INSECT HERBIVORES AND PLANT POPULATION DYNAMICS

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PERSPECTIVES AND OVERVIEW

Distinguishing Performance and Dynamics

It is one thing to show that herbivorous insects affect plant performance. It is an entirely different matter to demonstrate that insect herbivory affects plant population dynamics. There is a vast literature on insect pests of crop plants that shows how attack by defoliating, sucking, stem-mining, and gall-forming species can delay seed ripening, reduce seed production and individual seed weights, reduce the rates of shoot and root growth, increase the susceptibility of plants to disease, and reduce the competitive ability of plants relative to their unattacked neighbors. This literature tells us virtually nothing, however, about the importance of insects in natural communities, chiefly because we have so little information on the regulation of plant populations in the wild. For example, we do not know whether plant recruitment is seed limited, so we cannot predict whether there would be an increase in plant numbers if the simple experiment of sowing extra seeds were carried out. Information on the nature of population regulation is vital because if plant recruitment is not seed limited, then insects that reduce seed production will not have an important effect on plant population dynamics.

This review concentrates on material published from 1984 to 1987. Earlier material has been covered in other reviews (36, 64, 70, 94, 107, 121, 182, 206). The first part examines the impact of insect feeding on different aspects of plant performance. The second part examines two of the best sources of evidence on the impact of insect feeding on plant population dynamics: (a) the release of specialist insect herbivores against target weed species in classical
biological control projects and (b) the exclusion of insect herbivores from natural plant communities by the repeated application of chemical insecticides. The limitations and shortcomings of these bodies of evidence are also discussed.

**Background**

Until recently, conventional wisdom suggested that because the world was green, it was not possible that insect herbivores could be food limited (82, 167). The dramatic outbreaks of herbivorous insects that sometimes followed the indiscriminate use of broad-spectrum insecticides (51) lent credibility to the view that populations of insect herbivores are regulated at low densities by the actions of various natural enemies, notably predators, parasitoids, and diseases (87). At these low densities, the argument went, it was unlikely that insects could have an important effect on plant population dynamics.

The flaws in these arguments are numerous and have been discussed elsewhere (36, 62, 162). They can be summarized in three themes: (a) The world is not always green. (b) All that is green is not edible. (c) What is edible is not necessarily of sufficiently high quality to allow increase of the herbivore population. The evidence from natural populations does not provide convincing evidence in favor of the widespread importance of regulation by natural enemies (107) except in a handful of insect groups (e.g. leafminers, gall-formers, and some other small, sedentary species). Even in these few groups, however, direct experimental demonstration of population regulation by natural enemies by means of enemy exclusion has rarely been attempted.

It is possible, of course, that the assertion that insects have little impact on plant dynamics is correct, but for the wrong reasons. For example, recent work has shown that many herbivorous insects remain at low densities because of limited access to high-quality food (1, 3, 31, 83, 147, 150, 163, 175, 190, 211a, 212). They are food limited, but by the quality rather than the quantity of host plants available. Also, food quality and natural-enemy impact may be connected in that herbivore populations feeding on low-quality host plants will tend to have sufficiently low rates of increase that their populations could, at least in principle, be regulated by predators and parasites (124). A sudden rise in food quality might therefore trigger a population outbreak by inflating the rate of increase beyond the point at which the herbivore escapes natural-enemy control (174).

In any event, if insect herbivores are regulated by restricted access to high-quality food, it is not likely that they will be sufficiently abundant to have a profound effect on plant performance. Thus, insects may be food limited without imposing a substantial resource drain on their host plants, and quality-limited herbivores are not likely to be influential in plant population dynamics. While, in theory, low food quality might be expected to lead to
higher rather than lower rates of damage (as the insects attempt to compensate for low nutrient concentrations by feeding at a higher rate), in practice it appears that their capacity to compensate in this way is extremely limited (158).

Sometimes insect populations are limited by the amount of plant food available (54, 114, 202) and yet have little or no impact on the population density of their host plants. This asymmetry may come about because the growing season of the plant exceeds the feeding period of the insect, so that postdefoliation regrowth is possible (35, 86, 211). Alternatively, the plant might have a reserve of material that is physically inaccessible to the herbivore, and regrowth might occur from these reserves following defoliation. In yet other cases, the seed bank in the soil might be so large that even dramatic reductions in seed production would not lead to reduced seedling recruitment (41, 96, 186, 209).

The current view is that natural enemies probably maintain some herbivorous insects at population densities so low that their effect on plant dynamics would be immeasurably small (87). A further group of herbivorous insects (including many phloem feeders) are regulated by low food quality; their population densities are too low to have substantial effects on plant recruitment in most years (175). Low food quality and natural-enemy attack may interact with one another (124), so that a population may be enemy regulated in years when food quality is low, but may break free of enemy control in years of higher food quality. Other herbivorous insects are limited by the amount of food available to them and regularly defoliate their food plants (54). This does not mean that the insects necessarily have any important effect on plant dynamics, and the asymmetry observed in many field examples is such that plant recruitment is not herbivore limited even though herbivore populations are food limited (44, 47). A few herbivorous insects are known to have important effects on the population dynamics of their host plants [bark beetles (12), spruce budworm (14), beech bark insects (210a), and gypsy moth (201)]. Other herbivorous species, though not significant on their own, may have incremental effects that, along with effects of other insects, have substantial impact on plant dynamics (84, 225). Overall, however, it appears that plants have more impact on the population dynamics of insects than insects have on the population dynamics of plants.

**EFFECTS OF INSECT HERBIVORY ON PLANT PERFORMANCE**

*Flowering*

Insect feeding affects flower production both directly, by the destruction of flowers and flower buds, and indirectly, through various kinds of damage that
reduce bud production or bud burst. Flower and bud feeding are widespread among the main groups of herbivorous insects and are prevalent in all higher plant groups. Among coniferous trees, for example, a 40% female flower loss between May and August was attributed to insect feeding (mainly spruce budworm), with 22% of the surviving fruit crop showing signs of feeding damage (57). Cone-feeding insect populations often respond numerically to cone abundance, so attack in one year is reasonably predicted from a knowledge of the size of the cone crop in the previous year, which suggests that these insects are food limited. Whether or not their feeding influences the rate of flowering in future years has yet to be established (61, 105).

