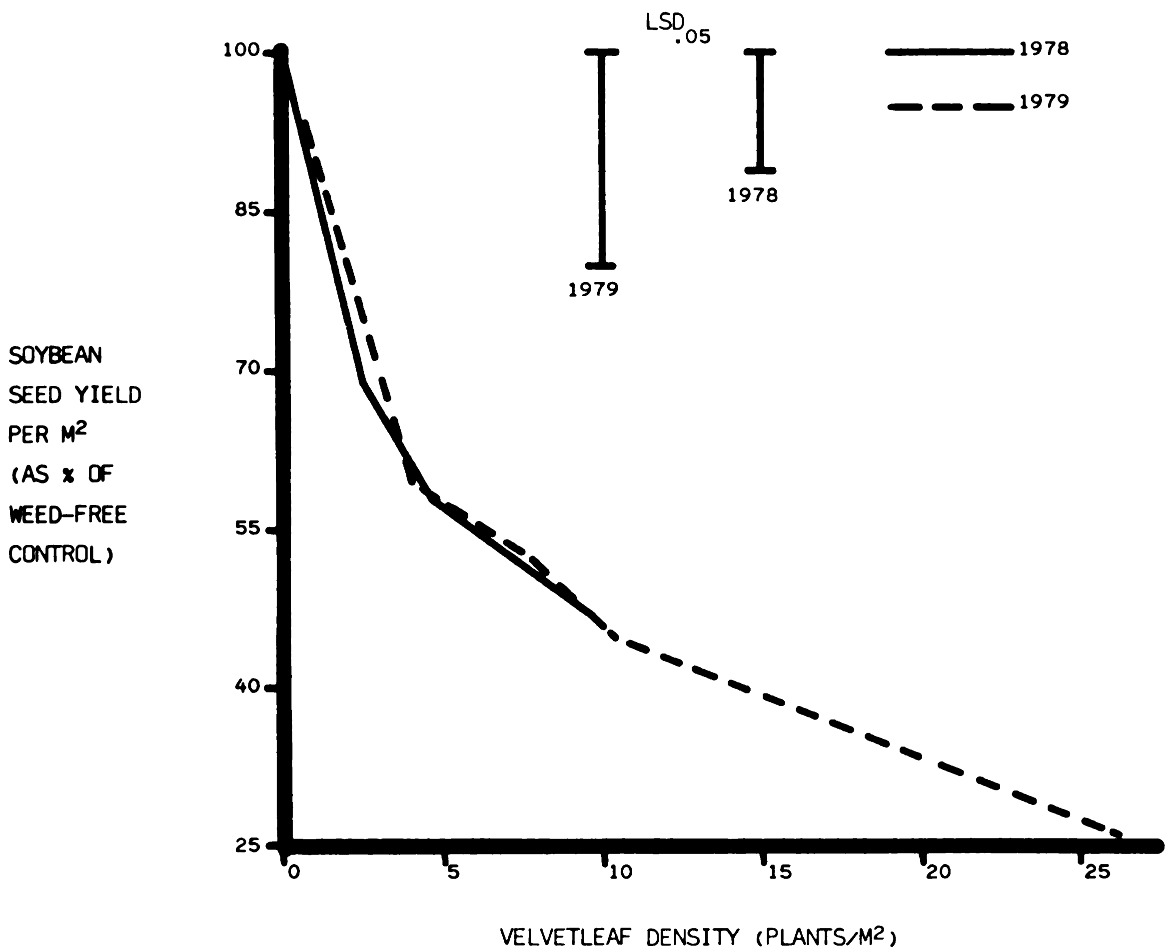


Figure 33. Effect of various velvetleaf densities on soybean seed yield/M^2 (expressed as a percent of the weed-free control) in a constant density soybean stand.

No differences in seed weights/m^2 were observed for either soybean or velvetleaf with changes in plant population from 5.8 to 83.3 plants/m^2. Soybean seed weight/m^2 was less than expected from monoculture yields in both years (1978 and 1979) in the high soybean-low velvetleaf ratio mixtures (Figure 34). The observed severe (ca. 70 to 25% of the weed-free control) soybean seed weight losses were due to the presence of velvetleaf, and not because of changes in plant population. Velvetleaf seed weight/m^2 yield was unaffected by the presence of soybean (Figure 34).

Reproductivity

The ways in which soybean and velvetleaf interact to alter their reproductive capacity can be characterized by two factors, seed number production and net reproductive effort.

Seed Number Production

Soybean seed number/m^2 decreased with the addition of low population (2.4 velvetleaf/m^2) of velvetleaf. The rate of loss decreased with added velvetleaf/m^2 (Figure 35). The losses observed in the data drawn from the additive design (Figure 35) were not due to changes in plant population. No differences in seed number/m^2 were observed for either soybean or velvetleaf with increases in plant population from 5.8 to 83.3 plants/m^2. In none of the mixtures tested were soybean seed number/m^2 different from what would be expected from the monoculture yield (Figure 35). Velvetleaf seed number/m^2 yields were as expected from the monoculture yield except for an increase with the 55% soybean - 45% velvetleaf mixture. Velvetleaf seed number/m^2 production was either

