

Many Little Hammers: Ecological Management of Crop-Weed Interactions

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I. Introduction

Despite the use of a considerable amount of technology and many hours of human labor, weeds cause substantial reductions in yields of crops grown in both industrialized and developing countries. In the United States, more than \$6 billion is spent annually on herbicides, tillage, and cultivation to control weeds in cropland (Chandler, 1991), yet annual crop losses due to weed infestation currently exceed \$4 billion (Bridges and Anderson, 1992). In many developing countries, hand labor for weed control may consume up to half of the total labor demand for crop production (Akobundu, 1991). Worldwide, Akobundu (1987) estimated that weeds reduce crop yields by 5% in the most developed countries, 10% in the less developed countries, and 25% in the least developed countries. Because weeds pose a recurrent and nearly ubiquitous threat to crop productivity and farm profitability, and because weeds respond dynamically to a wide range of farming practices, weed management has a key role in the design and function of agroecosystems.

Over the past four decades, weed management in the industrialized countries has been dominated by a focus on herbicide technology (Zimdahl, 1991; Wyse, 1992; Abernathy and Bridges, 1994). In the United States, yearly application of herbicides to agricultural land exceeds 200 million kg of active ingredients (Gianessi and Puffer, 1990) and accounts for more than 60% of the total mass of all agricultural pesticides applied (Aspelin,

1994). In many developing countries, amplification of crop production has been viewed as dependent on increased use of agrichemicals (Conway and Barbier, 1990), and government subsidy programs have often promoted the use of herbicides and other pesticides (Repetto, 1985).

Increased reliance on herbicides has generally been accompanied by marked improvements in crop productivity and farm labor efficiency. In recent years, however, several factors have led to a reappraisal of heavy emphasis on chemical weed control technology and to a growing interest in alternative management strategies that are less reliant on herbicides and more reliant on manipulations of ecological phenomena, such as competition, allelopathy, herbivory, disease, and responses to soil disturbance (Liebman and Dyck, 1993a; Wyse, 1994). We call these alternative approaches to suppressing weed survival, growth, and reproduction "ecological weed management."

In North America and northern Europe, a major factor propelling interest in ecological weed management has been recognition that herbicides, applied in the course of normal farming practices, are responsible for widespread contamination of ground and surface supplies of drinking water (Hallberg, 1989; Leistra and Boesten, 1989; NRC, 1989, pp. 101-109; Goolsby *et al.*, 1991, 1993; Thurman *et al.*, 1991; USEPA, 1992; Nelson and Jones, 1994). Public concern over this contamination has inspired strict groundwater regulations in Germany (Gassman, 1993), whereas other industrialized nations, e.g., Sweden (Weinberg, 1990; Bellinder *et al.*, 1994), the United Kingdom (Lawson, 1994), and Canada (Hamill *et al.*, 1994), have responded with policies to reduce or minimize the quantities of pesticides applied in crop production. In the United States, the Clinton administration announced its support for coordinated efforts to reduce pesticide use in food production in a 1993 joint statement from the Department of Agriculture, Environmental Protection Agency, and Food and Drug Administration (Gutfeld, 1993).

A second factor propelling interest in ecological weed management is the more than 1 million incidents of unintentional pesticide poisoning that occur throughout the world each year (WHO, 1990). Pesticide poisoning is most frequent in developing countries (WHO, 1990), although it is not uncommon in industrialized countries such as the United States (e.g., Stone *et al.*, 1988). Public health data from Costa Rica (Hilje *et al.*, 1992, p. 79; Dinham, 1993, p. 105) suggest that herbicides may contribute to a significant portion of pesticide poisonings in developing countries, where safe use is difficult because of unavailable or prohibitively expensive protective equipment, inadequate or insufficiently enforced safety standards, poor labeling, illiteracy, and insufficient knowledge of pesticide hazards by handlers and applicators (Pimentel *et al.*, 1992).

A third factor promoting interest in ecologically based weed management strategies is the likelihood that farmers will face increasingly intractable weed problems with fewer chemical control options. Herbicide resistance has been noted in more than 100 weed species (Warwick, 1991). This resistance has been measured to evolve under field conditions in 4 or 5 years (Holt, 1992) and is now appearing in new species at a rate equal to that observed for insecticide resistance in arthropod pests (Holt and LeBaron, 1990). Both older (e.g., triazine) and newer, more environmentally friendly (e.g., sulfonylurea) herbicide chemistries have been met with the evolution of resistance, and cross-resistances within single weed species to different classes of herbicides have been detected (Holt, 1992; Gill, 1995). In addition to resistance within weed populations, heavy reliance on herbicides has, in some instances, shifted the composition of weed communities toward species that are more difficult to control (e.g., nutsedges, *Cyperus* spp.; Keeley, 1987). Growing numbers of government regulations and restrictions and increasing costs of research, development, and registration are expected to reduce the availability of older herbicides and the rate at which new herbicides are introduced (Holt and LeBaron, 1990).

A final factor promoting greater attention to ecological weed management is wider recognition of farming systems that operate profitably and productively with little or no use of herbicides and other agrichemicals. Profitable reduced input and organic systems seem to be possible for most commodities; examples include production of row crops and small grains in South Dakota (Smolik *et al.*, 1993), mixed grain and livestock in the midwestern United States (Lockeretz *et al.*, 1981), mixed vegetable, fruit, and livestock in New Zealand (Reganold *et al.*, 1993), and rice in Japan (Andow and Hidaka, 1989). Although a paucity of data makes it difficult to assess the range of conditions under which reduced input and organic farming systems will be successful, it is clear that such systems offer important opportunities to study the effects of nonchemical weed management practices on the survival, reproductive success, and dispersal (in both time and space) of different weed species. The information generated by such studies is, in our view, extremely valuable for the development of broadly adaptable weed management strategies that promote adequate yields and profits while protecting human health and environmental quality.

II. Information and Approaches

Ecological weed management involves the use of diverse types of information and a variety of control tactics to develop strategies for subjecting weeds to multiple, temporally variable stresses. The goals of imposing these stresses are reductions in (i) the density of weed propagules and seedlings,

(ii) the rate of weed seedling emergence relative to crop emergence, (iii) the rate of weed dispersal between and within fields, (iv) the proportion of available resources consumed by weeds, and (v) the proportion of weed communities composed of particularly noxious genotypes and species (Aldrich, 1984, pp. 399–435). To achieve these goals there is particular value in information regarding spatial and temporal patterns of weed abundance, reductions in crop yield due to weeds, weed life histories, weed niche characteristics, mechanisms of resource competition, and predicted outcomes of simulation models.

Information about spatial and temporal patterns of weed abundance is critical for determining which species are present in different portions of a management area (field, farm, or region) and whether these species are increasing or decreasing over time in response to management. Such information is generated by continual monitoring and constitutes the foundation of any integrated pest management system (Bottrell, 1979). Information generated by monitoring forms the basis for evaluating the efficacy of previous management strategies and identifying areas within fields and across landscapes where control measures need to be intensified (Mortensen *et al.*, 1993; Johnson *et al.*, 1995).

Weed-related yield loss information describes the extent to which crop yield is reduced by weed populations and communities, with emphasis on their density, mass, or leaf area; species composition; time of emergence; and period of association with the crop (Zimdahl, 1980, pp. 29–93; Kropff and Lotz, 1993a). Although the mechanistic basis of crop–weed interactions is not addressed in yield loss–weed infestation relationships, additional information concerning environmental factors (e.g., soil moisture conditions) may be included to suggest why the outcome of crop–weed interactions may vary from year to year and place to place. Predictions of yield loss from early season measurements of weed seed and plant density might be used to indicate when and where control measures are justified by agronomic and economic criteria (Streibig *et al.*, 1989; Forcella *et al.*, 1993).

Life history information results from intensive study of weed life cycles, including stages of germination or resumption of growth, seedling establishment or shoot emergence, growth and resource use, sexual or vegetative reproduction, dispersal, and quiescence (Mortimer, 1983). Life history studies are valuable for identifying stages that are potentially the most susceptible to control measures (Maxwell *et al.*, 1993). They are also important for projection of increases or declines of weed populations over time in response to different management practices, such as tillage, cultivation, grazing, and crop rotation (Firbank *et al.*, 1985; Maxwell *et al.*, 1988; Jordan, 1993a; Jordan *et al.*, 1995).

Niche information is developed by quantifying weed and crop germination and growth responses to variations in biological, physical, and chemical

factors (e.g., Kennedy *et al.*, 1991; Ogg *et al.*, 1994). Such measurements help define the range of ecological conditions to which different weed and crop species (and genotypes) are best and least adapted. Of particular interest are possible differences between crops and weeds in germination and establishment and tolerance or susceptibility to manipulable environmental and management factors, such as mechanical disturbance, crop residue additions, herbivorous insects, and plant pathogens.

Mechanistic information concerning the ecophysiological basis of competition is generated through measurements of resource capture, resource conversion, growth, and allocation processes in crop and weed species grown in single-species stands and in mixture (Berkowitz, 1988; Kropff and Lotz, 1993b). Through intensive study of the mechanisms of crop–weed resource competition, management strategies may be developed to minimize stress on crops and maximize stress on weeds at particularly vulnerable stages of development.

A sixth type of information is generated by the integration of yield loss, life history, niche, and ecophysiological data into models with which to predict the outcome of crop–weed interactions when factors such as emergence time, plant height, and leaf area expansion rate are varied (Kropff *et al.*, 1993b). Such models may also aid efforts to breed crops with improved ability to tolerate or suppress weeds.

Guided by these diverse types of information, weed management strategies can be developed that employ nonselective and selective tactics. Nonselective tactics reduce weed numbers, growth, and reproduction through general herbivory, competition from rapidly growing cover crops, mowing, tillage, or the use of a broad spectrum herbicide such as glyphosate [*N*-(phosphonomethyl) glycine]. Because these manipulations can damage or kill a growing crop, they are carried out either before the crop is established or after it has been harvested to affect the weed pressure facing a subsequent crop. In contrast, selective techniques exploit differential responses between crop and weed species to control tactics such that the crop is favored and weeds are placed at a disadvantage. Examples of commonly used selective techniques include preemergence and postemergence herbicides and cultivation. Much less time and many fewer resources have been focused on the discovery and development of selective weed-suppression techniques that are based on ecological differences between crop and weed species, such as the use of weed pathogens and herbivores as biocontrol agents and rotation sequences that generate weed-suppressive crop residues. Nonetheless, available literature indicates that ecologically selective techniques can play key roles in suppressing weeds and promoting crop growth.

The full repertoire of possible tactics useful in ecologically based weed management strategies includes (i) different types and times of soil disturbance, through tillage and cultivation; (ii) diversification of crop vegetation,

through cover cropping, rotation sequences, intercropping, and green manuring; (iii) herbivory by livestock and weed-feeding insects; (iv) diseases caused by applied or indigenous weed pathogens; (v) improvements in crop competitive ability through the use of weed-tolerant and weed-suppressive varieties, and through manipulations of crop density and spatial arrangement; and (vi) manipulations of resource conditions, through irrigation and fertility management (Liebman and Janke, 1990; Regnier and Janke, 1990; Cardina, 1995). Herbicides are not excluded from the toolkit but are viewed as options rather than absolute requirements for crop production. They are used only when and where the concerted application of other control tactics fails to reduce and maintain weeds at acceptable levels, and they are used in a manner that poses minimal risks to humans, other nontarget organisms, and the environment.

III. Basic Principles Guiding Weed Management Strategies

A. Competition in Agroecosystems

Resource removal that affects another individual defines competition. The competitive interactions of greatest concern to farmers occur when resources necessary for crop growth are removed by weeds and yield is reduced (Kropff, 1993b). Allelopathy, another important plant-plant interaction in agricultural systems, describes the addition of phytotoxicants into the environment and the subsequent reduction in growth of susceptible plants. Although mechanistically distinct, competition and allelopathy are not easily distinguished in the field. Interference is used to describe the net effect of competitive (removal) and allelopathic (addition) interactions (Gliessman, 1986).