In angiosperms, flower loss attributable to insect attack ranges from less than 10% to almost 100%. For example, 80% of the bushes of the composite shrub *Gutierrezia microcephala* that were heavily attacked by the grasshopper *Hesperotettix viridis* failed to produce any flowers at all (171). Galling by *Euura lasiolepis* caused the loss of 43% of the reproductive buds in *Salix lasiolepis* (191). Grass-feeding aphids can cause greatly reduced flowering; *Holcaphis holci* feeding on tillers of the rhizomatous grass *Holcus mollis* can reduce the probability that a floral meristem is produced, and, at high aphid infestations, can preclude flowering altogether (J. Packham, personal communication). Feeding on buds and flowers by mirid bugs can cause heavy loss of fruit production (159). Mirids feeding on the flower stalks of grasses can cause silver top in which an entire panicle of unfilled seeds is produced as a result of blockage of the phloem (213). Flower consumption on the primary umbels of *Heracleum lanatum* by the moth *Depressaria pastinacella* leads to increased production of seeds from secondary umbels and to a change from male to female function in flowers on tertiary umbels (93).

Attack by the agamic generation of the cynipid gall wasp *Andricus quercus-calicis* caused 100% female flower mortality on certain trees of *Quercus robur*, with average rates of loss ranging between 26 and 47% over a 6-yr period (37). The sexual generation attacked the male flowers of a second host tree, *Quercus cerris*, and destroyed between 2 and 8% of its pollen production. This insect appears to be limited by the number of acorns available to the agamic generation on *Q. robur* and to have little impact on male flower function in *Q. cerris* (80).

Indirect effects of flower feeding on the rate of pollination, caused by reduced pollinator attraction, have received little attention. Given the balance of evidence that fruit set tends to be resource limited rather than pollination limited, reduced pollination may have little impact on plant population dynamics (52, 81, 101, 103, 178, 203, 205). It may, however, restrict the pollen choice of the female parent, and hence the genetic makeup of the progeny (145).

Plant size can affect the vulnerability of the plant to reduction of seed production by flower-feeding insects. For example, the host-specific moth
Heliodines nyctaginella causes a disproportionately great flower loss of small Mirabilis hirsuta plants because large plants flower early and thereby escape attack by the peak insect population (116). In other species, larger plants may flower longer than small ones, and may thus suffer a lower rate of flower loss to insects (200).

The factors determining the rate of flower loss in any given year, and the degree to which losses in one year influence the abundance of the insects and hence flower losses in subsequent years, have received little attention (152). Where density dependence in flower destruction has been investigated, either it has not been found (103) or flower attack rates have been found to be inversely density dependent (47, 56, 80). These results are consistent with the hypothesis that a fixed (or independently determined) number of insects attacks a variable number of flowers (where the number of flowers fluctuates in response to independent, external factors). Predator satiation therefore occurs in years of high flower production, but high rates of loss occur when low numbers of flowers happen to coincide with high insect densities.

**Fruit Production**

Feeding on ripening fruits and on seeds prior to dispersal accounts for massive losses in reproductive potential in many plant species. In others, the fruits are so well protected against insect attack (by a thick armor plating or an array of chemical toxins) that predispersal seed predation is minimal. Among conifers, fruit losses to insects of about 20% are commonplace (57, 61, 74, 142, 151, 198), but these may be substantially lower than losses attributable to mammals and birds (42, 199).

Angiosperms also lose many of their undispersed seeds to insect herbivores. Sucking insects such as aphids can greatly reduce the rate of fruit filling and can sometimes curtail fruit production altogether. Sheppard (196) sprayed the umbel rays of *Heracleum sphondylium* to exclude hogweed aphid, *Carvariella pastinacae*, and found that seed production and seed size both increased substantially. On the most heavily infested umbels there was no seed production at all. The aphid *Staticobium staticis* prevented seed production by sea lavender in those parts of a salt marsh where aphid densities were highest (68). Dramatic losses of pecan nut yield were attributable to leaf-feeding aphids (228). Attack on ripening fruits by mirid buds causes a more or less linear decline in seed production as insect numbers increase (159). In a long-term experiment on the broom *Cytisus scoparius*, Waloff & Richards (215) excluded herbivorous insects over an 11-yr period. Fruit production of the sprayed bushes increased an average of 2.5 fold chiefly as a result of the exclusion of the aphid *Acyrthosiphonpisum sparti* and two psyllids of the genus *Arytaina*.

A considerable amount of work has been carried out on the guild of herbivorous insects that attack the flowerheads (capitula) of thistles and
knapweeds. These plants are natives of southern Europe, and a number of them have become serious weeds when introduced into continental or Mediterranean climates elsewhere. Research has been aimed at discovering potential agents for biological weed control. There have been some notable successes, such as the introduction of the weevil *Rhinocyllus conicus* into Canada from France in 1968 to control the nodding thistle, *Carduus nutans* (231). Note that while the insect was able to control *C. nutans* in Canada, where the plant is alien, the same insect does not reduce the recruitment of the thistle in its native southern France, despite its inflicting over 90% seed losses. In addition, after sowing 1000 thistle seeds per m² no increase was observed in the number of thistle rosettes. Recruitment in this case appears not to be seed limited, though whether it is microsite limited or regulated by postdispersal seed predation or early seedling mortality is not yet clear (A. Sheppard, personal communication).