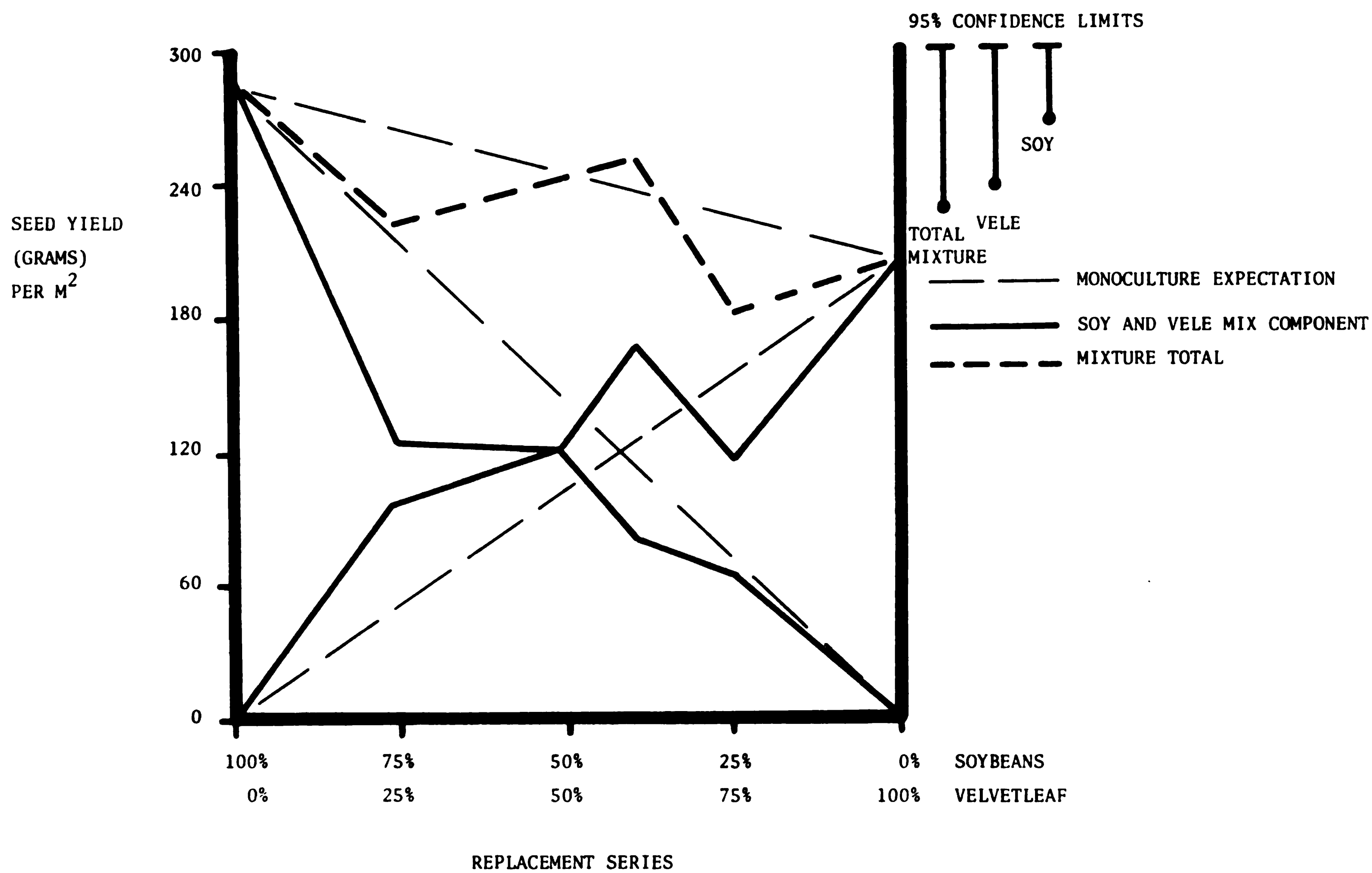


Figure 34A. Replacement series diagram of soybean and velvetleaf seed weight yield (grams) per M^2 in 1978 at a constant typical soybean field density.

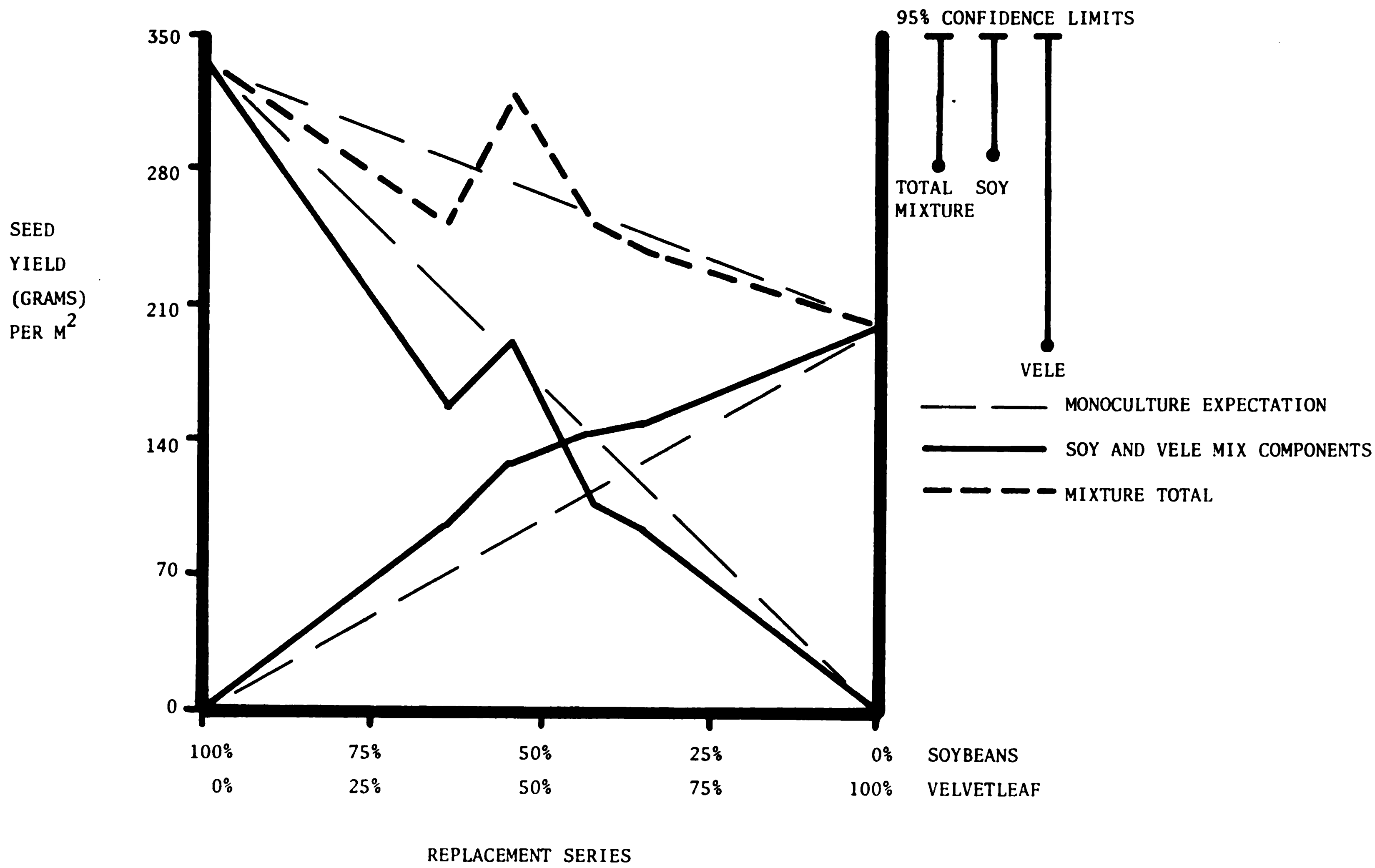


Figure 34B. Replacement series diagram of soybean and velvetleaf seed weight yield (grams) per M^2 in 1979 at a constant typical soybean field density.