Generally speaking, crops are planted at a constant density chosen to maximize economic yield per unit area (Radosevich and Roush, 1990). Although agricultural ecosystems are highly productive, intraspecific competition commonly limits the yield of individual crop plants, demonstrating that, even in a weed-free environment, supplies of certain resources are at suboptimal levels. Add to this environment weeds, and the total demand for resources, and therefore the intensity of resource competition, is increased. Interspecific competition is thus an intense and important interaction in agroecosystems.

Weed management has as its goals (i) exclusion of weeds from crop environments, (ii) killing of weeds before they interfere with crop growth and reproduction, and (iii) suppression of any surviving weeds. Interspecific resource competition and allelopathy are pivotal processes in obtaining the last of these three goals.

B. Effects of Weed Density, Duration, and Distribution

1. Yield Loss Relationships Results of experiments with a variety of weed-crop combinations, including wild oat (*Avena fatua* L.) with barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) (Cousens *et al.*, 1987), nightshade (*Solanum* spp.) with tomato (*Lycopersicon esculentum* Miller) (Weaver *et al.*, 1987), barnyard grass [*Echinochloa crus-galli* (L.) Beauv.] with sugar beet (*Beta vulgaris* L.) (Norris, 1992), common ragweed (*Ambrosia artemisiifolia* L.) with bean (*Phaseolus vulgaris* L.) (Chikoye *et al.*, 1995), redroot pigweed (*Amaranthus retroflexus* L.) with corn (*Zea mays* L.) (Knezevic *et al.*, 1994), and velvetleaf (*Abutilon theophrasti* Medikus.) with corn (Lindquist *et al.*, 1996), indicate that the relationship between crop yield loss and weed density often conforms to a rectangular hyperbola (Aldrich, 1987). Typical yield loss relationships are shown in Fig. 1 (Blackshaw, 1993a), which illustrates the effects of different densities (and age classes) of downy brome

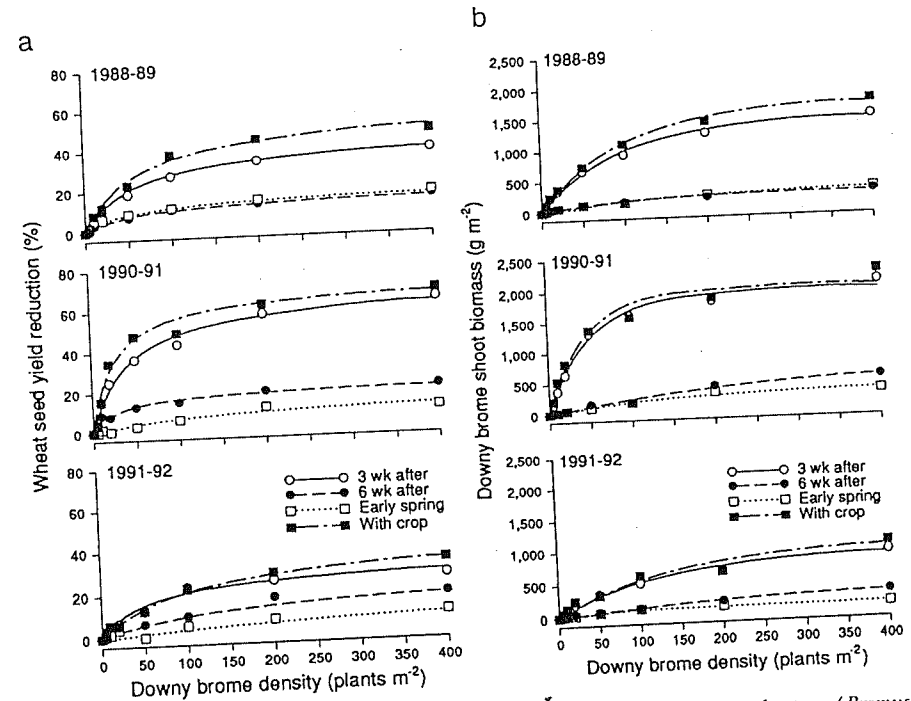


Figure 1 Winter wheat (*Triticum aestivum* L.) seed yield (a) and downy brome (*Bromus tectorum* L.) shoot biomass (b) as functions of downy brome density and times of emergence relative to wheat. Lines are fitted nonlinear regression curves for each emergence date (reproduced with permission from Blackshaw, 1993a).

(*Bromus tectorum* L.) on winter wheat. Drawn from such data sets is the first principle guiding weed management: *Reduce weed density.*

It can be seen in Fig. 1 that for a given age class of weeds, yield reduction due to weed infestation varied considerably among years: Weed competition was most damaging to wheat seed yield in 1990–1991, least damaging in 1991–1992, and intermediate in its effects in 1988–1989. Relationships between crop yield and weed density often vary considerably among environments and years, coincident with variation in temperature conditions, moisture availability, fertility source, and other factors (Aldrich, 1987; Mortensen and Coble, 1989; Bauer *et al.*, 1991; Liebman and Ohno, 1997; Lindquist *et al.*, 1996). For the experiments shown in Fig. 1, variation among years in the yield loss–weed density relationship was attributed to differences in the timing and quantity of rainfall (Blackshaw, 1993a). Thus, although general patterns of crop yield loss to varying densities and age classes of weeds appears consistent, specific outcomes are governed by a host of factors including weather, whose precise effects may be extremely difficult to predict without much larger data resources.

2. Critical Periods for Weed Control The experimental results illustrated in Fig. 1 indicate that earlier emerging weeds produced more biomass than later emerging weeds, and crop seed yield was inversely proportional to weed density. In general, weed populations that emerge earlier in the growing season are more damaging to crop yield than are populations that emerge later (Cousens *et al.*, 1987; Wyse, 1992). Thus, a second basic principle guiding weed management is: *Delay weed emergence relative to crop emergence.*

Crop species can differ greatly in their sensitivity to different durations of weed competition, as demonstrated in experiments in which purple nutsedge (*Cyperus rotundus* L.) was allowed to grow in several vegetable crops after weed-free conditions were maintained for varying numbers of weeks (William and Warren, 1975). Maintenance of nutsedge-free conditions for 3 weeks following planting was required to prevent yield reduction of transplanted cabbage (*Brassica oleracea* L.), whereas garlic (*Allium sativum* L.) yield was reduced unless nutsedge was excluded for more than 18 weeks. Other crops tested in this experiment gave intermediate results.

To better identify the period in a crop's life cycle when it must be kept weed free to prevent unacceptable yield loss, experiments can be conducted using two types of treatments: (i) Those in which the crop is first grown without weeds for specified periods of time and then weeds are allowed to grow for the remainder of the season (as in the purple nutsedge–vegetable experiments discussed above); and (ii) those in which the crop is first grown with weeds for specified periods of time and then weeds are excluded for the rest of the season (Oliver, 1988; Zimdahl, 1988). Data generated

from such experiments indicate that, in some cases, a crop may be unaffected by association with weeds during the early and late portions of the growing season if weeds are excluded during the middle period. When this pattern occurs, a clearly defined “critical weed-free period” is said to exist. For example, in a study conducted by Woolley *et al.* (1993) involving bean infested with weeds for different durations, crop yield loss did not exceed 3% if weeds were excluded during the interval of 15–60 days after the crop was planted.

In other cases, it is not possible to identify a critical weed-free period that occurs between periods of acceptable weed infestation. The important management issue then becomes how long weed exclusion efforts must be maintained before they can be relaxed. Van Acker *et al.* (1993a) noted, for example, that if weeds were prevented from growing in soybean from the time the crop was planted until it had four leaves (about 30 days after crop emergence), crop yield loss was <2.5% and weed biomass was reduced >97%. Similarly, no yield loss occurred in corn if redroot pigweed was prevented from growing until the crop reached the seven-leaf stage (Knezevic *et al.*, 1994).

As might be expected, the critical weed-free period for a given crop may vary considerably among sites and years, as was noted by Hall *et al.* (1992), who studied the effects of different durations of weed competition on corn grain yield. Factors contributing to variability in critical periods for weed control may include climatic and edaphic conditions affecting weed and crop emergence and growth rates, weed species composition, and weed density.

3. Growth Characteristics as Predictors of Weed Competition Variations between sites and years in weed and crop emergence times, growth rates, and densities would seem to preclude any unifying analysis of the effects of weed populations on crop yield or the ability to forecast the outcome of competitive interactions early enough in the season that cultivation or postemergence herbicides might still be used. A proposed solution to this problem is to use early season measurements of weed and crop leaf area to calculate a relative leaf area ratio with which to predict competitive outcomes. Theoretically, such an index could integrate variations in weed densities, emergence times, and growth rates into a quantifiable, consistent predictor of crop yield loss (Kropff and Spitters, 1991; Kropff *et al.*, 1992). Kropff and Lotz (1992) used data from five field experiments with different weed densities and times of emergence to demonstrate that leaf area measurements of sugar beet and lambsquarters (*Chenopodium album* L.) made 30 days after crop emergence could better predict crop yield loss than could weed density. Relative leaf area was also more successful than weed density in predicting soybean yield loss due to johnsongrass [*Sorghum hala-*

pense (L.) Pers.] (Vitta *et al.*, 1993), corn yield loss due to redroot pigweed (Knezevic *et al.*, 1995), and bean yield loss due to common ragweed (Chikoye and Swanton, 1995). Kropff and Lotz (1993a) provide further examples of the relative leaf area approach, including possible modifications to allow for time-dependent differences in growth characteristics such as leaf expansion rates.

The work of Lotz *et al.* (1994) is of particular interest from the standpoint of practical application of the relative leaf area approach in scouting farm fields. Because a large amount of labor is required to measure leaf area directly, the investigators tested the possibility of estimating leaf area using more rapid, nondestructive measurements of canopy cover and radiation reflectance. The study involved seven field experiments with spring wheat, sugar beet, and several weed species. Cover measurements made using a grid-quadrat frame were well correlated with direct measurements of leaf area until 3 or 4 weeks after crop emergence; reflectance measurements worked well in spring wheat but not in sugar beet. Based on results of this study, it would seem worthwhile to direct more research attention toward the development of rapid field techniques for estimating leaf area.

Other aspects of plant size that can be assessed easily early in the growing season may also prove useful for predicting the outcome of crop-weed interactions. For example, Bussler *et al.* (1995) grew corn with velvetleaf and common cocklebur (*Xanthium strumarium* L.) and found that 30–58% of the variation in corn seed production could be predicted from estimates of plant volume derived from nondestructive measurements of crop and weed densities, heights, and canopy widths made 23–28 days after planting.

Information regarding weed density and duration of competition might be used to establish thresholds and scouting methodologies but does not provide insight as to the mechanisms driving the crop-weed interactions. Mechanistic information requires a greater degree of reductionist investigation (see Section III,C,4).

4. Spatial Patterns A certain amount of variation in yield loss-weed density relationships may derive from variation in weed spatial distributions. As the result of innate and human-related dispersal patterns, weeds often occur in clumps within fields in a manner best described by the negative binomial distribution (Cousens and Mortimer, 1995, pp. 55–85, 217–242). It is thus important to consider that the local neighborhood of most crop plants within those fields is filled with many fewer weeds than the overall field average would suggest (Cardina *et al.*, 1995; Johnson *et al.*, 1995). For a given average density over a broad area, clumped weeds are expected to be less damaging to crop yield than are randomly or evenly distributed weeds (Auld and Tisdell, 1988; Brain and Cousens, 1990).

Clumped distributions of weeds within fields have two implications for management. First, if appropriate tools were available, weed control mea-

asures might be applied only in weedy areas within fields; weed-free areas could be ignored. For example, Johnson *et al.* (1995) used multiple small quadrat samples (0.76 m²) and geostatistical techniques to describe the spatial characteristics of weed populations in 12 commercial corn and soybean fields in Nebraska. In the interrow areas, where herbicides were not applied, 30% of the sample area was free of broadleaf weeds and 70% was free of grass weeds. Johnson *et al.* (1995) concluded that if herbicide application were linked to real-time weed-sensing technologies (Woeblbecke *et al.*, 1995; Mortensen *et al.*, 1997), considerable reductions in herbicide use might be achieved. On a slightly larger scale (e.g., sections of fields), knowledge of weed distributions might aid the deployment of other site-specific weed management tactics, such as the choice of particular crop sequences and tillage practices or the use of higher seeding rates (Mortensen *et al.*, 1997).