Chewing caterpillars can take a heavy toll of the capitula of some Compositae. Perhaps the best known example is the cinnabar moth, *Tyria jacobaeae*, which frequently strips all of the flower heads from ragwort plants on which egg batches are laid. Late-instar larvae, dispersing from defoliated plants, can inflict up to 90% loss of flower heads on nearby plants that escaped the attentions of ovipositing females. As with *C. nutans*, however, sowing 1000 seeds per m² did not increase the rate of recruitment of ragwort rosettes (46). Even though the insects cause large reductions in fruit survival, they do not appear to reduce the population density of the plants, at least in mesic grasslands (44) or the Breckland heaths of East Anglia (53). These dynamics contrast with those of the same plant species in more arid, open habitats on coastal sand dunes, where recruitment of new rosettes is reduced following years of heavy defoliation by the cinnabar moth (211).

In contrast to the two studies of Compositae described above, sowing 1000 hogweed seeds per m² did lead to increased recruitment. Thus ray-feeding aphids may well have reduced the number of hogweed rosettes that became established in the following spring. Plots sown with extra seed in 1982 (196) were still supporting conspicuously higher plant densities in 1988 (M. J. Crawley, unpublished results).

Other effects of insect herbivory on plant reproduction include reductions in the numbers of seeds per fruit (118) and delays in the timing of fruit maturation (140, 210). Ant-attended plants lost 33% of their fruits to insect herbivores, with the loss rising to 66% when the ants were experimentally excluded (100).

Insect herbivory frequently leads to reduced seed size (46, 93, 208), with potential effects on seedling competitiveness (see below). Insect herbivores may also influence the evolution of seed size, both by exhibiting feeding preferences for seeds of particular sizes (143, 164) and by inflicting a higher
death rate on some sizes of seeds than on others. For example, the acorn weevil *Curculio glandium* kills a significantly greater proportion of small acorns than of larger acorns from the same tree (67).

Some insects cause such inconspicuous damage that assessment and attribution of seed losses is remarkably difficult. Heteroptera such as *Lygus* spp. can cause seed losses of more than 50% in umbelliferous vegetable crops such as carrot, celery, dill, fennel, parsley, and parsnip by killing the embryo without disturbing other parts of the seed (65).

Like flower losses, fruit losses appear more often to be inversely density dependent than directly density dependent. Thus, larger fruit crops suffer a lower loss rate than small ones (16, 152, 180, 200), presumably because insect abundance and fruit density are not closely coupled or are coupled with a substantial time lag. Inverse density dependence even occurs within multi-seeded fruits. The probability of death of an individual seed declines as the number of seeds per fruit increases (95) even though insects may show a preference for larger fruits (118, 141). Insect feeding may also increase the rate of abortion of partially filled fruits, though whether this causes a net reduction in the total seed crop is not clear (117, 203, 205).

Insect attack on fruits can reduce the attractiveness of fruits to seed dispersers (34, 138). As with so many other aspects of plant performance, however, no link has yet been established between reduced dispersal efficiency and reduced plant recruitment.

**Postdispersal Seed Mortality**

Detailed field studies on the fate of seeds have been published for umbellifers (93, 196, 208), oaks (67, 80, 148), thistles (210b, 211b, 231), crucifers (59, 134), leguminous trees (6, 106), desert annuals (48–50), and many other plants. Attention has been paid to the selection of seeds of different sizes (20, 221) and to the growth and competitive ability of seedlings from seeds of different sizes (28, 46, 143).

Of the insect groups, most attention has been paid to beetles and ants (chiefly the desert harvester ants) (20, 27, 48, 137, 160). These studies are notable for the fact that some attempt has been made to demonstrate the effects of seed removal on plant recruitment (2, 9, 27, 49, 97, 119, 155, 165, 178, 184, 229). Where exclusion experiments have been carried out in the field, it has typically been found that seed predation by vertebrates is more important than insect granivory in affecting plant population dynamics (42, 49, 50). In other cases, despite predator satiation, plant recruitment is limited by rare, pulsed conditions (often of rainfall) (219). The view that dispersal of seeds by ants can target the seeds to locally improved soil conditions around ant nests (185), although an attractive hypothesis, has received little support from critical field studies (9, 183).
Once buried, seeds become exceptionally difficult to study, and virtually no work has been carried out to determine the loss of seeds that can be attributed to soil-dwelling insect herbivores (186).

**Seedling Mortality**

Molluscan and vertebrate herbivores are traditionally regarded as the major seedling predators (36, 108), but several insect groups are important seedling feeders. These insects either kill the seedlings outright or seriously reduce their growth and competitive ability (153). Sawflies are pests of seedlings in gardens, but their role in natural vegetation is not clear. Mirid and pentatomid bugs can damage seedlings (76). Psyllids reduced the growth rate of *Ceanothus* seedlings in California, impairing their competitiveness with *Adenostoma* seedlings. In this case, exclusion of small mammals had a greater effect on seedling performance than insect exclusion (154). Frit flies (*Oscinella spp.*) are severe pests of spring-sown cereals and short-term grass leys, where the young larvae attack seedlings before the four-leaf stage. Attack later in the season, once the plant has tillered, is rarely lethal (108, 161). Repeated defoliation of seedlings of *Quercus robur* by lepidopteran caterpillars spinning down from mature trees overhead may be one of the main factors preventing recruitment of oaks beneath the canopy of parent trees (195). However, vertebrate herbivores such as sheep and rabbits are usually more likely to prevent regeneration of oaks from seed (41, 173, 181).

Failure of buried seed to produce an emergent seedling is usually attributed to germination failure, simply as a matter of convenience. How many of these losses result from attack by soil insects on very young seedlings, prior to their emergence above soil level, is unknown. Large-scale, frequent, and destructive sampling would be required to answer this question.