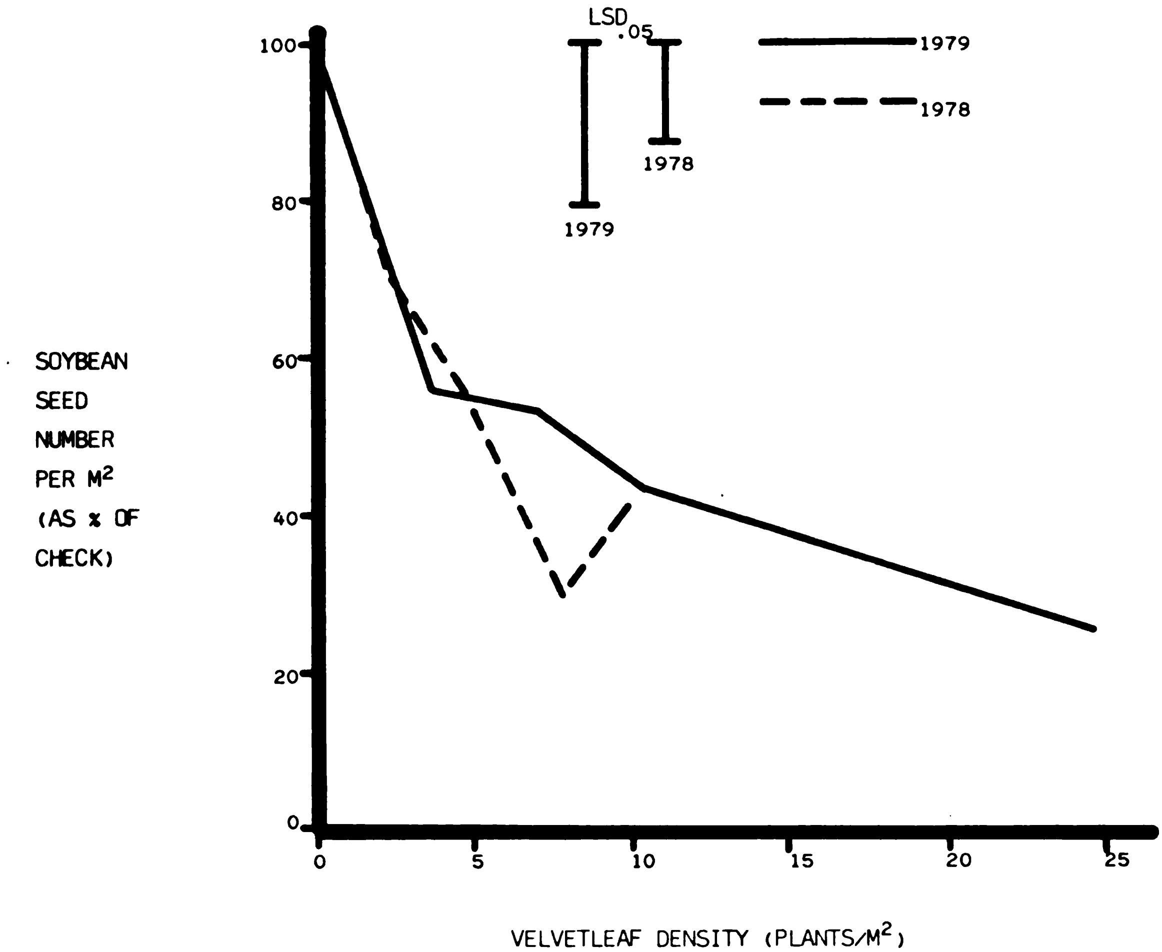
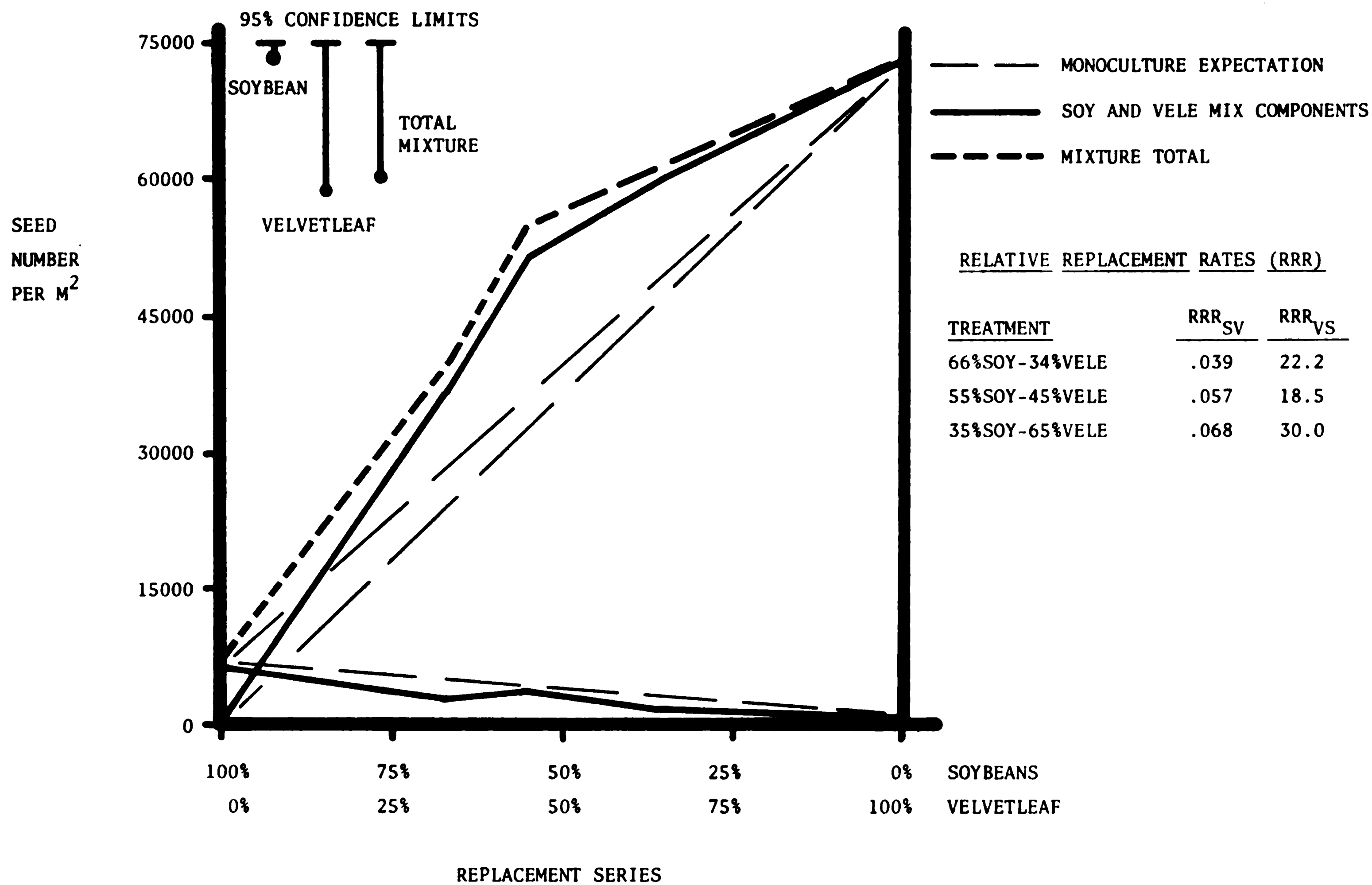


Figure 35A. Effect of various velvetleaf densities on soybean seed number/M^2 (expressed as a percent of the weed-free control) in a constant density soybean stand.