The second, and corollary, implication of clumped weed distributions is that managing weed dispersal within fields can be an important strategy in a weed management system. Simulation models suggest that (i) if weed seed dispersal from local patches can be restricted during activities such as tillage and harvest, then the rate of weed population increase may be reduced (Ballare *et al.*, 1987); and (ii) management of weed dispersal may have greater influence on crop yield than the relative competitive ability of the weed with respect to the crop (Maxwell and Ghersa, 1992). Thus, we suggest a third principle for weed management: *Limit the dispersal of weed propagules.*

C. Mechanisms of Resource Competition

1. A Conceptual Model Resource capture, resource conversion, and biomass allocation are key processes affecting plant growth and reproduction (Mooney and Chiariello, 1984; Berkowitz, 1988). A conceptual model that incorporates these processes and provides a means of organizing information concerning resource competition between crops and weeds is shown in Fig. 2. As shown in the model, resources (e.g., light, water, and nutrients) may be either generally accessible to both crops and weeds, in which case competition for limited quantities may occur, or selectively accessible to either crop or weed species, as in mixtures of legumes, which use atmospheric N, and nonlegumes, which lack access to this N source. Because plant biomass accumulation and reproductive effort are strongly linked to resource consumption, we suggest a fourth principle for weed management: *Maximize the proportion of available resources consumed by crops and minimize the proportion consumed by weeds.*

For both generally accessible and selectively accessible resources, the capture of one resource (e.g., nitrogen) may affect capture of other resources (e.g., light) through feedback loops involving growth and biomass

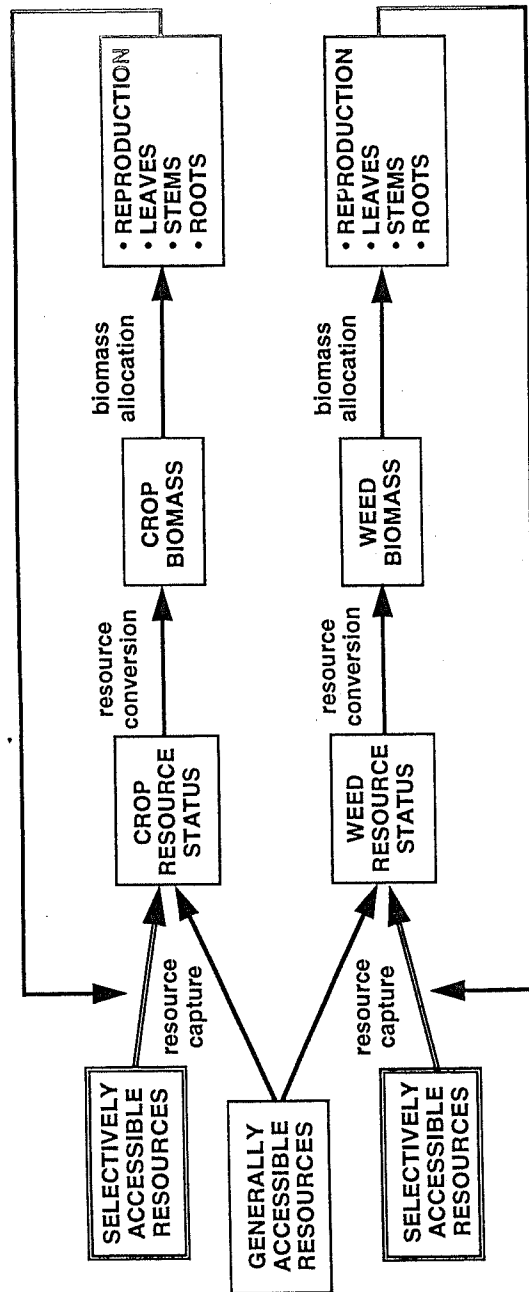


Figure 2 The iterative process of resource competition.

allocation. Biomass, representing seed or vegetative structures present at the start of crop-weed interactions, may be viewed as the starting point of the model, although its importance in determining competitive outcomes has been questioned (Wilson, 1988a).

The model shown in Fig. 2 includes state and rate variables that can be quantified (Kropff and Spitters, 1992; Kropff, 1993a). State variables, boxed in Fig. 2, might include concentration of inorganic N in the soil, plant N content, total biomass, and biomass of individual plant organs; examples of rate variables include canopy light interception per unit time, photosynthetic carbon (C) gain per unit of N absorbed, photosynthetic C gain per unit of water transpired, and biomass partitioning coefficients. Abiotic and biotic environmental factors, such as temperature, precipitation, incident photosynthetically active radiation, and pathogens, can affect resource availability and physiological processes of resource capture and conversion, but for simplicity are not included here. Kropff (1993a) describes a mechanistic, ecophysiological model of crop-weed competition that includes environmental factors at the crop-weed system's boundaries as driving variables.

Direct measurements of resource availability, capture, conversion, and allocation can be made using instruments to quantify gas exchange, radiation interception throughout the canopy, soil and plant water potentials, nutrient concentrations, and other ecophysiological parameters (e.g., Pearcy *et al.*, 1991). Growth analysis techniques may also prove useful in examining rates of biomass accumulation and canopy production and efficiencies of biomass production calculated on the basis of leaf area, nutrient content, and other state variables (e.g., Evans, 1972; Hunt, 1982; Van Acker *et al.*, 1993b). In both field and glasshouse experiments, techniques to partition shoots and roots can be used to determine whether the locus of competitive interactions is above or below ground (Snaydon, 1979; Wilson, 1988b; Exley and Snaydon, 1992; Bozsa and Oliver, 1993).

One of the advantages of using a resource-based model to organize investigations of crop-weed interactions is that it encourages acquisition of information with which to differentiate crop *tolerance* of weeds ("competitive response") from crop *suppression* of weeds ("competitive effect") (Goldberg and Landa, 1991). Tolerance involves the ability to maintain growth through (i) high resource conversion efficiency at depleted resource levels or (ii) access to a selectively available pool of resources. In contrast, suppression involves the ability to preempt the use of generally accessible growth resources from competitors (Goldberg, 1990). Strategies to minimize crop yield loss to weed infestation might emphasize improved tolerance of weeds, whereas strategies to minimize weed growth and reproduction would prioritize improved suppression of weeds (Jordan, 1993b). Because weed-tolerant crop varieties may not be those with the strongest ability to suppress weed growth, and because a variety's ability to suppress

weeds may carry a yield penalty (Jordan, 1993b), a resource-based model of crop-weed competition may facilitate resolution of potentially contradictory crop breeding objectives.

2. Resource-Related Effects of Weeds on Crops Resource-related mechanisms of weed competition against crops help to identify those resources that might be better manipulated to a crop's advantage.

Experiments conducted by Cruz *et al.* (1983) and Graham *et al.* (1988) illustrate the effects of varying weed density on crop resource use. In a study conducted under dryland conditions with rice (*Oryza sativa* L.) and a mixture of weed species, Cruz *et al.* (1983) observed that leaf water potential of the crop decreased (i.e., moisture stress increased) as weed density increased. Graham *et al.* (1988) reported that leaf area, interception of photosynthetically active radiation, net photosynthesis, total biomass, and seed production of sorghum (*Sorghum vulgare* L.) were reduced as density of pigweed (*Amaranthus* spp.) increased.

A study conducted by Young *et al.* (1983) with quackgrass [*Elytrigia repens* (L.) Nevski] and soybean illustrates how resource availability may be manipulated to help identify factors for which competition may be occurring. The investigators observed that addition of irrigation water could offset the weed's detrimental effect on crop leaf water potential but could not eliminate all of the weed's negative effects on yield. Macronutrient content of soybean leaves was not affected by the presence of quackgrass; competition for light by the weed against the crop was inferred from measurements of plant height.

Weed infestation can result in reductions in crop macronutrient uptake and yield, as shown in experiments with corn (Vengris *et al.*, 1955) and wheat (Soni and Ambasht, 1977). A study conducted by Volz (1977) demonstrates the value of monitoring nutrient availability as well as crop and weed nutrient uptake. Volz (1977) showed that corn N concentration and uptake were depressed by the presence of yellow nutsedge (*Cyperus esculentus* L.), but that nutsedge N uptake failed to account for the depression. Measurements of soil inorganic N concentration and denitrifying bacteria population densities led the investigator to suggest that nutsedge reduced N availability to corn by increasing losses through denitrification. Results of this study emphasize that interactions between crops and weeds are not necessarily limited to resource competition.

3. Resource-Related Effects of Crops on Weeds By understanding how to create resource deficits in a weed's immediate environment, and how a weed responds to such deficits, crop and soil management strategies may be devised to reduce weed growth and reproduction. Research efforts following this approach have generally focused on weed-crop canopy relations

and light deficits, but management of soil resources may offer additional options.

Shetty *et al.* (1982) used bamboo frames to manipulate light conditions in a field experiment and reported that shading reduced height, leaf area, dry matter production, and tuber production of purple nutsedge. Height, leaf area, and seed production of several other annual weeds were also reduced by shading. The investigators concluded that by manipulating crop canopies to create desired levels of shading, substantial weed suppression could be achieved.

Resource deficits may create desirable shifts in allocation patterns of weed biomass. In two field experiments in which screen cloth was used to create shaded conditions, Williams (1970) observed that shading of quackgrass resulted in an 11–16% reduction in shoot dry weight but a 47–51% decrease in rhizome weight. Williams (1970) suggested that selecting crops that shade the weed "would most help in its control."

Lotz *et al.* (1991) demonstrated that shading reduces shoot biomass and tuber production in yellow nutsedge, and that crops differ in their ability to shade the weed. Compared to a crop-free control, tuber number per nutsedge plant was reduced 25% by winter rye (*Secale cereale* L.), 69% by winter barley, 96% by corn, and 100% by hemp (*Cannabis sativa* L.). Reductions in nutsedge tuber production were reflected in decreased competition from nutsedge (i.e., higher yields) in a subsequent corn crop. Lotz *et al.* (1991) concluded that use of crops that produce dense canopy cover during a long period of the growing season may result in a considerable decrease in nutsedge population density on infested farmland.

Liebman and Robichaux (1990) examined the effects of N and light deficits on the photosynthetic performance, growth, and seed production of white mustard (*Brassica hirta* Moench) in field experiments in which the weed was grown alone, in mixture with barley sole crops, or in mixture with barley-field pea (*Pisum sativum* L.) intercrops. Barley had no effect on the amount of photosynthetically active radiation (PAR) reaching the weed, but it did reduce the weed's leaf N concentration, photosynthetic surface area, net photosynthesis, and biomass production. In contrast, barley-pea intercrops reduced both weed leaf N concentrations and the amount of PAR incident on weed leaves. Reductions in N status and PAR interception were accompanied by reductions in photosynthetic surface area, net photosynthesis, biomass, and seed production. Compared to use of a short statured pea variety with small leaves, use of a taller pea variety with larger leaves increased shading of the weed and further decreased its growth and seed production. Thus, cultivar choice may have important effects on a crop's ability to suppress growth of associated weed species through shading.

In a field competition experiment in which both the crop and the weed were tree species [Douglas fir (*Pseudotsuga menziesii* Franco.) and red alder (*Alnus rubra* Bong.), respectively], Shainsky and Radosevich (1992) demonstrated dynamic interactions between plant population density, competition for water, and competition for light. Red alder grew taller than Douglas fir, consequently reducing the fir's access to PAR and thereby its growth rate. However, when the investigators increased the density of Douglas fir, leaf water potential and leaf area of red alder decreased. The reduction in alder leaf area resulted in less shading of Douglas fir and a concomitant increase in Douglas fir's leaf area and growth rate. The combination of population and ecophysiological approaches presented in this study is exceptional and would be extremely useful in studies of annual crop and weed species.