**Defoliation**

The rates of defoliation attributable to insect herbivores are traditionally considered to lie within the range of 5-10% of leaf area per year (15, 37, 79, 139). Average rates of defoliation may be higher in certain Australian eucalyptus forests (average about 15%), and within Australia defoliation rates increase with altitude (73). Critics have argued, however, that these percentages represent a serious underestimate of defoliation rates (135, 166) because they fail to account for leaf turnover during the growing season (i.e. for the appearance and disappearance of leaves between one sampling period and the next). It is certainly true that far too many estimates of defoliation have been based on a single sample of leaves, taken toward the end of the growing period once insect feeding was assumed to have ceased. Such studies have provided no estimates of the numbers of leaves that were consumed completely, leaving no trace, or of the effect of partial damage on the rate of
premature abscission of leaves. In a detailed study of herbivory and leaf turnover in water lilies, for example, it was discovered that feeding by adult and larval *Pyrrhalta* beetles reduced average leaf longevity from 45 to 17 days. This degree of leaf turnover would have led to severe underestimation of primary production had a simple method such as the use of peak leaf standing crop been employed (214).

Studies involving careful, frequent measurements on large samples of individually marked leaves have been rare. In work on cohorts of individually marked birch leaves (*Betula pendula*), Zakaria (230) measured every leaf every day and found that 11% of leaves produced from April to mid July fell prematurely or were consumed entirely, so that no trace of their existence remained by the date that a single damage sample would have been taken. Between mid July and August a further 6% were lost. Premature losses of leaves varied from tree to tree between 0 and 35%. Of the total annual leaf production, 13–35% of leaves were produced after the first spring flush was complete and would not have been detected if a single cohort of leaves had been tagged in spring.

Other studies have discovered even higher rates of within-season leaf loss, and it is clear that considerable care must be exercised to ensure that leaf turnover rates are known. For example, a number of studies on evergreen and semievergreen trees have shown that attack by herbivorous insects (notably by leafminers) can cause a substantial rise in the rate of premature leaf fall (24, 111, 176, 224). Attack by leaf-mining weevils causing premature leaf fall over successive years may eventually kill the host tree (102).

Refoliation following leaf loss to herbivorous insects is commonplace, especially in woody angiosperms (90, 91). It is important, therefore, in studies of leaf loss that these regrowth leaves be distinguished from primary leaves. Not only might failure to distinguish the classes of leaves lead to underestimates of leaf consumption, but since insect performance is often different on diets of regrowth and primary foliage (45, 88, 223), it might also lead to confusion over the cause of differences between the survival and fecundity of early and late insect cohorts.

**Growth and Reproduction**

Plant growth rate, plant shape, and the allocation of resources to seed production are all influenced to a greater or lesser extent by insect herbivory. Even relatively low levels of insect herbivory can, if sustained, have a significant effect on the growth of young trees [e.g. *Acer pseudoplatanus* (218)]. Chronic levels of insect herbivory modified both plant shape and sex expression in pinon pine, *Pinus edulis* (222). In some cases, insect herbivores reduce growth without causing any reduction in sexual reproduction. For example, Karban (113) found that the cicada *Magicicada septendecim* caused
a 30% reduction in ring width in *Quercus ilicifolia* oak wood without causing any reduction in acorn production. In other work on *Q. robur* (37), however, exclusion of insects using insecticides had no effect on ring width, but caused a marked increase in acorn production. Clearly there have been too few studies to allow any generalizations about the order in which different components of plant performance are impaired under attack by insect herbivores.

While insect attack is often the cause of reduced plant growth rate (91, 112), the rate of plant growth may itself influence both the probability and the consequences of insect attack (60, 120, 204, 217). For instance, stressed plants may be more susceptible to insect herbivory (see section on competitive ability, below). Similarly, individual plants that have slow growth rates by reason of their age (204) or the soil conditions in their particular microhabitat (125) might be more prone to insect attack or may suffer greater loss of performance with each individual insect they support.

The effect of insect feeding on plant performance is typically described by plotting a damage function. This is a graph of plant growth or seed production against insect population density. The shape of the damage function provides information on the nature and extent of plant compensation (36). Most insect-plant relationships are adequately described by simple, linear damage functions (7, 169). A smaller number are better described by curvilinear functions, which suggest plant compensation for low levels of insect feeding (18, 156, 159). Some studies have distinguished explicitly between effects on primary growth and on the extent of regrowth following defoliation (45, 93, 105, 157). Some insect species perform better on a diet of regrowth foliage (87, 177, 223), while other species perform less well (71, 126).

The current controversy as to whether and under what circumstances herbivory could ever benefit individual plants (8, 39, 146) rests largely on semantic issues. While there have been a few reports of increased plant performance following insect herbivory (i.e. a humped damage function) (17, 147, 168), I have found no detailed experimental study that has reported greater recruitment from plants attacked by insect herbivores than from unattacked control plants growing under the same competitive circumstances. One study currently in progress aims to test whether attack by the weevil *Curculio glandium* increases the fitness of *Q. robur*. Weevil attack causes death of the acorn in about 90% of cases. Intact acorns, however, suffer almost 100% predation from various vertebrate herbivores including rabbits, mice, squirrels, jays, and wood pigeons. Most of these animals reject weevily acorns, so the probability of an acorn producing a seedling might be higher for a weeviled than for an unweeviled acorn (67).

Clearly, the potential for regrowth and compensation depends critically upon the timing of insect attack (114, 156, 202). In general, the earlier the attack, the greater the possibility for regrowth. For example, an identical 3%
loss of final cabbage yield was caused by 25% defoliation early in the growing season and by as little as 5% defoliation at the time of heading (227). Late-season attack leaves no time for regrowth and may also cause grazed plants to enter the unfavorable season in a more vulnerable condition (e.g. more likely to succumb to frost or drought) (85).

A certain amount of insect damage inevitably escapes recognition because of its obscure effects and the small size of the individual animals. In such cases losses are wrongly attributed to other factors such as drought, fungi, frost, or deficiencies in soil nutrients that produce similar, nondistinctive symptoms. These misattributions of damage are especially likely when small sucking insects such as froghoppers and aphids attack plants such as grasses that are not usually thought to suffer severe invertebrate herbivory (25). In fact, insect herbivory may be profoundly important in the population dynamics of grasses (29, 30, 92).