RELATIVE REPLACEMENT RATES (RRR)

TREATMENT	RRR_{SV}	RRR_{VS}
66%SOY-34%VELE	.039	22.2
55%SOY-45%VELE	.057	18.5
35%SOY-65%VELE	.068	30.0

Figure 35B. Replacement series diagram of soybean and velvetleaf seed number per M^2 in 1979 at a constant typical soybean field density; with associated relative replacement rates, of soybean with respect to velvetleaf (RRR_{SV}), and of velvetleaf with respect to soybean (RRR_{VS}).

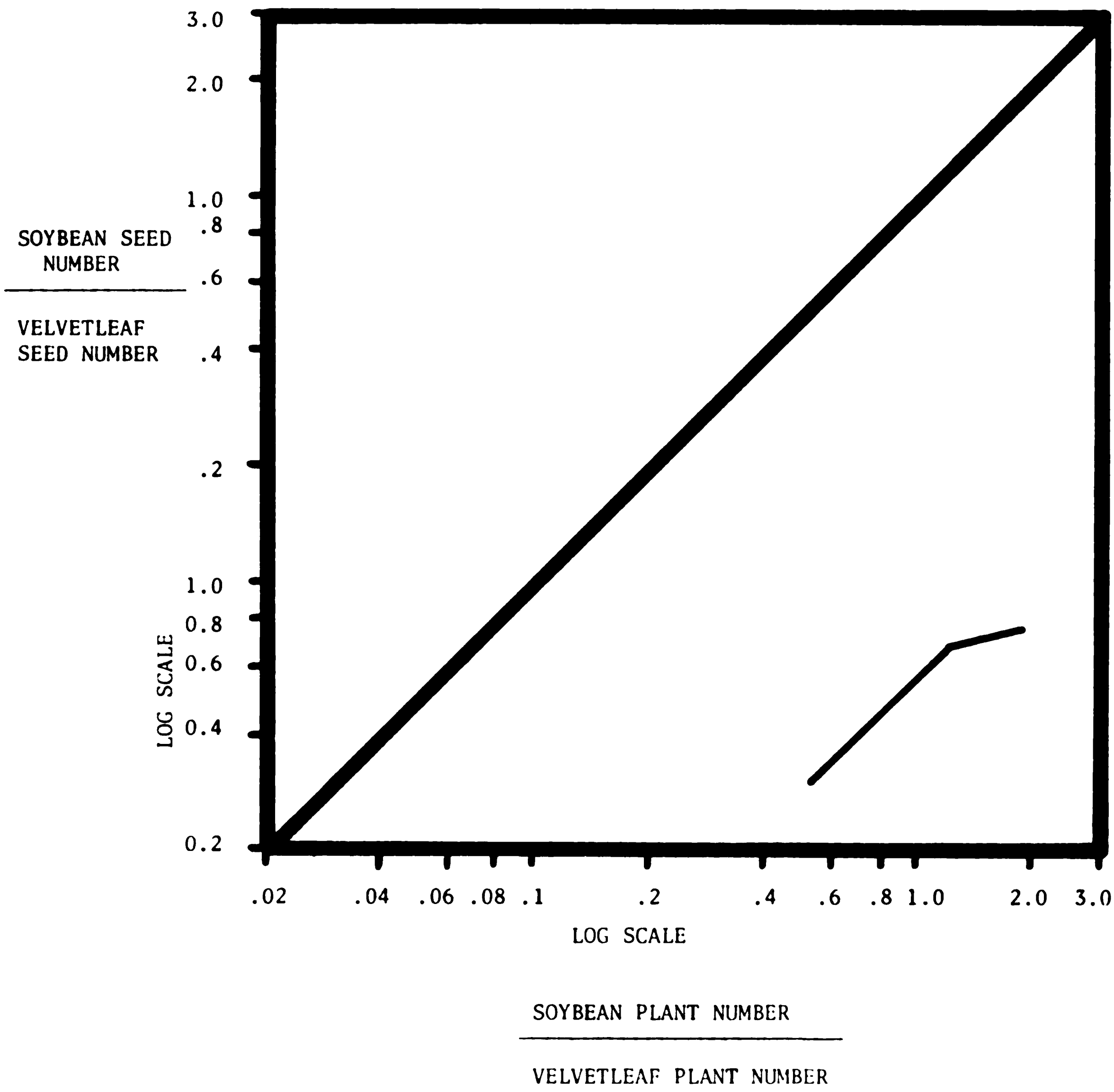


Figure 36. Ratio diagram of the ratio of soybean to velvetleaf seed number versus the ratio of soybean to velvetleaf plant number.