4. Ecophysiological Simulation Models of Resource Competition With an adequate amount of ecophysiological information, conceptual models of crop-weed competition for resources, such as that shown in Fig. 2, can be developed into quantitative simulation models. Ecophysiological simulation models of crop-weed competition typically start with characterizations of each species grown in pure stand, and then predict growth and yield in mixture based on height and canopy characteristics affecting interspecific shading and light-driven transpiration rates. Similarly, root length or mass may be used to predict the outcome of competition for nutrients.

In the INTERCOM model described by Kropff and Spitters (1992), model parameters include functions describing vertical leaf area profile; light distribution throughout the canopy; carbon dioxide assimilation and light response curves of individual leaves at different heights in the canopy; maintenance respiration rates; phenological patterns of growth and development driven by accumulated heat units; dry matter partitioning patterns; leaf area development and senescence patterns; plant height; and transpiration rates. INTERCOM and similar models have been used to study competition for light between winter wheat and wild oat (Weaver *et al.*, 1994); competition for light and nitrogen between rice and barnyard grass (Graf and Hill, 1992); and competition for light and water between soybean and common cocklebur, rice and barnyard grass, corn and barnyard grass, sugar beet and lambsquarters, and tomato and eastern black nightshade (*Solanum ptycanthum* Dun.) (Wilkerson *et al.*, 1990; Wiles and Wilkerson, 1991; Kropff *et al.*, 1993c).

Concordance between observed and predicted responses in these studies has generally been very good. Thus, it can be hoped that ecophysiological simulation models will be useful for (i) developing hypotheses concerning mechanisms of resource competition, (ii) examining variability in the outcome of crop-weed interactions between years and environments, and

(iii) evaluating potential impacts of alternative weed management practices at a cost considerably lower than that incurred by multisite, multiyear field experiments. For example, simulation models of rice-barnyard grass competition conducted by Kropff *et al.* (1993a) indicated that using a rice cultivar with 5% increases in leaf area expansion rate and height parameters could reduce crop yield loss to weed competition by 6%. Because considerable genetic variation exists in rice for these traits, "there may be potential for breeding for higher competitive ability." As this example demonstrates, simulation can be useful for suggesting useful directions and hypotheses—it must, however, be substantiated by research in the field.

IV. Managing Crop-Weed Interactions

A. Strategies to Reduce Weed Propagule and Seedling Densities

As indicated in Fig. 1, factors that reduce weed population density and that delay weed emergence relative to crop emergence can be expected to improve crop performance and increase the competitive dominance of the crop over associated weeds. A variety of existing practices can be used to achieve these objectives and numerous ecological relationships exist with potential for exploitation as components of weed management strategies.

1. Crop Rotation and Use of Cover Crops Crop rotation is one of the most powerful cultural management techniques available to farmers for reducing weed seed and seedling densities (Liebman and Dyck, 1993b; Liebman and Ohno, 1997). When rotation sequences include crops that differ in planting and maturation dates, competitive and allelopathic characteristics, and associated management practices (e.g., tillage, cultivation, mowing, and grazing), weeds can be confronted with an unstable and frequently inhospitable environment that prevents their proliferation. Figure 3 illustrates marked reductions in weed seed and seedling densities when corn was grown in rotation with winter wheat compared with corn grown as a continuous monoculture (Covarelli and Tei, 1988). Rotation of corn with soybean was also found to reduce weed seed and seedling densities compared with continuous corn (Forcella and Lindstrom, 1988). Although crop rotation is a well-known and long-used method of maintaining or increasing crop yields, more research is needed to understand factors affecting weed demography in different rotation systems and to identify rotation strategies that are especially effective for weed management.

Cover crops are often planted to control erosion and, when leguminous species are used, to improve soil productivity through N fixation. Cover crops may also be used to suppress weeds. For example, lower weed densities were observed when various vegetable crops were planted without tillage

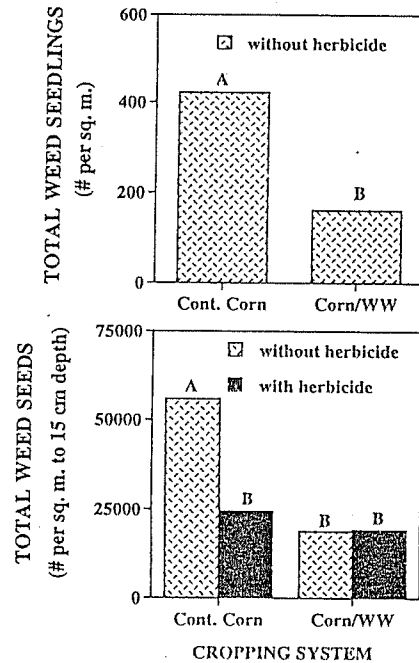


Figure 3 Effect of crop rotation and herbicide application on weed plant (upper panel) and seed densities (lower panel). Continuous corn was compared to a wheat/corn rotation, each with and without herbicides used for weed control. The predominant weed species were *Amaranthus retroflexus* L., *Chenopodium album* L., and *Echinochloa crus galli* L. Different letters above bars indicate significant differences ($P < 0.05$) in mean values (adapted with permission from Covarelli and Tei, 1988).

into the residues of gramineous cover crops compared to when the vegetables were planted into a tilled seedbed or an untilled bed without cover crop residues (Putnam and DeFrank, 1983; Putnam *et al.*, 1983). The investigators attributed much of this effect to allelopathic compounds released from the cover crops that selectively suppressed weed emergence.

Other data indicate that physical characteristics of cover crop residues may also affect weed emergence. Teasdale and Mohler (1993) reported that residues of rye and hairy vetch (*Vicia villosa* Roth.) cover crops on the soil surface reduced light transmittance and soil temperature amplitude sufficiently to reduce weed emergence. The investigators noted, however, that maintenance of soil moisture beneath cover crop residues could enhance weed emergence. Results of greenhouse and field studies indicated that hairy vetch residue used as a surface mulch reduced emergence of some weed species but not others (Teasdale *et al.*, 1991; Teasdale, 1993).

Cover crops that are incorporated into the soil may also affect weed emergence. Boydston and Hang (1995) reported that weed density was

reduced 73–85% and crop yield was increased 10–18% when potato was grown after rapeseed (*Brassica napus* L.) compared with after fallow. Glucosinolate compounds released or derived from rapeseed residues were suggested as possible agents of weed suppression. In a field experiment examining weed-related effects of a crimson clover (*Trifolium incarnatum* L.) cover crop and synthetic N fertilizer, Dyck and Liebman (1994) found that soil-incorporated clover residue strongly suppressed emergence of common lambsquarters but only slightly reduced emergence of sweet corn (Table I). Nitrogen fertilizer was found to stimulate emergence of the weed but to reduce corn emergence when clover residue was present. The investigators concluded that use of crimson clover as a N source provided weed control benefits both as a direct suppressant of weed emergence and as a substitute for N fertilizer.

2. Tillage and Cultivation Tillage, for seedbed preparation, and cultivation, for weed control, can affect established plants and reproductive structures. Tillage practices can range from nearly complete soil inversion, with moldboard plowing, to minimal soil disruption, with the use of zero-tillage (direct drilling) techniques. In addition to determining characteristics of soil disturbance and residue incorporation, tillage practices can have important effects on weed density and species composition (Buhler, 1995; Froud-Williams, 1988). Factors determining tillage effects on weeds include (i) depth of seed burial, (ii) seed survival at different soil depths, (iii) seed dormancy responses to burial, (iv) seedling ability to emerge from different burial depths, and (v) the quantity of new seeds added to the soil seedbank (Mohler, 1993). Because weed species may differ in these factors, responses to tillage are often species specific. For example, in a study comparing moldboard plow, chisel plow, and no-tillage systems for soybean production, Buhler and Oplinger (1990) observed that lambsquarters densities were not greatly influenced by tillage systems, whereas redroot pigweed densities were generally highest in the chisel plow system. Giant foxtail (*Setaria faberi* Herrm.), an annual grass species, was most abundant in the no-tillage system and least abundant in the moldboard plow system. In contrast, velvetleaf, an annual broadleaf species, was most abundant in the moldboard plow system and least abundant in the no-tillage system. Similarly in corn production systems, Buhler (1992) observed that density responses to tillage differed among weed species. Derksen *et al.* (1993) have suggested that changes in weed communities are influenced more by location and year than by tillage systems, but it appears that tillage is potentially useful for reducing weed density if choice among tillage practices is based on knowledge of the full spectrum of ecological sensitivities of different weed species.

Because seeds of many weed species require exposure to light to germi-

Table 1 Effect of Crimson Clover (*Trifolium incarnatum* L.) Residue and Nitrogen (N) Fertilizer on Emergence of Common Lambsquarters (*Chenopodium album* L.) and Corn (*Zea mays* L.)^a

Fertilizer treatment (kg N ha ⁻¹)	Total emergence (plants m ⁻²)				Time to 50% emergence (days after planting)			
	Lambsquarters		Corn		Lambsquarters		Corn	
	Without residue	With residue	Without residue	With residue	Without residue	With residue	Without residue	With residue
0	215	150	7.8	7.6	11.3	16.5	7.1	7.4
60	357	287	7.8	6.2	14.4	18.1	7.0	8.0
120	382	260	7.9	7.1	14.0	15.7	6.8	8.6
180	360	257	7.7	6.8	14.9	17.7	6.8	7.3
ANOVA								
Residue		$P < 0.001$						$P < 0.01$
N fertilizer ^b		$P < 0.001$						NS
Residue *N fertilizer		NS						NS

^a Adapted from Dyck and Liebman (1994), by permission of Kluwer Academic Publishers.
^b Contrast of 0 kg N ha⁻¹ vs (60 + 120 + 180 kg N ha⁻¹)/3. NS, not significant.

nate, attention has been directed recently toward the possibility of preparing crop seedbeds at night or during the day using tillage equipment covered with light-excluding hoods. In field trials Ascard (1994) observed that, compared to daylight tillage, both of the aforementioned dark-tillage techniques reduced weed density.

In some farming areas, germination of common weed species may occur in predictable flushes that are driven by accumulated heat units and rainfall (e.g., Harvey and Forcella, 1993). Because weed seedlings are extremely vulnerable to tillage operations, Forcella *et al.* (1993) conducted experiments in the north central United States to determine whether synchronicity in weed emergence could be exploited for management purposes. Delaying final tillage operations—the so-called stale seedbed strategy—allowed the investigators to kill a very high percentage of weed seedlings before planting corn and soybean and, consequently, to reduce weed competition against the crops.

Following planting, cultivation can be used before and after crop emergence to reduce weed densities between and within crop rows (Terpstra and Kouwenhoven, 1981; Buhler *et al.*, 1992; Rasmussen, 1992; Rydberg, 1993; Mulder and Doll, 1994; Rasmussen and Svenningsen, 1995; Vangessel *et al.*, 1995). Increased interest in alternatives to herbicides has resulted in a number of new cultivation implements, some of which are capable of working under high residue conditions and therefore are compatible with soil conservation objectives (Eadie *et al.*, 1992). Interest has also increased in machinery for flame weeding, which kills weed seedlings through cell rupture rather than incineration (Daar, 1987). Flame weeding can be used to destroy weeds emerging before crop emergence (Ascard, 1995a,b); post-emergence flaming, long practiced in cotton (*Gossypium hirsutum* L.), is also possible in certain other crops such as onion (*Allium cepa* L.) and corn (Daar, 1987).