**Competitive Ability**

Indirect effects of feeding by insect herbivores, leading to reduced plant vigor and impaired competitive ability, are thought to be paramount in affecting plant population dynamics, especially by practitioners of biological weed control (78, 85, 193, 216). Defoliating insects, phloem-feeding aphids, whitefly or scale insects, various sap-feeding Heteroptera, and stem-boring flies, moths, and beetles have all been charged with reducing the vigor of their host plants sufficiently that the plants were unable to compete with more vigorous, unattacked, neighboring plants (references below). Few critical manipulative experiments have been carried out on this important topic (32, 33), however, and it is easy to overlook other, less obvious factors that might be the direct cause of the plants’ decline. For instance, there have been numerous reports of proliferation of insect herbivores on plants stressed by air pollution (58, 66), drought (11, 35, 122, 130, 220), soil acidity or impeded drainage (13, 125, 134), shade (131, 136), soil nutrient deficiency (123, 192), resistant plant genotypes (127), previous defoliation (71, 84, 126, 170, 177, 187, 194), or previous low plant growth rate due to intense plant competition (60, 120, 204, 217). It is not clear to what extent, if any, the insect attack exacerbated the loss in vigor that the plants would have suffered in any case. Recent field studies using controlled release of air pollutants (SO₂) have, however, pointed to extra yield losses attributable to enhanced feeding by cereal and conifer aphids (66).

Several reports have suggested that differential rates of insect attack can relax or even reverse the competitive relationships between plant species in natural communities (69, 128, 175, 179, 226). For example, the grass aphid *Holcaphis holci* reduced the rate of tillering of its host plant *Holcus mollis*, and this reduction led to increases in the abundance of the low-growing herb
*Galium saxatile* in years when (or in places where) the aphid was abundant. In low-aphid years, the grass advanced at the expense of the herb (J. Packham, personal communication). Defoliation by insect herbivores reduced the competitive ability of certain shrubs in the Chilean matorral, effectively excluding them from plant communities (75). Defoliation by the chrysomelid beetle *Gastrophysa viridula* altered the outcome of competition between *Rumex crispus* and *Rumex obtusifolius* (10, 33).

These effects are by no means universal, and insect exclusion has been shown to have no measurable effect on interspecific plant competition in a number of studies where broad-spectrum insecticides have been applied to seminatural plant communities (see Table 4). Analysis of insecticide application experiments is necessarily rather crude, given the number of plant species present and the variety and trophic positions of insects excluded. Thus it is possible that there are responses in plant growth to reduced insect feeding, but they cancel one another out. This topic is discussed in more detail below.

### Death Rate of Established Plants

It is unusual for insect herbivores to cause the death of established perennial plants. Increased mortality has resulted from bark beetle attacks on mature coniferous trees (12, 188), attack by spruce budworm on balsam fir, *Abies balsamea* (14), and attack by gypsy moths on deciduous hardwood trees (201). In the last case, plant death rates are little affected unless individual trees suffer more than 50% defoliation for three or more consecutive years (90). Most deciduous hardwoods have substantial powers of regrowth following complete defoliation, and several species can withstand repeated defoliation even within the same growing season (e.g. *Q. robur*) (43).

Increased plant death rates as a result of insect herbivory have led to successful biocontrol of the ragwort *Senecio jacobaea* by the cinnabar moth, *T. jacobaeae*, in eastern Canada (86). Plants that have been severely defoliated by cinnabar moths are killed by the characteristically early frosts in this part of Canada. In other regions frosts occur later in the autumn, and ragwort regrowth appears after cinnabar moths have pupated. Plants that have been allowed more protracted regrowth prior to the first frosts do not suffer significantly higher death rates than undefoliated plants, and weed control is much less successful. When levels of plant competition experienced by the arid-land shrub *Gutierrezia microcephala* were reduced experimentally by removing neighboring individuals, the death rate of plants decreased from 47 to 22% on plots exposed to intense herbivory by the grasshopper *Hesperotettix viridis*. Ungrazed plants, protected with cages, showed no response to reduced competition; their death rate was 8% whether or not their neighbors were removed (172).
EFFECTS ON PLANT POPULATION DYNAMICS

Despite the mass of evidence on the effects of herbivorous insects on plant performance, there is woefully little data on the effects of insect herbivory on plant population dynamics. Without a knowledge of the key factors acting at each stage in the plant's life cycle and which (if any) of these factors act in a density-dependent manner, it is impossible to predict how insect feeding will affect plant abundance.

Evidence From Biological Weed Control

Releases of imported insects for the biological control of weeds represent some of the most impressive, large-scale ecological field experiments that have ever been carried out. Even though these attempts were not planned as experiments and tend to be neither replicated nor randomized (38, 40), it is important that we use the information they provide on insect-plant interactions to the full. The material presented in this section was assembled as part of the Silwood Project on the Biological Control of Weeds (see acknowledgments), which augmented Julien’s catalog (110) of published weed-biocontrol results with firsthand, unpublished accounts. One aim of this work was to document control attempts that failed, either because the agent failed to establish or because, having established successfully, it failed to make any impact on the abundance of the target weed (78, 85, 193, 216).

INSECT TAXONOMY

The most frequently repeated successes in biological control are listed in Table 1, and the most successful individual cases are given in Table 2. It is difficult to generalize about the taxonomy of the insects involved. The Opuntia cacti, for example, have been controlled by species as different as a relatively large, chewing insect, Cactoblastis cactorum, and a tiny sucking species, the cochineal insect Dactylopius ceylonicus. Cochineal insects have been responsible for successful control much more frequently than moths (8:3 in Table 1; 7:1 in Table 2). Cochineal insects might even have been effective in the classic textbook example of cactus control in Queensland, Australia, had C. cactorum not been introduced before D. ceylonicus became firmly established. Out of the top 11 weed control cases, seven involved leaf or cladode suckers, three involved leaf-chewing insects, and only one involved a seed head–feeding insect (Rhinocyllus conicus). Leafminers, stem borers, and root feeders are not represented among these most successful cases (Table 2).