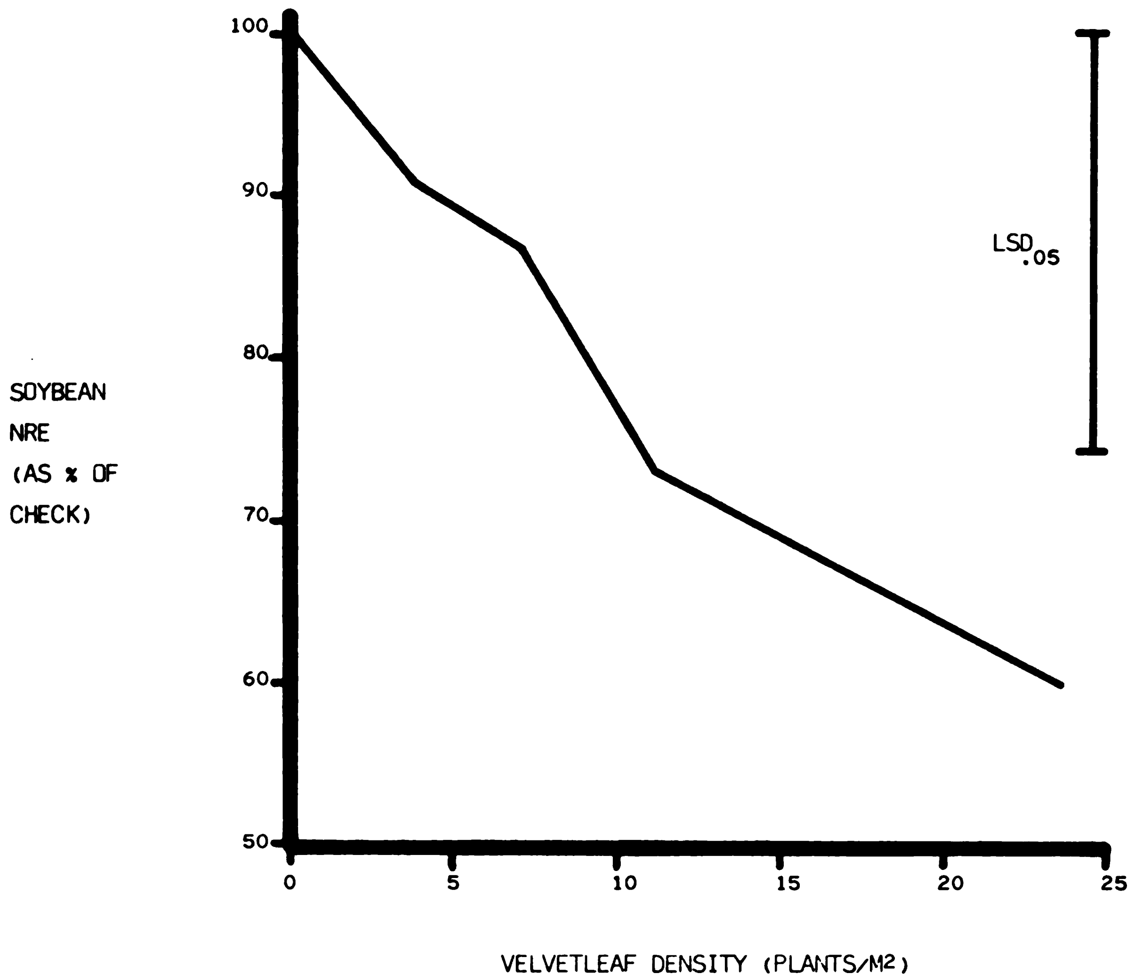


Figure 37. Replacement series diagram of soybean and velvetleaf net reproductive effort (NRE) at a constant typical soybean field density in 1978.

unaffected, or increased, by the presence of soybean. A possible explanation for the observed soybean seed number production losses (Figure 35) could be a cumulative effect of changes in both species composition (proportion) and in plant population.

The seed replacement equilibrium potential of a mixed stand of soybean and velvetleaf in terms of seed number overwhelmingly favors velvetleaf (Figure 36). The relative replacement rate of velvetleaf compared to soybean (RRR_{VS}) is relatively independent of mixture proportion (Figure 35). This equilibria is not realistic in the sense that soybean is replanted every year. It is realistic in terms of the evolutionarily dominant position it gives to velvetleaf. With the reproductive replacement equilibria this far in the favor of velvetleaf, the potential for long term survival, and development of herbicide resistance, is great.

Net Reproductive Effort

The amount of effort devoted to soybean reproductive parts decreased with the addition of medium populations (11.1 velvetleaf/m^2) of velvetleaf (Figure 37. The losses observed in the data drawn from the additive design (Figure 37) were not due to changes in plant population. No differences were observed in either soybean or velvetleaf net reproductive effort (NRE) with increases in plant population from 5.8 to 83.3 plants/m^2. In none of the mixtures tested was the soybean NRE different from the monoculture expected effort (Figure 37). The velvetleaf NRE was as expected from the monoculture effort except for an increased NRE in the 76% soybean 24% velvetleaf mixture.

Velvetleaf NRE is either unaffected, or increased, by the presence of soybean plants. Because neither changes in plant population, nor the presence of velvetleaf, can alone explain the observed losses (figure 38), a possible interaction of the two could be the cause.

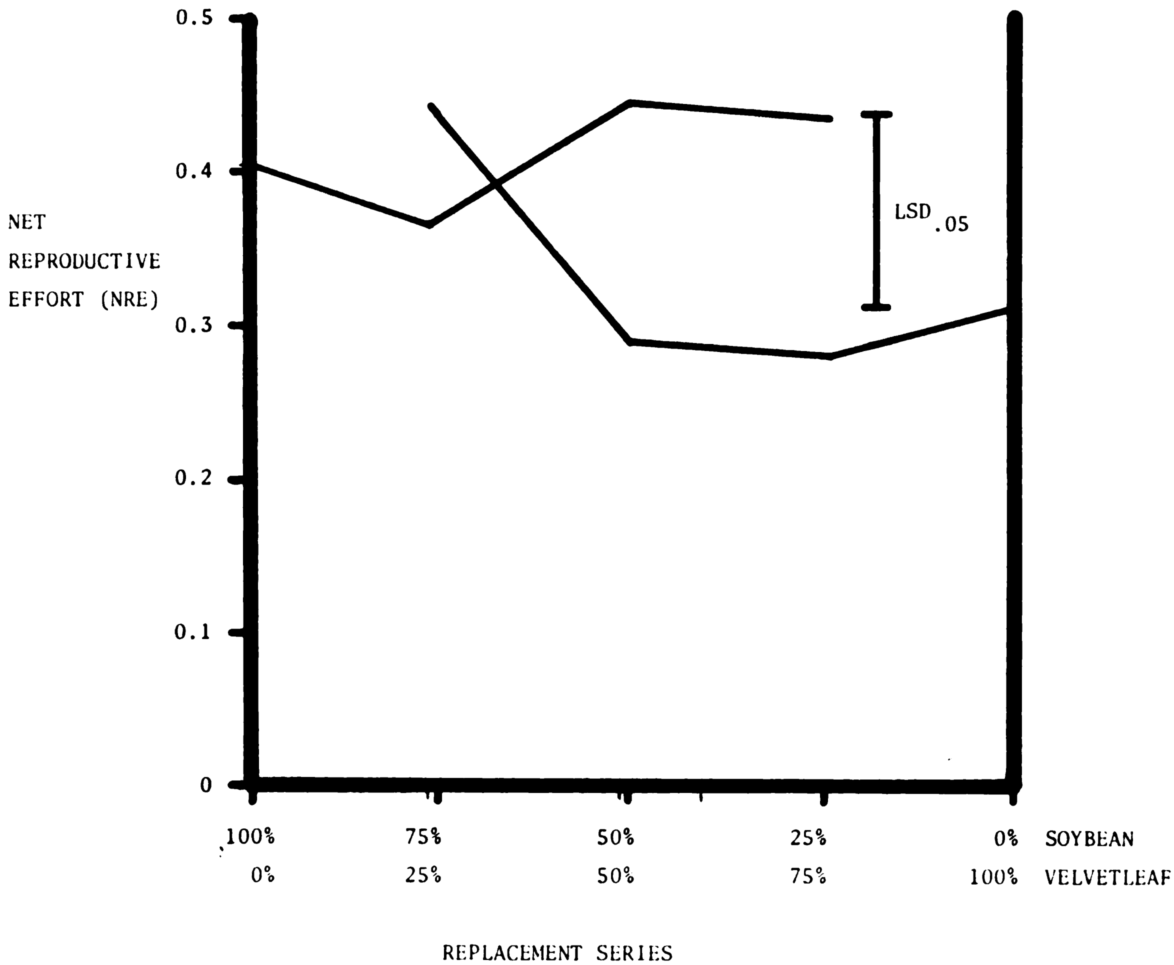


Figure 38. Effect of various velvetleaf densities on soybean net reproductive effort (NRE) (expressed as a percent of the weed-free control) in a constant density soybean stand (1979).