3. Seed Predators and Pathogens Seed predation by insects, rodents, and birds can greatly reduce weed seed and seedling density, particularly in reduced tillage systems, which characteristically have greater amounts of residue cover (House and Brust, 1989). For example, Brust and House (1988) reported that, over a 5-week period, indigenous weed seed predators consumed 68% of seeds placed as baits in a zero-tillage soybean production system containing grain straw on the soil surface, but consumed only 27% of the seeds placed as bait in a clean-tilled soybean system. Weed seed predators may be indigenous (Lund and Turpin, 1977; Brust and House, 1988) or they may be cultured and released (Kremer and Spencer, 1989a,b). Weed seed predators exhibit species-specific preferences and thus may affect the relative abundance of different weed species (Brust and House, 1988; House and Brust, 1989). Pathogens, acting with (Kremer and Spencer,

1989a,b) or without (Kennedy *et al.*, 1991; Kremer, 1993) insects attacking seeds, can also be important for reducing weed seed and seedling densities. Despite data indicating weed seed predators and pathogens can be manipulated and augmented to desirable ends, optimum management strategies exploiting these interactions have not yet been developed.

4. Soil Solarization In areas with extended periods of hot weather, use of plastic tarps to heat moist soil prior to planting (soil solarization) has proven useful as a means of killing weed seeds and reducing weed seedling densities in subsequent crops (Egley, 1983; Horowitz *et al.*, 1983; Standifer *et al.*, 1984; Elmore *et al.*, 1993). Kumar *et al.* (1993) provided data indicating the positive effects of soil solarization on both weed suppression and crop yields, although the effect on crop yield might be attributed to reductions in pathogen populations as well as reduction in weed pressure (Stapleton and DeVay, 1986).

B. Strategies to Limit Weed Dispersal

The exclusion of weed seeds and other propagules from habitats and fields where they have previously been absent has long been recognized as an important means of reducing weed problems. Sanitation methods for limiting weed dispersal into new areas include using only crop seed free of weed contamination; composting of manures to kill weed seeds; cleaning of tillage and harvest equipment between operations in different fields; and mowing, cultivating, or spraying to kill weeds in areas bordering crop fields (Walker, 1995).

More problematic is the prevention or reduction of weed dispersal on a more local scale, i.e., between patches within fields. Perimeter portions of a cropped field may contain higher densities of weeds than more central portions (Wilson and Aebischer, 1995). Thus, site-specific control methods, such as higher seeding rates, different tillage practices, and different rates or types of herbicides, might be applied to field margins to control weed propagule production and subsequent movement into the rest of the field (see Section III,B,4). Where high densities of weeds occur in scattered "hot spots", the elimination of the propagules through hand roguing and spot spraying can be important in preventing further colonization. Combine harvesters clearly have the ability to spread weed seeds throughout a field (Cousens and Mortimer, 1995; pp.79-84); their ability to act as weed "seed predators", however, has received very little attention. Maxwell and Ghera (1992) and Cousens and Mortimer (1995, p. 290) have emphasized the need for more integrative work by weed managers and agricultural engineers to develop better machinery for harvesting and removing weed seeds.

C. Strategies to Manipulate Resource Availability and Resource Capture

Manipulating access to water, nutrients, and light can provide opportuni-

ties to a crop's advantage. Access to resources can be manipulated in spatial, temporal, and physiological dimensions.

1. Spatial Aspects Manipulating access to water can have powerful effects on crop and weed performance in arid areas. Figure 4 illustrates how selective placement of irrigation water improved weed management in tomato production systems studied in California (Grattan *et al.*, 1988). Three irrigation systems were compared: sprinkler irrigation, which spread

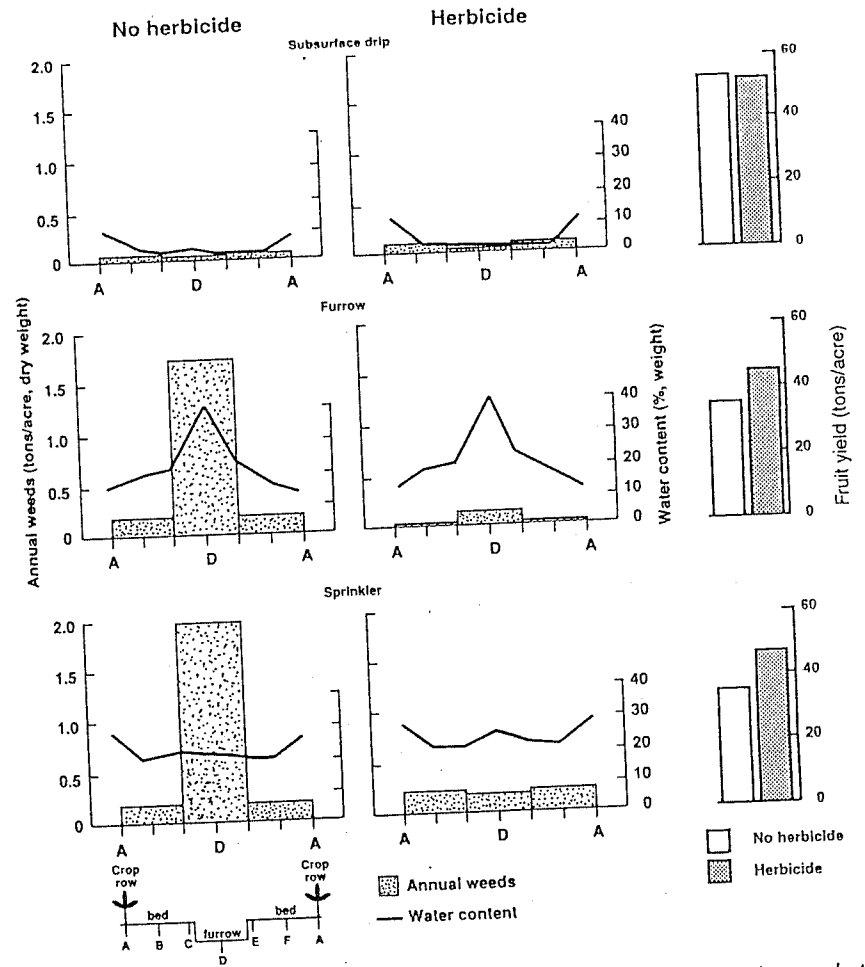


Figure 4 Biomass of annual weeds, soil water content, and tomato (*Lycopersicon esculentum* Miller) fruit yield as affected by herbicide application and three types of irrigation. The crop row (A) and bed furrow separating the raised beds (D) are depicted schematically at the bottom of the figure (adapted with permission from Grattan *et al.*, 1988).

water uniformly over the entire plot; furrow irrigation, which concentrated water between crop rows; and subsurface drip irrigation, which concentrated water directly beneath the crop. In the absence of herbicides, weed growth in the sprinkler and furrow irrigation systems was substantial, and tomato yield was reduced by weed competition. In contrast, when subsurface drip irrigation was used, weed growth was extremely low, even in the absence of herbicides, and crop yield was unaffected by weed competition. It should be noted that the experiment was conducted at a site at which precipitation during the tomato production season is nil or extremely low.

Seed placement may affect the availability of soil moisture and the outcome of crop-weed interactions. In a review of weed management tactics useful for production of agronomic crops in Nebraska, Bender (1994, p. 37) identified planting conditions as optimum when adequate moisture to germinate the crop is present below the soil surface but the surface is sufficiently dry to prevent germination of weeds until the next rain. In this case, seed placement in moister soil provides a competitive advantage to the crop by permitting it to emerge before the weeds.

Manipulating the location of nutrients appears to offer some potential as a means of increasing both crop yield and weed suppression. In a review of the effects of fertilizer placement on crop and weed performance, DiTomaso (1995) noted that banding fertilizers within the crop row of bean (*Phaseolus vulgaris* L.), soybean, peanut (*Arachis hypogaea* L.), wheat, alfalfa (*Medicago sativa* L.), Lincoln brome grass (*Bromus inermis* Leyss.), littleseed canary grass (*Phalaris minor* Retz.), and rice not only increased crop yield compared to broadcast applications but also reduced weed density. Application of nutrients in a deep band (e.g., 7 cm below seed level) appeared to be more effective for improving crop yield and weed suppression than did application of nutrients in a band on the soil surface.

In a field study conducted in Florida, banded applications of P (5 cm depth) failed to increase lettuce yield compared to broadcast P but did reduce the strength of weed competition measured as the percentage difference between weed-free and weed-infested crop yield (Shrefler *et al.*, 1994). However, lower rates of P were applied in the banded treatment than in the broadcast treatment, thus confounding fertilizer rate with placement effects.

Reinartsen *et al.* (1984) compared the effects of surface broadcasting and deep banding (5 cm depth) N fertilizer in a no-tillage winter wheat production system in eastern Washington. Banding N increased wheat yield but had no effect on wild oat biomass. In the same area of Washington, Cochran *et al.* (1990) compared the effects of broadcasting and banding (5 cm depth) N fertilizer on yield of winter wheat and biomass production of two grass weeds, downy brome and jointed goat grass (*Aegilops cylindrica* Host.). Comparisons were made in three tillage systems: moldboard plow-

ing, shallow rototilling, or no-tillage prior to planting. Wheat grain yields were higher with band-applied N compared to broadcast N in all tillage systems, with or without the presence of grass weeds. Weed biomass did not differ between the two fertilizer application treatments in the moldboard plow and no-tillage systems, but less weed growth occurred with banded N in the rototilled system. Cochran *et al.* (1990) suggested that the lack of weed suppression they observed with banded N in the moldboard plow and no-tillage systems may have resulted from inherently high soil fertility conditions; greater weed suppression would be expected when unfertilized surface soil limited weed growth and deep banded fertilizer relieved nutrient deficits for crops. Alternatively, crop performance (competitive response) may not have been closely linked to weed suppression (competitive effect). Mechanistic studies of nutrient competition are needed to address this issue.

Rasmussen *et al.* (1996) found that banding nitrogen fertilizer 5 cm below the depth at which spring barley was sown decreased weed biomass 55% and increased grain yield 28% compared with broadcast fertilizer application. Supporting the notion that fertility placement effects should be more pronounced in low relative to high fertility soils, the yield increase from fertilizer placement, averaged over 3 years, was 17% on sandy loam compared with 38% on coarse sand. Although all treatments were subjected to spring tine harrowing for weed control, the authors' opinion was that "fertilizer placement favored the crop at the expense of the weeds."

2. Temporal Aspects Because many weed species are capable of earlier and more rapid uptake of nutrients than are associated crops (Alkamper, 1976), some research effort has focused on whether delayed application of nutrients deprives weeds of nutrients early in the growing season and better matches the timing of crop uptake ability. Data indicate that temporal differences in nutrient supply can be important in determining competitive interactions between certain weed and crop species, but that results may not be consistent. In pot experiments with corn, wild mustard [*Sinapis arvensis* L. syn. *Brassica kaber* (DC) L.C. Wheeler var. *pinnatifida* (Stokes) L.C. Wheeler], and common lambsquarters grown in mixture, Alkamper *et al.* (1979) observed that applying half a dose of NPK fertilizer at planting and the remainder at corn ear emergence improved crop growth and reduced weed growth compared with application of the full nutrient dose at planting. In field competition experiments with rice and barnyard grass, Smith and Shaw (1966) reported that application of N fertilizer after barnyard grass had reached the reproductive stage increased rice yields much more than earlier application; effects on the weed were not reported, however. In field experiments with winter wheat infested with downy brome, effects of delayed application of N fertilizer on weed growth and crop yield varied

between years in a manner that was suggested to reflect variations in precipitation (Anderson, 1991). In experiments with two competing weed species (*Abutilon theophrasti* Medic. and *Datura stramonium* L.) supplied with nutrients at different times, Benner and Bazzaz (1987) concluded that "the timing of nutrient availability may influence plant growth and competition, but its effects are not readily predictable, and they appear to be less important than the effects of factors such as emergence time" (p. 243).