On host plants other than Opuntia and Lantana species, the insect group responsible for the largest number of conspicuous successes is the beetles. Weevils have controlled plants as different as the aquatic fern Salvinia molesta, the waterweed Eichhornia crassipes, and terrestrial weeds such as
Table 1  The most frequently repeated successes of biological weed control up to 1980*

<table>
<thead>
<tr>
<th>Rank</th>
<th>Plant</th>
<th>Insect</th>
<th>S</th>
<th>E</th>
<th>R</th>
<th>%S</th>
<th>%E</th>
<th>Insect life history</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Lantana camara</td>
<td>Teleonemia scrupulosa</td>
<td>9</td>
<td>26</td>
<td>29</td>
<td>31</td>
<td>90</td>
<td>Leaf feeding tingid</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Uroplopa girardi</td>
<td>5</td>
<td>11</td>
<td>17</td>
<td>29</td>
<td>65</td>
<td>Chrysomelid beetle</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hypena strigata</td>
<td>3</td>
<td>6</td>
<td>7</td>
<td>43</td>
<td>86</td>
<td>Noctuid moth</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Three others</td>
<td>4</td>
<td>14</td>
<td>24</td>
<td>17</td>
<td>58</td>
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</tr>
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<td>Hypericum perforatum</td>
<td>Chrysolina quadrigemina</td>
<td>4</td>
<td>7</td>
<td>8</td>
<td>50</td>
<td>88</td>
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<td></td>
<td></td>
<td>Chrysolina hyperici</td>
<td>3</td>
<td>6</td>
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<td>30</td>
<td>60</td>
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<tr>
<td></td>
<td></td>
<td>Zeuxidioplasis giardi</td>
<td>2</td>
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<td>33</td>
<td>83</td>
<td>Cecidomyiid midge</td>
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<tr>
<td></td>
<td></td>
<td>Three others</td>
<td>5</td>
<td>6</td>
<td>10</td>
<td>50</td>
<td>60</td>
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</tr>
<tr>
<td>3</td>
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<td>Neocheineae eichhorniae</td>
<td>5</td>
<td>6</td>
<td>10</td>
<td>50</td>
<td>60</td>
<td>Pyralid moth</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sameodes albigenalis</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>40</td>
<td>60</td>
<td>Pyralid moth</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Neocheineae bruchi</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>33</td>
<td>66</td>
<td>Curculionid beetle</td>
</tr>
<tr>
<td>4</td>
<td>Opuntia vulgaris</td>
<td>Dactylisopius ceylonicus</td>
<td>6</td>
<td>7</td>
<td>9</td>
<td>66</td>
<td>78</td>
<td>Cochineal insect</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cactoblastis cactorum</td>
<td>1</td>
<td>20</td>
<td>22</td>
<td>5</td>
<td>91</td>
<td>Pyralid moth</td>
</tr>
<tr>
<td>5</td>
<td>Cordia macrostachya</td>
<td>Metrogaleruca obscura</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>100</td>
<td>100</td>
<td>Chrysomelid beetle</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Eurytoma attiva</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>66</td>
<td>100</td>
<td>Eurytomid wasp</td>
</tr>
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<td>6</td>
<td>Centaurea diffusa</td>
<td>Urophora affinis</td>
<td>4</td>
<td>6</td>
<td>6</td>
<td>66</td>
<td>100</td>
<td>Tephritid fly</td>
</tr>
<tr>
<td>7</td>
<td>Opuntia dillenii</td>
<td>Dactylisopius opuntiae</td>
<td>2</td>
<td>16</td>
<td>23</td>
<td>9</td>
<td>70</td>
<td>Cochineal insect</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cactoblastis cactorum</td>
<td>2</td>
<td>20</td>
<td>22</td>
<td>9</td>
<td>91</td>
<td>Pyralid moth</td>
</tr>
<tr>
<td>8</td>
<td>Alternanthera phloxoides</td>
<td>Agasicles hygrophiens</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>100</td>
<td>100</td>
<td>Chrysomelid beetle</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vogtia malloia</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>100</td>
<td>100</td>
<td>Pyralid moth</td>
</tr>
<tr>
<td>9</td>
<td>Tribulus cistoides</td>
<td>Microlarinus lypriformis</td>
<td>3</td>
<td>10</td>
<td>10</td>
<td>30</td>
<td>100</td>
<td>Curculionid beetle</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Microlarinus lareynii</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>20</td>
<td>60</td>
<td>Curculionid beetle</td>
</tr>
<tr>
<td>10</td>
<td>Linaria vulgaris</td>
<td>Gymnaetron antirrhini</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>66</td>
<td>100</td>
<td>Curculionid beetle</td>
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<tr>
<td></td>
<td></td>
<td>Brachypterolus pulicarius</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>50</td>
<td>100</td>
<td>Curculionid beetle</td>
</tr>
</tbody>
</table>

*From Reference 110 and the Silwood Project on Weed Biocontrol.

bS = Number of releases leading to successful control.

E = Number of releases leading to established insect populations.

R = Total number of releases up to 1980.

%S = Percentage of releases leading to successful control.