CONCLUSIONS

Table 4 is a summary of the results obtained for each factor evaluated that might influence soybean and velvetleaf community productivity. The results indicate that for all three major factors (mortality, plastic growth, and reproductivity) velvetleaf interferes effectively with soybean, and will continue to do so. Because of contemporary breeding programs, soybean has lost the adaptive ability of using judicious mortality as a means of vigorous survival. Velvetleaf uses this characteristic to exploit and dominate soybean production. Severe soybean seed weight losses were incurred due to the presence of velvetleaf. This interference was most apparent in the inhibition of soybean flowering node productivity, less so with soybean dry matter accumulation, and was obscure in soybean branching node production. Velvetleaf seed number production favors it to survive and continue dominating soybean production. This characteristic will give it time to adapt to manmade pressures, as herbicide use; with the possible consequence of herbicide resistance development.

Under conditions of good soil fertility any explanation of the mechanism of velvetleaf interference probably does not include interference for macro- and micronutrients, or for early season interference of solar radiation. Evidence presented (figure 32) could support a hypothesis implicating allelopathic interference by means of soybean reproductive organ abortion; or one implicating interference with soybean water relations (17,31,86,87,88,89).

Table 4. Summary of the results of possible factors influencing soybean and velvetleaf community productivity.

Factor		Results	Consequences[1] for the Productivity of: Soybean	Velvetleaf
I. Mortality				
	A. Life	high soybean survival predisposes it to smaller, less productive, plants	-	+
	B. Death	velvetleaf mortality enables it to reach optimally interferring population at typical soybean field populations		
II. Plastic growth				
	A. Dry wt.	soybean decreased due to presence of velvetleaf, esp. in high soybean-low velvetleaf proportioned mixtures	-	+ or =
		velvetleaf not hurt, or is stimulted	- or =	+
		interference for macro- or micronutrients not implicated	+	+
	B. Branching nodes	effect obscure, variable between years; where soybean losses do occur due to changes in plant population	= or -	= or +
	C. Flowering nodes	soybean severely decreased with velvetleaf present, in all mixtures, all season long	-	+ or =
		velvetleaf unaffected	=	=
	D. Seed wt.	soybean severely decreased due to presence of velvetleaf, esp. in high soybean-low velvetleaf proportioned mixtures	-	+ or =
		velvetleaf unaffected	=	=

Table 4 (Continued)

Factor	Results	Consequences[1] for the Productivity of: Soybean	Velvetleaf
III. Reproductivity			
A. Seed number	soybean decreased; unclear whether population, velvetleaf, or interaction	-	= or +
	velvetleaf unaffected or increased; due to presence of soybean	= or -	+ or =
	long term seed replacement equilibria favors velvetleaf	-	+
B. Net reproductive effort	soybean decreased; unclear whether population, velvetleaf, or interaction	-	= or +
	velvetleaf unchanged or increased due to presence of soybean	= or -	+ or =

[1]Key: - harmful; = no effect or effect not apparent; + helpful.

LIST OF REFERENCES

1. Aberg, E., I. J. Johnson and C. P. Wilsie. 1943. Associations between species of grasses and legumes. J. Am. Soc. Agron. 35:357-369.

2. Allee, W. C., A. E. Emerson, O. Park and K. P. Schmidt. 1949. Principles of Animal Ecology. Philadelphia.

3. Baeumer, K. and C. T. de Wit. 1968. Competitive interference of plant species in monoculture and mixed stands. Neth. J. Agric. Sci. 16:103-122.

4. Bakhuis, J. A. and H. J. Kleter. 1965. Some effects of associated growth on grass and clover under field conditions. Neth. J. Agric. Sci. 13:280-310.

5. van den Bergh, J. P. and C. T. de Wit. 1960. Concurrentie tussen timothee en reukgras. Meded. Inst. Biol. Scheik. Onderz. Landb. Gewass. 121:155-165.

6. van den Bergh, J. P. and W. T. Elberse. 1962. Competition between *Lolium perennee* L. and *Anthoxanthum odoratum* L. at two levels of phosphate and potash. J. Ecol. 50:87-95.

7. van den Berg, J. P. 1968. An analysis of yields of grasses in mixed and pure stands. Versl. Landbouwkd. Onderz. No. 714:1-71.

8. Black, J. N. 1960. An assessment of the role of planting density in competition between red clover (*Trifolium pratense* L.) and Lucerne (*Medicago sativa* L.) in the early vegetative stage. Oikos 11:26-42.

9. Blackman, G. E. and W. G. Templeman. 1938. The nature of the competition between cereal crops and annual weeds. J. Agric. Sci., Camb. 28:247-271.

10. Bleasdale, J. K. A. 1960. Studies on plant competition. *In*: The Biology of Weeds, J. L. Harper ed., Blackwell Scientific Publications, Oxford. pp. 133-142.

11. Borthwick, H. A. and M. W. Parker. 1938. Influence of photoperiods upon the differentiation of meristems and the blossoming of Biloxi soybeans. Bot. Gaz. 99:825-839.

12. Bradley, R. T., J. M. Christie and D. R. Johnson. 1966. Forest management tables. Bookl. For. Comm. 16.

13. Burdon, J. J. and L. D. Pryor. 1975. Interspecific competition between Eucalypt seedlings. Aust. J. Bot. 23:225-229.

14. Buttery, B. R. 1969. Effect of plant population and fertilizer on the growth and yield of soybeans. Can. J. Plant Sci. 49:659-673.

15. Cochran, W. G. and G. M. Cox. 1957. Experimental Designs. John Wiley and Sons, New York.

16. Cody, M. L. 1966. The general theory of clutch size. Evolution, N.Y. 20:174-184.

17. Colton, C. C. and F. A. Einhellig. 1977. Allelopathic mechanisms of velvetleaf on soybeans. M.S. Thesis, University of South Dakota.

18. Darwin, C. 1859. The Origin of Species. Mentor ed.

19. Dekker, J. H. and W. F. Meggitt. 1978. Herbicide trials on velvetleaf in soybeans. In: Weed Control Results in Field Crops, Department of Crop and Soil Sciences, Michigan State University. pp. 18-28.

20. Dekker, J. H. and W. F. Meggitt. 1979. Herbicide trials on velvetleaf in soybeans. In: Weed Control Results in Field Crops, Department of Crop and So8l Sciences, Michigan State University. pp. 19 A-F.

21. van Dobben, W. H. 1951. Enkele beschouwingen naar aanleiding van veldproeven met mengcultulir. Maandbl., Landbvoorldienst. 8:89-100.

22. Dominguez, C. and D. J. Hume. 1978. Flowering, abortion and yield or early-maturing soybeans at three densities. Agron. J. 70:801-805.

23. Donald, C. M. 1951. Competition among pasture plants. I. Intraspecific competition among annual pasture plants. Aust. J. Agric. Res. 2:355-376.