Crop-weed interactions can be tilted in favor of the crop through higher seeding densities (Blackshaw, 1993b; Carlson and Hill, 1985; Tollenaar *et al.*, 1994a; Wilson *et al.*, 1995) and narrower row widths (Teasdale and Frank, 1983), which often increase early season light capture by the crop (Teasdale and Frank, 1983; Yelverton and Coble, 1991; Forcella *et al.*, 1992; Egli, 1994; Board and Harville, 1994) and which may also increase early season water and nutrient capture (Sojka *et al.*, 1988). Several caveats apply to this approach, however: (i) If preemergence herbicides are not used, early season cultivation or postemergence herbicides may still be needed, in which case row spacing or plant vigor must accommodate this traffic; (ii) density cannot be increased too greatly in crops for which the size of each marketable unit is negatively density dependent; (iii) in nonirrigated areas with high evapotranspiration potential, excessive crop density and early season canopy cover may exhaust limited moisture supplies and reduce yield because of late season moisture deficits; and (iv) in humid areas, dense canopy cover may increase susceptibility to certain pathogens because of changes in microclimate.

3. Physiological Aspects Most leguminous crop species have access to atmospheric N through bacterial fixation; nonleguminous weeds do not. Because of this physiological difference, legume crops may effectively shade and suppress associated nonleguminous weeds under conditions of low soil N availability, as was observed by Liebman (1989) in studies with barley-pea intercrops grown in competition with white mustard. Conversely, weeds may be more competitive toward legume crops under conditions of high soil N availability. Staniforth (1962) reported that weed growth and resulting soybean yield reductions were greater when N fertilizer was applied to a previous year's corn crop than when it was not applied. Dotzenko *et al.* (1969) observed that weed seed and seedling densities in sugar beet increased with increasing rates of N fertilizer applied to previous crops of barley, corn, or bean. Thus, manipulation of soil N fertility levels may be an important component of weed management in crop rotations containing legumes and other crops. For example, a fall cover crop that immobilized soil N following corn harvest might improve the competitive performance of a subsequent soybean crop.

Species can also differ in their response and sensitivity to forms of mineral nitrogen. Teyker *et al.* (1991) fertilized corn and pigweed with ammonium

or nitrate nitrogen. Corn biomass was unaffected by N source; however, use of ammonium and the addition of a nitrification inhibitor reduced pigweed shoot dry weight by 75% compared with the nitrate N source. Thus, the form of nitrogen fertilizer applied may be chosen so as to benefit the crop over certain weeds.

4. Intercropping Crop species that differ spatially, temporally, and physiologically in their patterns of resource use can often capture more light, water, and nutrients when planted in mixtures (intercrops) than when planted as single-species stands (sole crops) (Ofori and Stern, 1987; Willey, 1990; Fukai and Trenbath, 1993; Keating and Carberry, 1993; Morris and Garrity, 1993a,b). Complementarity in resource use between intercrop components can limit competition between them and can lead to higher yields per unit land (Vandermeer, 1989, pp. 68-105; Willey, 1990; Liebman, 1995). Conversely, resource complementarity between intercrop components can also lead to greater resource preemption from weeds and less weed growth compared to sole crops (Liebman and Dyck, 1993b). In a field study integrating ecophysiological and agronomic measurements, Abraham and Singh (1984) observed that a sorghum-fodder cowpea intercrop captured more macronutrients, intercepted more light, suppressed weed growth more effectively, and provided higher crop yield than did a sorghum sole crop.

Because intercrop mixtures are often planted at higher total density than those used for the component species grown as sole crops, it can be difficult to ascertain whether intercrop weed control advantages are results of increased crop diversity or increased crop density. Results of replacement series experiments, in which total crop density is maintained constant for both intercrops and sole crops, indicate that some intercrops can reduce weed growth below levels obtained from sole crops of the components without an increase in total crop density (Fleck *et al.*, 1984; Sharaiha and Gliessman, 1992), whereas in other cases, weed growth in intercrops is intermediate between that obtained from the most weed-suppressive and least weed-suppressive sole crops (Shetty and Rao, 1981; Mohler and Liebman, 1987). Increases in crop density in intercropping systems definitely contribute to improved weed suppression (Liebman and Dyck, 1993b) and can increase total yield of intercrops assessed on a unit land area basis (Willey, 1979; Ofori and Stern, 1987).

Although intercropping practices are widely used in tropical areas, they are employed in limited ways in many mechanized, temperate farming systems. Examples include forage grasses and legumes intercropped with corn, soybean, barley, oat, or wheat; soybean intercropped with wheat; field pea intercropped with barley, oat, or wheat; and grasses and legumes planted as understories in fruit and nut orchards (Liebman, 1995). Expan-

sion of opportunities to use intercropping practices would be enhanced by more attention from agricultural engineers (Vandermeer, 1989, pp. 199–201).

D. Strategies to Exploit Differential Growth Responses and Susceptibilities

Differential responses may exist between crop and weed species to abiotic and biotic environmental factors. Abiotic factors, such as temperature, moisture, fertility, and light conditions, may result in differential growth responses, reflecting differential responses at levels of resource capture, conversion, or allocation. Alternatively, biotic factors, such as pathogens, herbivores, and crop residues, may have species-specific effects in suppressing plant growth. Identification of differential responses may allow field conditions to be manipulated to the benefit of crops and detriment of weeds.

1. Temperature Conditions The outcome of interspecific competition between plants can be markedly affected by temperature conditions (Pearcy *et al.*, 1981; Flint and Patterson, 1983; Holt, 1988; Radosevich and Roush, 1990; Wall, 1993). Although very little research effort has been directed toward exploiting differential responses to temperature in weed management strategies, results of an experiment conducted by Weaver *et al.* (1988) indicate that more attention to this subject could be worthwhile. After quantifying differences between tomato and four weed species in their germination and emergence responses to temperature, Weaver *et al.* (1988) predicted the sowing temperatures at which tomato would emerge before the weeds and consequently experience less competition from them. In addition to choosing planting times based on soil temperature as a means of improving weed control, soil temperature might be manipulated intentionally for weed management purposes. Significant differences can occur, for example, between tillage systems in early season soil temperature characteristics (Johnson and Lowery, 1985; Cox *et al.*, 1990; Dwyer *et al.*, 1995) that affect crop, and probably, weed emergence.

2. Moisture Conditions Competitive interactions between crops and weeds may also be affected by moisture conditions. For example, Ogg *et al.* (1994) reported that mayweed chamomile (*Anthemis cotula* L.) was more aggressive in reducing growth of pea under conditions of low moisture availability than under conditions of greater moisture availability because of differential susceptibility to moisture stress between the crop and weed species. Conversely, cocklebur was more detrimental in its effects against soybean in wetter years than in drier years (Mortensen and Coble, 1989). This effect was ascribed to (i) greater reduction in vegetative growth of cocklebur, compared to soybean, under dry conditions and consequently reduced

canopy growth and reduced light competition; and (ii) reduced yield potential of soybean under dry conditions. Water management and moisture conditions have a strong impact on the species composition of weeds infesting rice and the outcome of rice–weed competition (Moody and Drost, 1983; Sarkar and Moody, 1983; Seaman, 1983). Because weed species adapted to particular irrigation (flooding) regimes build up rapidly with repeated production of rice under the same set of management conditions, variation in crop establishment techniques and irrigation practices may be necessary to prevent weed proliferation where rice is grown in near-continuous monocultures.

3. Fertility Conditions Application of nutrients (especially N) may either increase or alleviate competitive suppression of crops by weeds. Supporting Alkamper's (1976) contention that weeds are often more responsive to fertilizer application than are crops, Carlson and Hill (1985) found that application of N to wild oat–spring wheat mixtures increased wild oat growth and decreased wheat yields. Yield reductions of wheat due to interference from Italian ryegrass (*Lolium multiflorum* Lam.) were greater under N fertilized conditions than under unfertilized conditions (Appleby *et al.*, 1976). Conversely, Tollenaar *et al.* (1994b) found that applying N to corn and a mixture of weed species resulted in lower weed biomass and increased corn yields, suggesting greater crop interference against the weeds at higher fertility levels. Wells (1979) reported that application of N fertilizer to wheat in Australian experiments increased wheat yield and had no effect on the strength of weed interference against the crop. A mechanistic, resource-based explanation is needed to reconcile these opposing types of competitive outcomes. As discussed previously, timing of nutrient availability may be a critical factor affecting differential responses between crop and weed species. Results may also depend on crop cultural practices, such as planting date; the identities of the species and genotypes involved and their intrinsic growth responses to N; and differential responses to other environmental factors, including ratios of N to other nutrients (Tilman, 1982, pp. 139–189).

4. Light Conditions Coffee (*Coffea arabica* L.), cocoa (*Theobroma cacao* L.), and tea (*Thea sinensis* L.) are well adapted to production in the shaded understory of taller tree species (Willey, 1975). Production of these crops in shade may confer weed control advantages. In an experiment conducted in Mexico, Nestel and Altieri (1992) reported that weed biomass in shaded coffee systems was substantially less than that in unshaded coffee or in control plots without coffee or shade trees. In Nicaraguan coffee plantations, shading has been observed to reduce the proliferation of particularly aggressive weed species and to shift composition of the weed community

toward species that are less competitive toward the crop (C. P. Staver, personal communication).

5. Pathogens and Herbivores Differential susceptibility to pathogens and herbivores can reduce weed growth and shift competitive interactions between crop and weed species to favor the crop. Exploitation of this principle serves as the core component of weed biocontrol strategies. A large number of microbe species are potentially available as inundative biocontrol agents for weeds (Charudattan and DeLoach, 1988; Charudattan, 1991). Less attention has been directed toward the use of herbivores as weed biocontrol agents, except in rangeland systems.

In field trials conducted in California, Pantone *et al.* (1989a,b) observed that addition of fiddleneck flower gall nematode [*Anguina amsinckiae* (Steiner and Scott, 1935) Thorne, 1961] to mixtures of wheat and coast fiddleneck (*Amsinckia intermedia* Fischer and Meyer) greatly increased wheat's ability to suppress fiddleneck's flower and seed production. Conversely, addition of the nematode reduced fiddleneck's negative effect on wheat and increased wheat seed yield. The nematode does not attack wheat and is considered a possible biocontrol agent for the weed (Pantone *et al.*, 1985).

Rhizobacteria can be selective in their effects between weeds and crops. Kennedy *et al.* (1991) conducted laboratory and fieldwork to examine the effects of *Pseudomonas fluorescens* strain D7 on the weed downy brome. Downy brome is a major pest in winter wheat regions of the northwestern United States and there is a lack of effective chemical practices with which to control it. Application of the bacterial isolate reduced germination, biomass production, and seed production of downy brome but did not have inhibitory effects on wheat. In plots infested with downy brome, wheat seed yields were increased significantly at two of three sites by application of D7. The suppressive effect of the bacterial isolate has been attributed to a phytotoxin produced by strain D7 (Tranel *et al.*, 1993; Gurusiddaiah *et al.*, 1994). Although much more work needs to be conducted to establish the widescale efficacy of this approach, it merits attention. The ability of soil microbial factors to suppress or convey resistance to crop pathogens has been documented by van Bruggen (1995); it follows that "weed suppressive soils" may exist, a phenomenon that could offer unique opportunities for management. To bring this concept to fruition, however, requires greater understanding of interactions between soil microbes, weeds, crops, and various environmental factors.

Foliar pathogens may also serve as weed biocontrol agents. Paul and Ayres (1987) conducted field experiments with lettuce (*Lactuca sativa* L.), the weed common groundsel (*Senecio vulgaris* L.), and a rust fungus (*Puccinia lagenophorae* Cooke) that attacks the weed. Lettuce fresh weight was

significantly reduced by competition from uninfected groundsel at sowing densities from 250 to 65,000 seeds m^{-2} but was not reduced by rust-infected groundsel until the weed sowing density exceeded 4000 seeds m^{-2} . Lettuce yield in plots with infected groundsel was two or three times greater than that in plots in which the weed had not been infected with the pathogen. The strength of competitive suppression of groundsel by lettuce was increased by rust infection. Auld and Morin (1995) noted that mycoherbicides have great potential in tropical regions of high humidity and predictable rainfall. Furthermore, traditional production of fermented foods offers expertise that could be used on-farm or in cottage industries for the production of local supplies of weed control pathogens.