%E = Percentage of releases leading to established insect populations.
Table 2 The most successful individual biocontrol releases, ranked by the degree of control, the area over which control was obtained, and the initial severity of the weed infestation*

<table>
<thead>
<tr>
<th>Rank</th>
<th>Plant</th>
<th>Insect</th>
<th>Location, year</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Opuntia vulgaris</td>
<td>Dactylopius ceylonicus</td>
<td>India, 1795</td>
</tr>
<tr>
<td>2</td>
<td>O. vulgaris</td>
<td>D. ceylonicus</td>
<td>Sri Lanka, 1795</td>
</tr>
<tr>
<td>3</td>
<td>Opuntia dillenii</td>
<td>Dactylopius opuntiae</td>
<td>India, 1926</td>
</tr>
<tr>
<td>4</td>
<td>Carduus nutans</td>
<td>Rhinocyllus conicus</td>
<td>Canada, 1968</td>
</tr>
<tr>
<td>5</td>
<td>Hypericum perforatum</td>
<td>Chrysolina quadrigemina</td>
<td>USA, 1946</td>
</tr>
<tr>
<td>6</td>
<td>O. vulgaris</td>
<td>D. ceylonicus</td>
<td>South Africa, 1913</td>
</tr>
<tr>
<td>7</td>
<td>Opuntia elatior</td>
<td>D. opuntiae</td>
<td>Indonesia, 1935</td>
</tr>
<tr>
<td>8</td>
<td>Opuntia sp.</td>
<td>D. opuntiae</td>
<td>Madagascar, 1923</td>
</tr>
<tr>
<td>9</td>
<td>Opuntia tuna</td>
<td>D. opuntiae</td>
<td>Madagascar, 1928</td>
</tr>
<tr>
<td>10</td>
<td>Opuntia triacantha</td>
<td>Cactoblastis cactorum</td>
<td>Nevis, West Indies, 1957</td>
</tr>
<tr>
<td>11</td>
<td>Salvinia molesta</td>
<td>Cyrtobagous salviniae</td>
<td>Australia &amp; New Guinea, 1980</td>
</tr>
</tbody>
</table>

*Maximum scores represent complete control of weeds that had previously formed impenetrable monocultures over large areas. Low scores represent local or patchy control of weeds that had low cover prior to release of the control agent. All the insect species in the table were recorded as having brought about “complete” control of the weed in question. Changing the definition of “successful control” alters the ranking slightly but does not have a marked effect on the weed species included as having been controlled.

the spiny-fruited Tribulus terrestris and the thistle C. nutans. Chrysomelids have controlled Hypericum perforatum, Alternanthera philoxeroides, and Cordia macrostachya (Table 1). Other insect groups previously thought to have little or no potential in weed biocontrol have produced some spectacular results in recent introductions. For example, the pteromalid gall wasp Trichilogaster acaciaelongifolii was introduced into South Africa from Australia in an attempt to control the invasive Australian tree Acacia longifolia. The insects were considered so sensitive and delicate on first release that doubts were raised about whether they could even be successfully established. Since 1982, however, they have increased to such densities that tree branches are now weighed down by galls, and seed production has been reduced by over 95% (55).

Taxonomic mistakes have an interesting history in weed biocontrol. A number of failures in cactus control have been attributed to failure in identification of the host plant that resulted in the collection and release of insects from the wrong native strain. Ironically, other cases have led to successful control, apparently because of the small degree of taxonomic mismatching. Hokkanen & Pimentel (99) suggested that successful control would be more likely if the insect were not too closely adapted to the host plant, basing their argument on the notion that prolonged coevolution leads to
Table 3 Most frequently repeated failures of biological weed control (zero success rate)

<table>
<thead>
<tr>
<th>Rank</th>
<th>Plant Insect</th>
<th>E</th>
<th>R</th>
<th>%E</th>
<th>Plant life history</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Lantana camara</em></td>
<td>1</td>
<td>11</td>
<td>9</td>
<td>Verbenaceae: perennial, straggling shrub with prickly stems, spread by seed, but regrows vigorously after cutting</td>
</tr>
<tr>
<td></td>
<td><em>Diastema tigris</em></td>
<td>4</td>
<td>11</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Leptobyrsa decora</em></td>
<td>13</td>
<td>20</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ophiomyia lantanae</em></td>
<td>0</td>
<td>5</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Teleonemia elata</em></td>
<td>17 others</td>
<td>34</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Hypericum perforatum</em></td>
<td>2</td>
<td>7</td>
<td>29</td>
<td>Hypericeaeae: protocryptophyte, hemicryptophyte, perennial</td>
</tr>
<tr>
<td></td>
<td><em>Agrilus hyperici</em></td>
<td>0</td>
<td>3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Chrysolina varians</em></td>
<td>2</td>
<td>5</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4 others</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td><em>Salvinia molesta</em></td>
<td>1</td>
<td>5</td>
<td>20</td>
<td>Polypodiaceae: annual or perennial floating fern, spread by fragmentation</td>
</tr>
<tr>
<td></td>
<td><em>Cyrtobagous singularis</em></td>
<td>7</td>
<td>10</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Paulinia acuminata</em></td>
<td>1</td>
<td>3</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Samea multiplicalis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td><em>Cirsium arvense</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>Compositae: geophyte with root buds, rhizomatous perennial spread by seed and by rootstock fragments</td>
</tr>
<tr>
<td></td>
<td><em>Altica carduorum</em></td>
<td>2</td>
<td>5</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Urophora cardui</em></td>
<td>2</td>
<td>2</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ceutorhynchus litura</em></td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lema cyanella</em></td>
<td>27</td>
<td>42</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td><em>Opuntia littoralis</em></td>
<td>3</td>
<td>6</td>
<td>50</td>
<td>Cactaceae: spread by seed and cladodes</td>
</tr>
<tr>
<td></td>
<td><em>Chelinidea vittiger</em></td>
<td>0</td>
<td>9</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Meligita prodenialis</em></td>
<td>27</td>
<td>42</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4 others</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td><em>Cyperus rotundus</em></td>
<td>1</td>
<td>7</td>
<td>14</td>
<td>Cyperaceae: rhizomatous perennial spread by seed and tubers from rootstock</td>
</tr>
<tr>
<td></td>
<td><em>Athesapeuta cyperi</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bactra minima</em></td>
<td>2</td>
<td>5</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bactra venosana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td><em>Opuntia ficus-indica</em></td>
<td>4</td>
<td>4</td>
<td>100</td>
<td>Cactaceae: spread by seed and cladodes</td>
</tr>
<tr>
<td></td>
<td><em>Archlagocheirus funestus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Meligita dodalis</em></td>
<td>0</td>
<td>3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Meligita prodenialis</em></td>
<td>0</td>
<td>9</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 others</td>
<td>6</td>
<td>8</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td><em>Chromolaena odorata</em></td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>Compositae: short-lived, scrambling perennial spread by seed</td>
</tr>
<tr>
<td></td>
<td><em>Apion brunneonigrum</em></td>
<td>1</td>
<td>6</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pareuchaete pseudoinsulata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td><em>Senecio jacobaea</em></td>
<td>4</td>
<td>9</td>
<td>44</td>
<td>Compositae: biennial or perennial, rosette-forming hemicryptophyte spread by seed and root fragments</td>
</tr>
<tr>
<td></td>
<td><em>Tyria jacobaeae</em></td>
<td>2</td>
<td>4</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Hylemyia seneciella</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Longitarsus jacobaeae</em></td>
<td>3</td>
<td>3</td>
<td>100</td>
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### Table 3 (Continued)