24. Donald, C. M. 1962. In search of yield. J. Aust. Inst. Agric. Sci. 28:171-178.

25. Donald, C. M. 1963. Competition among crop and pasture plants. Adv. Agron. 15:1-118.

26. Duff, G. 1966. Yield tables for unthinned stands of the "green" varieties of Pinus contorta in New Zealand. Tech. Pap. Forest Res. Inst. N.A. 50.

27. Durrant, A. 1965. Analysis of reciprocal differences in diallel crosses. Heredity 20:573-607.

28. Eaton, B. J., O. G. Russ and K. C. Feltner. 1976. Competition of velvetleaf, prickly sida and Venice mallow in soybeans. Weed Sci. 24:224-228.

29. Enyi, B. A. C. 1973. Effect of plant population on growth and yield of soybean. J. Agric. Sci. 81:131-138.

30. Esau, K. 1977. Anatomy of seed plants. John Wiley and Sons, New York.

31. Evetts, L. L. and O. C. Burnside. 1973. Early root and shoot development of nine plant species. Weed Sci., 21:289-291.

32. Frazee, R. W. and E. W. Stoller. 1974. Differential growth of corn, soybean and seven dicotyledonous weed seedlings. Weed Sci. 22:336-339.

33. Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland.

34. Gleeson, A. C. and C. A. McGilchrist. 1978. Analysis of plant competition data from an incomplete mixture diallel experiment. J. Agric. Sci., Camb. 91:416-426.

35. Gressel, J. B. and L. G. Holm. 1964. Chemical inhibition of crop germiantion by weed seeds and the nature of inhibition by <u>Abutilon theophrasti</u>. Weed Res. 4:44-53.

36. Hall, R. L. 1974. Analysis of the nature of interference between plants of different species. I. Concepts and extension of the de Wit analysis to examine effects. Aust. J. AGric. Res. 25:739-747.

37. Hall, R. L. 1974. Analysis of the nature of interference between plants of different species. II. Nutrient relations in a nandi <u>Seteria</u> and greenleaf <u>Desinodium</u> association with particular reference to potassium. Aust. J. Agric. Res. 25:749-756.

38. Harper, J. L. 1957. Ecological aspects of weed control. Outlook on Agric. 1:197-205.

39. Harper, J. L. and A. P. Chancellor. 1959. The comparative biology of closely related species living in the same area. IV. Rumex: interference between individuals in populations of one and two species. J. Ecol. 47:679-695.

40. Harper, J. L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15:1-39.

41. Harper, J. L. and D. Gajic. 1961. Experimental studies of the mortality and plasticity of a weed. Weed Res. 1:91-104.

42. Harper, J. L. and I. H. McNaughton. 1962. The comparative biology of closely related species living in the same area. VII. Interference between individuals in pure and mixed populations of Papaver species. New Phytol. 61:175-188.

43. Harper, J. L. 1964. The nature and consequence of interference amongst plants. Proc. IX Int. Conf. Genet. pp. 465-481.

44. Harper, J. L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55:247-270.

45. Harper, J. L. and J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to Senecio vulgaris L. J. Ecol. 586581-698.

46. Harper, J. L. 1977. Population Biology of Plants. Academic Press, N.Y.

47. Hayman, B. I. 1954. The analysis of variance of diallel tables. Biometrics 10:235-244.

48. Hayman, B. I. 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.

49. Helsel, Z. R. and L. O. Copeland. 1978. Seeding practices for Michigan crops. Mich. St. Univ. Cooper. Ext. Bull. E-489.

50. Hildebrand, S. L., R. E. Lucas and R. G. White. 1975. Producing soybeans profitably in Michigan. Mich. St. Univ., Cooper Ext. Bull. E-362.

51. Hill, J. and Y. Shimamoto. 1973. Methods of analyzing competition with special reference to herbage plants. I. Establishment. J. Agric. Sci., Camb. 81:77-89.

52. Hill, J. 1973. Methods of analyzing competition with special reference to herbage plants. II. Effects of associate plants. J. Agric. Sci., Camb. 81:91-98.

53. Hinson, K. and W. D. Hanson. 1962. Competition studies in soybeans. Crop Sci. 2:117-123.

54. Hirano, S. and T. Kira. 1965. Influence of autotoxic root exudation on the growth of higher plants grown at different densities. J. Biol. Osaka City Univ. 16:27-44.

55. Hiroi, T. and M. Monsi. 1966. Dry matter economy of Helianthus annuus communities grown at varying densities and light intensities. J. Fac. Sci. Tokyo Univ. III 9:241-85.

56. Holliday, R. 1960. Plant population and crop yield. Nature, London 186:22-24.

57. Hozumi, K., T. Asahira and T. Kira. 1956. Intraspecific competition among higher plants. VI. Effect of some growth factors on the process of competition. Jour. Inst. Polytech. Osaka City Univ. 7:15-34.

58. Hozumi, K., K. Shinozaki and Y. Tadaki. 1968. Studies on the frequency distribution of the weight of individual trees in a forest stand. I. A new approach toward the analysis of the distribution function and the -3/2 power distribution. Jap. Jour. Ecol. 18:10-20.

59. Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:767-788.

60. Jinks, J. L. and B. I. Hayman. 1953. The analysis of diallel crosses. Maise Genet. Cooperation Newsletter 28:48-54.

61. Joyce, P. M. and G. Gallagher. 1966. Provisional yield tables for Contorta pine (coastal) in Ireland. Dublin.

62. Kira, T., H. Ogawa and N. Sakazaki. 1953. Intraspecific competition among higher plants. I. Competition - density - yield interrelationship in regularly dispersed populations. J. Inst. Polytech. Osaka City Univ. D4:1-16.

63. Koyama, H. and T. Kira. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. J. Inst. Polytech. Osaka Univ. D7:73-94.

64. Lehman, W. F. and J. W. Lambert. 1960. Effect of spacing of soybean plants between and within rows on yield and its components. Agron. J. 52:84-86.

65. Lerner, I. M. 1965. Genetic homoeostasis. Edinburgh.

66. Little, T. M. and F. J. Hills. 1978. Agricultural Experimentation. John Wiley and Sons, New York.

67. Lysenko, T. D. 1946. Natural selection and intraspecific competition. Lysenko, T. D.: Agrobiology, Moscow, 1954.

68. Mackenzie, A. M. 1962. The Bowmount Norway spruce sample plots 1930-60 (Picea abies karst. syn. P. excelsa Link). The effects of thinning treatment on growth. Forestry 35:129-138.

69. Martin, J. H. and W. H. Leonard. 1967. Principles of field crop production. MacMillan Co., New York.

70. McGilchrist, C. A. 1965. Analysis of competition experiments. Biometrics 21:975-985.

71. McGilchrist, C. A. 1971. Relationship algebra of an incomplete diallel cross. Sankhya Series B. 33:225-234.

72. McGilchrist, C. A. and B. R. Trenbath. 1971. A revised analysis of plant competition experiments. Biometrics 27:659-671.