In a field study investigating impacts of insects introduced as biocontrol agents of tansy ragwort (*Senecio jacobaea* L.), both herbivory and plant competition proved important for control of this weed species (McEvoy *et al.*, 1993). At the local scale of small plots used in the experiment, competition from existing meadow vegetation acted in an additive manner with herbivory by ragwort flea beetle (*Longitarsus jacobaeae* Waterhouse) to eliminate all ragwort individuals, except those within the soil seedbank, in a period of months.

Crop management practices may determine whether herbivores attack weeds selectively. In an assessment of weed biocontrol agents in rice cropping systems, Templeton (1983) noted that tadpole shrimp (*Triopus* spp.), which feed on seedlings and disturb their roots by agitation of the soil, can have both deleterious and beneficial effects depending on planting practices. If rice is seeded directly into water, as is the practice in California, tadpole shrimp are considered pests because they feed on both rice and weed seedlings. However, the problem is avoided in transplanted rice because the plants are larger and their roots are adequately covered with soil. Populations of 20–30 tadpole shrimp m^{-2} have significantly reduced weed populations in transplanted rice fields. Field trials suggested that use of tadpole shrimp as weed biocontrol agents could reduce hand labor requirements for weed control in rice by 70–80% (Templeton, 1983).

6. Crop Residue Crop residues may selectively reduce weed growth. For example, Liebl *et al.* (1992) demonstrated that use of a rye cover crop in conjunction with minimum tillage was a highly effective approach for limiting weed competition in soybean with minimal reliance on herbicides. Weed growth in the rye mulch system was significantly lower than that in a corn stubble system. The weed-suppressive effect of rye was attributed to allelopathy as well as shading, cooling, and physical obstruction effects of mulch on the soil surface. Compared to the corn stubble treatment, rye residue had no direct effect on soybean yield. Similarly, Mohler (1991) reported that the presence of a rye mulch decreased weed biomass and had no detrimental effect on sweet corn yield.

Anderson (1993) reported that growth of jointed goat grass (*A. cylindrica* Host) was reduced 70–85% by incorporated residues of wheat, corn, millet (*Pennisetum glaucum* L.), safflower (*Carthamus tinctorius* L.), and sorghum. Wheat growth was reduced 50–70% by the same five crop residues. Suppression of goat grass by crop residues could be overcome by adding N fertilizer, suggesting that N immobilization was responsible for the observed suppression; recovery of the wheat crop was not investigated. Anderson (1993) suggested that the combination of weed-suppressive, N immobilizing crop residues with band application of N to foster the growth of the crop was a possible management strategy to reduce weed growth while maintaining crop performance.

Soil-incorporated residues of hairy vetch and crimson clover were shown to be more detrimental for emergence and dry matter production (at 4 weeks after planting) of pitted morningglory (*Ipomoea lacunosa* L.) than of corn, an effect attributed to soluble allelopathic compounds (White *et al.*, 1989). In contrast to corn, cotton was suppressed by the legume residues, indicating that the selectivity of residue effects is species specific.

Differential responses between corn and common lambsquarters to crimson clover residue were demonstrated in a field study conducted by Dyck *et al.* (1995). Soil management treatments consisted of (i) crimson clover that was grown for 2 months before incorporation into the soil as a N source and (ii) bare fallow that was maintained for 2 months before being amended with different rates of synthetic N fertilizer. Following the clover and bare fallow regimes, sweet corn was grown alone and in combination with a fixed density of common lambsquarters in each soil management treatment. The resulting patterns of corn and common lambsquarters biomass production are shown in Fig. 5.

In the absence of the weed, crimson clover supplied an estimated 58 kg N ha⁻¹ to the corn crop (data not shown) and increased corn biomass 6% compared to the unfertilized bare fallow treatment (Fig. 5A). In contrast, in the presence of the weed, corn biomass in the crimson clover treatment was 35% higher than that in the unfertilized bare fallow treatment and 20% higher than that in bare fallow plots fertilized with 45 or 90 kg N ha⁻¹. The substantial increase in corn biomass observed in the crimson clover treatment reflected a reduction in weed competition, as estimated by the difference in corn biomass between weed-free and weed-infested plots. Common lambsquarters competition reduced corn biomass by 2% in the crimson clover treatment compared to 23, 21, and 22% reductions in the bare fallow treatments amended with 0, 45, and 90 kg N ha⁻¹, respectively (Fig. 5B). Common lambsquarters biomass was least in the crimson clover treatment and increased with increasing N application in the bare fallow treatments.

Results of this study and others (Liebman and Ohno, 1997) suggest that leguminous crop residues can have important effects as selective weed-

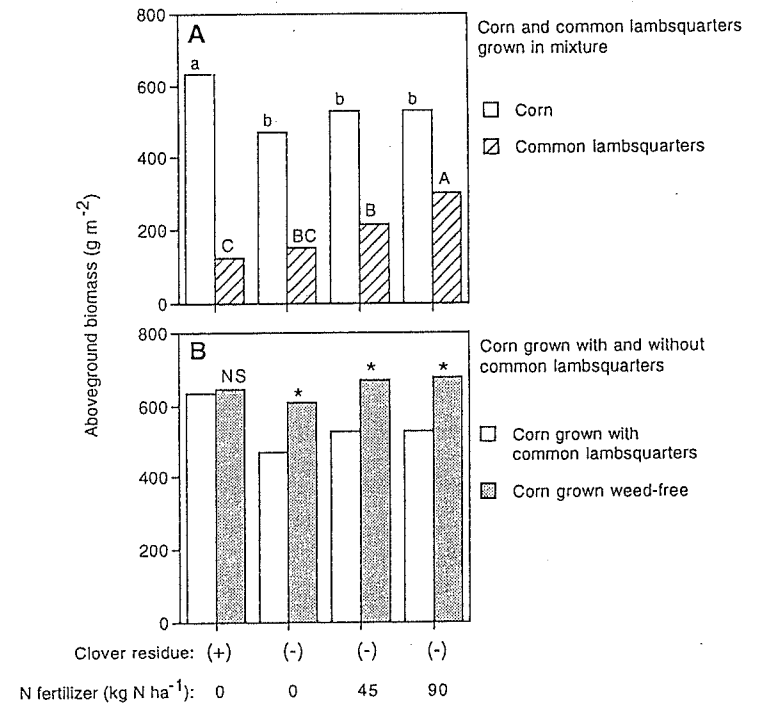


Figure 5 Effects of crimson clover residue and nitrogen (N) fertilizer on biomass of corn and common lambsquarters (*Chenopodium album* L.) grown in mixture (A); bars denoted by common letters of the same case are not significantly different at $P = 0.05$. Comparing corn growth with and without common lambsquarters (B) demonstrates yield loss due to weed competition; NS, not significant; *, significant weed effect ($P = 0.05$). Aboveground crimson clover biomass (4758 kg ha⁻¹), with a calculated N equivalence value of 58 kg N ha⁻¹, was incorporated 1 day before planting corn and common lambsquarters. Established densities were 7.3 corn plants m⁻² and 81 common lambsquarters plants m⁻². Aboveground crop and weed biomass were harvested at 86 days after planting (adapted with permission from *Agric. Ecosyst. Environ.* Dyck, E., Liebman, M., and Erich, M. S., Cropweed interference as influenced by a leguminous or synthetic fertilizer nitrogen source. I. Doublecropping experiments with crimson clover, sweet corn, and lambsquarters. Copyright 1995, Vol. 56, pp. 93–108, Elsevier Science B. V., Amsterdam. The Netherlands).

suppressive agents as well as sources of N fertility. However, the efficacy of legume residues for reducing weed growth and competition may be a function of residue quality. In contrast to the high level of weed suppression obtained from immature, fresh crimson clover (Dyck and Liebman, 1994; Dyck *et al.*, 1995), weaker and less consistent weed suppression was obtained when winter-killed, weathered clover residue was used (Dyck and Liebman, 1995). More research attention is needed to identify the biological, chemi-

cal, and physical characteristics of legume residues that may result in selective and effective weed suppression.

E. Strategies Employing Weed-Tolerant and Weed-Suppressive Cultivars

Crop varieties can differ greatly in their abilities to tolerate weeds (i.e., sustain the presence of weeds with little or no yield loss compared to weed-free control treatments) and suppress weeds (i.e., reduce weed emergence, growth, and reproduction). Although few efforts have previously been made to exploit these differences for weed management, there is now increasing interest in choosing and breeding cultivars for use as components of ecologically based weed management strategies (Berkowitz, 1988; Callaway, 1992; Callaway and Forcella, 1993; Jordan, 1993b). One of the crucial steps for making better use of crop genetic resources in weed management is the identification of heritable characteristics that confer greater ability to tolerate or suppress weeds.

Potter and Jones (1977) compared three crop and six weed species and reported that partitioning of dry matter into new leaf area was highly correlated with rapid growth. Thus, the use of crop varieties with high initial leaf area partitioning and expansion rates may be particularly important in weed management strategies (Forcella, 1987; Wortmann, 1993; Callaway and Forcella, 1993). Other characteristics, such as rates of shoot and root extension and ion absorption efficiencies, may also be important (Seibert and Pearce, 1993).

Callaway and Forcella (1993) selected for a soybean genotype with a high rate of leaf area expansion and were successful in developing a line that was superior in suppressing weed growth and providing high yield under both weed-infested and weed-free conditions. Blackshaw (1993a) showed that semidwarf cultivars of winter wheat were more susceptible to yield reduction by downy brome than were taller cultivars; taller cultivars intercepted more light and were better able to suppress growth of downy brome. However, Wicks *et al.* (1986) identified short statured wheat cultivars with superior ability to suppress summer annual weeds. Comparisons of different rice cultivars indicated that weed growth was least and weed-infested crop yield was highest for taller, leafier cultivars (Garrity *et al.*, 1992). Kropff and Spitters (1992) conducted evaluations of the INTERCOM model that indicated morphological characteristics, such as leaf area expansion rate, specific leaf area, and plant height, rather than physiological characteristics such as maximal photosynthetic rate largely determined ability to maintain yield in the presence of weeds. Lindquist and Kropff (1996) used INTERCOM to simulate competition for light between barnyard grass and irrigated rice, evaluating leaf area relative growth rates, i.e., LAI per LAI per growing degree day (RGRL). In these simulations, several items of importance to plant breeders wishing to improve the competitive ability of rice cultivars

were noted: (i) Increasing rice RGRL improved tolerance and barnyard grass suppressive ability, (ii) benefits of improved tolerance and suppressive ability varied with barnyard grass density, and (iii) the magnitude of variation in rice RGRL required to improve tolerance and suppressive ability was found to be within the range of values expected to exist in rice genotypes currently available for breeding work.

In addition to the development of new cultivars, weed management efforts could benefit from information on the competitive abilities of currently available cultivars. Herbicide dose, for example, could be reduced for cultivars that are highly competitive with weeds (Christensen, 1994). Alternatively, several management tactics may have to be invoked if an uncompetitive cultivar is planted into a field that contains high weed pressure. In Maine, dry bean farmers typically grow any of four locally adapted varieties—"Jacob's Cattle", "Marafax", "Soldier", or "Yellow Eye"—although others such as "Midnight Black Turtle" could be chosen. Although the locally adapted varieties show a high degree of morphological similarity, they differ in their abilities to tolerate and suppress wild mustard (*S. arvensis* L.), a common weed problem in Maine (Fig. 6; E. R. Gallandt, unpublished results). Black Turtle, Yellow Eye, and Jacobs Cattle, for example, showed greater tolerance to wild mustard (Fig. 6, top), as well as greater suppression of wild mustard (Fig. 6; bottom) compared to Marafax. Yield loss was greatest with Soldier (Fig. 6, top). In this instance, although choice of variety will continue to be market driven, the decision should probably affect a grower's weed management plan; e.g., cultivation efforts should be increased in a crop of Marafax or Soldier beans relative to Black Turtle, Yellow Eye, or Jacob's Cattle if fields are known to contain wild mustard.

The recent mechanistic experiments of Kropff and Spitters (1992) and Callaway and Forcella (1993), by identifying specific breeding objectives, could encourage future research on competitive cultivars. Because the yield- and weed-related costs and benefits of using weed-tolerant and weed-suppressive cultivars are not known (Jordan, 1993b), studies that compare conventional and competitive cultivars in various management systems are needed to determine the potential role of competitive cultivars in ecologically based weed management systems.

V. Many Little Hammers

As pointed out by Medd (1987), weeds are influenced by almost every aspect of crop production, including the obvious "direct controls" of herbicide application and cultivation as well as "indirect controls," such as crop genotype, time of sowing, nutrition, and other cultural factors. By understanding and organizing these direct and indirect controls into crop-

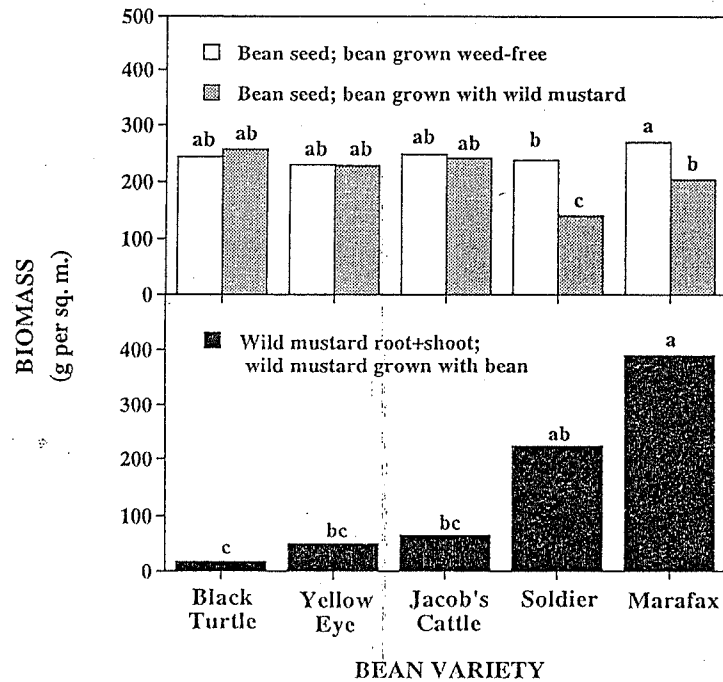


Figure 6 Seed yield of five bean (*Phaseolus vulgaris* L.) varieties grown either weed-free or with wild mustard (*Sinapis arvensis* L.) (top) and total biomass (root plus shoot) of wild mustard grown with the different bean varieties (bottom). Plants were harvested 104 days after planting. Bean varieties were established at 24 plants m^{-2} and were grown with wild mustard at 6 plants m^{-2} or under weed-free conditions. Weed-infested bean seed yields were inversely correlated with mustard total biomass ($P < 0.001$) (E. R. Gallandt, unpublished results).

ping strategies that reduce weed problems, environmental and economic objectives of weed management may be more readily met.

There are significant advantages to reliance on a combination of different methods, i.e., the use of “many little hammers”, over a single pest control tactic, i.e., “one large hammer”. The use of a combination of methods can lead to (i) acceptable control through the additive, synergistic, or cumulative action of tactics that may not be effective when used alone; (ii) reduced risk of crop failure or serious loss by spreading the burden of protection across several methods; and (iii) minimal exposure to any one tactic and consequently reduced rates at which pests adapt and become resistant to the methods (Bottrell and Weil, 1995). The philosophy of using a combination of methods to regulate pest populations is congruent with integrated pest management concepts that were introduced in the early

1970s (Bottrell, 1979). Although the philosophy of using many little hammers to manage weeds does not exclude use of direct controls (the large hammers), it shifts the focus of weed management to the many indirect controls and many possible interactions that can lead to successful management.

At the heart of this approach is the hypothesis that multiple and temporally variable stresses can be imposed on weeds that will result in acceptable crop yield and quality. This approach has been formalized in the “cumulative stress” approach for knapweed (*Centaurea* spp.) control in North America (Müller-Schärer and Schroeder, 1993). The impetus in this instance is likely the lack of economically viable “single hammer” approaches in rangeland ecosystems. The approach could prove useful, however, in all agroecosystems.

Modeling efforts to understand the combined action of plant stresses, although focused on a crop response to pests (e.g., Browde *et al.*, 1994), may help select specific tactics to impose on weeds. Mechanistic models link pest or damage levels to an appropriate physiological or demographic coupling point, e.g., leaf area index, stand density, intercepted light, photosynthesis, assimilated carbon, translocation rate, growth of different organs, and leaf senescence. Simulations in both rice (Pinnschmidt *et al.*, 1995) and potato (Johnson, 1992) showed that the effects of multiple stresses were less than additive and suggested that important pest-pest interactions were occurring. Although certain combinations may evoke a synergistic response, other tactics may be less than additive or antagonistic; many stresses may therefore be required to achieve a cumulative response and attain a desired level of weed suppression.

Because considerable genetic variability may exist within and among weed populations (Barrett, 1988), weeds often have the capacity to evolve resistance to or tolerance of management practices. Although attention has focused largely on variation in herbicide resistance, differences in weed responses to other factors may reflect genetic variation. For example, Tardif and Leroux (1992) observed significant differences among quackgrass genotypes in their shoot and rhizome responses to N application. The evolution of weed genotypes that mimic crop coloration, phenology, seed size, and other characteristics has been noted for a number of weed species (Barrett, 1983). Thus, changes in weed management practices can be expected to be met with dynamic responses in weeds that result in their continued adaptation and persistence. The use of multiple tactics in a concerted manner may be particularly important in limiting the rate of these changes in weed populations and in preventing shifts in the species composition of weed communities toward particularly noxious species. In the study conducted by Covarelli and Tei (1988), for example, using crop rotation (wheat-corn) rather than monoculture (continuous corn) re-

duced both the total weed density and the dominance of the weed community by the most abundant species (barnyard grass).

As the number of species within a community increases so does the potential for interactions. In a study of weed dynamics in potato cropping systems, Liebman *et al.* (1996) found that significant interspecific interactions occurred among weed species. *Brassica rapa*, *Sinapis arvensis*, and *Raphanus raphanistrum*, as a group, suppressed the growth of lambsquarters, the other dominant weed in the system; this interaction explained why the authors found either no relationship or a weak relationship between lambsquarters plant density and shoot biomass. Clements *et al.* (1994), in an insightful review, discuss the value of viewing weeds as a community rather than as individual species. Through increased understanding of the relationships between management and community structure and function, weed diversity may be strategically manipulated to suit crop production purposes.

What might a many little hammers weed management strategy look like? A two-hammer approach is common and most often includes the direct controls—herbicides and cultivation (Buhler *et al.*, 1992, 1993; Poston *et al.*, 1992; Mulder and Doll, 1993; Burnside *et al.*, 1994). In general, these studies have shown that herbicide applications and/or rates can be reduced if combined with well-timed cultivation. Less common are studies that include two indirect controls, for example, tactics aimed at processes such as interspecific competition, seed production, dispersal, seed survival, or seedling recruitment.

Combinations of direct controls with indirect tactics that are focused on interspecific competition and seedling mortality have shown that the competitive ability of a crop can assume some of the burden of weed control from a herbicide application. In Denmark, with recent political directives to reduce herbicide use, Christensen (1994) has shown that weeds may be controlled effectively in “competitive” cereal varieties with lower herbicide doses than those required for less competitive varieties. For example, spring rape (*Brassica napus* L.), used as a surrogate weed, was controlled in a competitive spring barley variety with one-third the herbicide required for control in the least competitive variety (Christensen *et al.*, 1990).

Additional bitactical strategies may or may not include herbicides combined with other tactics. Herbicides or plant growth regulators have been employed at low rates to enhance biocontrol programs using weed-feeding insects (Messersmith and Adkins, 1995) and weed pathogens (Scheepens, 1987; Hodgson *et al.*, 1988; Wymore and Watson, 1989). Insect defoliation of weeds and interspecific competition against weeds may also prove to be a useful combination of tactics (Ang *et al.*, 1994).

Examples of three little hammers, although relatively infrequent in the literature, demonstrate some creative management strategies. The common

feature of most three-tactic strategies is that they exploit interspecific competition, a pivotal process that can influence both weed seedling mortality and seed production. Teasdale (1995) found that reduced herbicide rates (1/4X) provided weed control and corn yield as good as full herbicide rates (X) if corn was grown with narrow row spacing and the crop population was doubled. Thomsen *et al.* (1996) reported that suppression of yellow starthistle (*Centaurea solstitialis* L.) growth and seed production through grazing and mowing was enhanced by planting subterranean clover (*Trifolium subterraneum* L.) to compete against the weed. Other examples of three-tactic strategies, which have achieved varying degrees of success, include combinations of herbicide banding, cultivation, and intercropping (Samson and Coulman, 1989); crop cultivar, row spacing, and seeding density (Malik *et al.*, 1993); and crop cultivar, tillage intensity, and mulch (Shilling *et al.*, 1995).

The closest one may come to viewing the action of many little hammers is probably demonstrated by studies that examine the effects of crop rotation on crop–weed interactions and weed population dynamics. Rotation increases system diversity, and hence the number of possible ecological interactions and stresses, and is often successful at suppressing weeds (Liebman and Dyck, 1993b; Liebman and Ohno, 1997). Although rotation has been examined in combination with practices such as tillage (Buhler *et al.*, 1994; Blackshaw *et al.*, 1994) or tillage plus herbicides (Young *et al.*, 1994), rotation itself can affect many demographic processes, supporting the notion that many little hammers can be useful for ecologically managing weeds.

VI. Summary and Conclusions

Conventional weed management in the latter half of the 20th century has had a relatively narrow focus on methods to reduce weed seedling recruitment (through the use of preemergence herbicides) and/or weed seedling survival (through the use of postemergence herbicides and cultivation). The many other factors in agroecosystems known to influence weed population dynamics and crop–weed interactions have been largely ignored. The increased incidence of herbicide resistance and greater demands for environmental stewardship signal that a shift from chemical technologies toward ecologically based strategies is now desirable, and that a broader focus for weed management efforts is necessary. Broader, well-integrated weed management strategies that exploit the full range of factors determining weed performance need to include tactics that affect crop–weed competition, weed seed production, seed dispersal, and seed survival. The use of such tactics could (i) lessen the burden placed on management

at the seedling stage; (ii) reduce requirements for off-farm inputs, and (iii) retard the adaptation of weeds to the stresses imposed upon them.

Shifting to more integrated approaches that exploit diverse stress and mortality factors will not be easy. In contrast to the simple testing and development of single- or two-tactic management strategies, a major difficulty facing the designers of ecologically based weed management systems is the complexity of interactions involving multiple stresses and mortality factors. As noted by Levins and Vandermeer (1990): "[agroecosystems] might very well exhibit behavior so complicated that even a deep understanding of the way the system is put together will not necessarily ensure that we can predict what will happen under different management strategies" (p. 349).

Comparative cropping systems studies could play an important role in understanding and testing weed management via many little hammers. A large-scale experiment with a historical database can serve as a site for evaluating discoveries made in smaller component studies, which can examine mechanisms of interactions between two or three factors. Perturbation of weed dynamics would demonstrate the effect of a tactic within the context of many interacting factors. This hierarchical approach to research, which includes studies at levels ranging from single factors to the level of the cropping system, is critical to the development of multiple stress weed management systems.

Inspired by the desire to compare conventional with alternative management strategies within an ecosystem context, cropping systems studies are being conducted in the United States (King and Buchanan, 1993; Smolik *et al.*, 1993; Temple *et al.*, 1994; Alford *et al.*, 1996) and Europe (Vereijken, 1989; Besson and Niggli, 1991; Lebbink *et al.*, 1994). Weed scientists have, as yet, played little or no role in evaluating interactions within these systems. We hope that situation will soon change.

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