73. Mitscherlich, E. A. 1919. Ein beitrag zur standraumweite unserer landwirtschaftlichen kulturpflazen in Gefassen und im freien lande, Bei reinstat und mengsaat. Landw. Jb. 53:341-360.

74. Monsi, M. 1968. Mathematical models of plant communities. In: Functioning Models of Terrestrial Ecosystems at the Primary Production Level, F. E. Eckardt ed., Paris. pp. 131-149.

75. Mulluerstedt, R. 1963. Untersuchungen uber die keimung von unkrautsamen in abhangigkeit von sauerstoff partialdruk. Weed Res. 3:154-163.

76. Niciporovic, A. A. 1954. 15th Timirjazev Lecture. U.S.S.R. Acad. Sci. (Precis by J. N. Black and D. T. Watson, 1960) Fld. Crop Abstr. 13:169-

77. Norrington-Davies, J. 1967. Applications of diallel analysis to experiments in plant competition. Euphytica 16:391-406.

78. Norrington-Davies, J. 1968. Diallel analysis of competition between grass species. J. Agric. Sci., Camb. 71:223-231.

79. Oliver, L. R. 1979. Influence of soybean planting date on velvetleaf competition. Weed Sci. 27:183-188.

80. Pandey, J. P. and J. H. Torrie. 1973. Path coefficient analysis of seed yield components in soybeans. Crop Sci. 13:505-507.

81. Pavlovsky, Q. and T. H. Dobzhansky. 1966. Genetics of natural populations. XXXVII. The coadapted system of chromosomal variants in a population of Drosophila spuedoobscura. Genetics, Princeton 53:843-54.

82. Pavlychenko, T. K. and J. B. Harrington. 1935. Root development of weeds and crops in competition under dry farming. Scient. Agric. 16:151-160.

83. Potter, J. R. and J. W. Jones. 1977. Leaf area partitioning as an important factor in growth. Plant Physiol. 59:10-14.

84. Puckridge, D. W. and C. M. Donald. 1967. Competition among wheat plants sown at a wide range of densities. Aust. J. Agric. Res. 18:193-211.

85. Putnam, A. R. and W. B. Duke. 1978. Allelopathy in Agroëcosystems. Ann. Rev. Phytopathol. 16:431-451.

86. Raynal, D. J. and F. A. Bazzaz. 1973. Establishment of early successional plant populations on forest and prairie soil. Ecology 54:1335-1341.

87. Retig, B. and L. G. Holm. 1971. Influence of four weeds on enzyme components of cabbage, tomato and lettuce seedlings. Weed Sci. 19:735-739.

88. Retig, B. 1971. Studies of the interactions between weed species and crop seedlings. Ph.D. Thesis, University of Wisconsin.

89. Retig, B., L. G. Holm and B. E. Struckmeyer. 1972. Effects of weeds on the anatomy of roots of cabbage and tomato. Weed Sci. 20:33-36.

90. Sakai, K. 1955. Competition in plants and its relation to selection. Cold. Spring Harb. Symp. Quant. Biol. 20:137-157.

91. Sakai, K. I. 1957. Studies on competition in plants. VII. Effect on competition of a varying number of competing and non-competing individuals. J. Genet. 55:227-234.

92. Sakai, K. I. 1961. Competitive ability in plants: Its inheritance and some related problems. Symp. Soc. Exp. Biol. 15:245-263.

93. Shinozaki, K. and T. Kira. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. J. Inst. Polytech. Osaka City Univ. D7:35-72.

94. Shinozaki, K. and T. Kira. 1961. The C-D rule, its theory and practical uses. J. Biol. Osaka City Univ. 12:69-82.

95. Staniforth, D. W. and C. R. Weber. 1956. Effects of annual weeds on the growth and yield of soybeans. Agron. J. 48:467-471.

96. Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Co., N.Y.

97. Stern, W. R. and D. R. Beech. 1965. The growth of safflower (Carthamus tinctorius L.) in a low altitude environment. Aust.

98. Sukatschev, U. N. 1928. Plant communities (in Russian). In: The Struggle for Existence, G. F. Gause ed., 1934, Baltimore, p. 272.

99. Tamm, C. E. 1948. Observations on reproduction and survival of some perennial herbs. Bot. Notiser. 3:305-321.

100. Tamm, D. O. 1956. Further observations on the survival and flowering of some perennial herbs. Oikos 7:273-292.

101. Thomas, U. J. 1970. A mathematical approach to fitting parameters in a competition model. J. Appl. Ecol. 7:487-496.

102. Trenbath, B. R. and J. L. Harper. 1972. Neighbor effects in the genus Avena. I. Comparison of crop species. J. Appl. Ecol. 10:379-400.

103. Trenbath, B. R. 1974. Biomass productivity of mixtures. Adv. Agron. 26:177-210.

104. Trenbath, B. R. 1975. Neighbor effects in the genus Avena. III. The diallel approach. J. Appl. Ecol. 12:189-200.

105. Tripathi, R. S. and J. L. Harper. 1973. The comparative biology of Agropyron repens (L.) Beauv. and A. caninum (L.) Beauv. I. The growth of mixed populations established from tillers and from seeds. J. Ecol. 61:353-368.

106. Wearden, S. 1964. Alternative analyses of the diallel cross. Heredity. 19:669-680.

107. Welbank, P. J. 1963. A comparison of competitive effects of some common weed species. Ann. Appl. Biol. 51:107-125.

108. White, J. and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58:467-485.

109. Williams, E. J. 1962. The analysis of competition experiments. Aust. J. Biol. Sci. 15:509-525.

110. Winter, D. M. 1960. The development of the seed of Abutilon theophrasti. I. Ovule and embryo. Amer. Jour. Bot. 47:8-14.

111. de Wit, C. T. 1960. On competition. Versl. Landbouwk. Onderz. 66(8):1-82.

112. de Wit, C. T. 1961. Space relationships within populations of one or more species. Symp. Soc. Exp. Biol. 15:314-329.

113. de Wit, C. T. and J. P. van den Bergh. 1965. Competition between herbage plants. Neth. J. Agric. Sci. 13:212-221.

114. de Wit, C. T., P. G. Tow and G. C. Ennik. 1966. Competition between legumes and grasses. Versl. Landbouwkd. Onderz. No. 687:1-30.

115. Yoda, K., T. Kira and K. Hozumi. 1957. Intraspecific competition among higher plants. IX. Further analysis of the competitive interaction between adjacent individuals. Jour. Inst. Polytech. Osaka City Univ. 8:161-178.

116. Yoda, K., T. Kira, H. Ogawa and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ. 14:107-129.

117. Zimdahl, R. L. 1980. Weed-crop competition. International Plant Protection Center. Univ. of Oregon.

APPENDIX

APPENDIX A

Typical Michigan Soybean Production Area Velvetleaf Infestation Levels

	Velvetleaf/M^2
Mean stand	20.6
Range of infestations	2.2-39.5
Two most frequent infestations	4.0 (Low)
	28.0 (High)