<table>
<thead>
<tr>
<th>Rank</th>
<th>Plant</th>
<th>Insect</th>
<th>E&lt;sup&gt;a&lt;/sup&gt;</th>
<th>R&lt;sup&gt;b&lt;/sup&gt;</th>
<th>%E&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Plant life history</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Euphorbia × pseudovirgata</td>
<td>Chamaesphecia tenthrediniformis</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>Euphorbiaceae: rhizomatous perennial protohemicryptophyte</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hyles euphorbiae</td>
<td>3</td>
<td>4</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oberea erythrocephala</td>
<td>2</td>
<td>2</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chamaesphecia empiformis</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>E = Number of releases leading to establishment.  
<sup>b</sup>R = Number of release attempts.  
<sup>c</sup>%E = Percentage of releases leading to establishment.  

---

reduced virulence. Although this argument has been refuted by ecologists working with animal parasites [who point out that natural selection can lead to increases or decreases in virulence, depending upon the precise circumstances (38)], little work has been carried out with plants. A striking counterexample to Hokkanen & Pimentel’s hypothesis is provided by the successful control of *Salvinia molesta*. At first both the fern and the insect were misidentified, and attempts at weed control brought little success (Table 3). Once the plant had been correctly identified, however, insect collection was carried out in its correct native range, and in due course weevils were collected that brought about spectacularly successful control of the weed in both Australia and Papua New Guinea. It later transpired that the successful insect was not the species it was thought to be, but a local endemic, new to science (207). Here, a level of control that had proved impossible with the more distantly related form was achieved using the more closely adapted species.

The most frequently repeated failures of biological weed control (Table 3) fall into two clear categories. The first two plants also top the list of repeated successes (Table 1); they are weeds whose control is possible but relatively unpredictable (and in the case of *Lantana camara*, control often involves several insect species), so that there have been many attempts, and many of these have led to failure. In the second category are plant species that for one reason or another are more difficult to control. All of the cases listed in Table 3 had success ratings of zero, either through failure of the insect to establish or because the established population had no impact on weed abundance. The table may tell us more about the optimism of biocontrol workers than about the ecology of the insect herbivores employed.

### PLANT TAXONOMY

Given that most targets for biocontrol are nonnatives, it might be expected that the taxonomy of target weeds would reflect the
invasive tendencies of different plant families (40). Some families, such as Compositae, are abundant in both native and alien floras and are not significantly overrepresented as aliens. Some families produce proportionately more invasive aliens than others (e.g. Labiatae, Cruciferae, and Caryophyllaceae). Some families are significantly underrepresented as aliens (e.g. Cyperaceae, Ericaceae, Orchidaceae, Juncaceae, and Polypodiaceae). Interestingly, biocontrol is rarely targeted against weeds from the overrepresented families of aliens, perhaps because so many of their species are annuals and therefore tend to be less serious weeds. In addition, annual plants may be less likely to succumb to biocontrol using insect herbivores (78, 84).

Leaving aside the Opuntia cacti and Lantana camera (which together account for over 40% of all weed biocontrol releases), most biocontrol projects have been targeted against weeds from Compositae (e.g. Centaurea, Carduus, Senecio, Eupatorium, and Chromolaena species). All the plants controlled successfully were perennials, and most were weeds of open habitats such as badly managed, semiarid pasturelands where there was little competition from native perennials. Another open habitat in which conspicuous success was achieved using insect biocontrol was lentic freshwater, where plants such as alligator weed (A. philoxeroides), water hyacinth (E. crassipes), and floating fern (S. molesta) have been dramatically reduced in abundance.

Repeated attempts to control weeds from certain plant families have led only to repeated failures (Table 3). Despite numerous attempts using a variety of insect species, nutsedge (Cyperus rotundus) and creeping thistle (Cirsium arvense) have never been successfully controlled, even though many of the insects have successfully established quite large populations. Indeed, the weevil Apion ulicis, introduced to control gorse (Ulex europaeus) in New Zealand, has become one of that country’s most abundant insects, frequently destroying over 90% of the seed crop (96). It fails as a control agent partly because gorse has such a large and long-lived seed bank and partly because the weevil has no deleterious effect on the growth or survival of the parent plant. In other cases, control agents have become established, but remain scarce as a result of attack by generalist natural enemies, inclement weather, disturbance, and other disasters (19). Insects that feed on the outside of plants are especially vulnerable to predation of their eggs by ants, and this is a frequent cause of failure of biocontrol releases in tropical environments (38).

The difficulty experienced in controlling certain pasture weeds (e.g. Euphorbia × pseudovirgata) may result partly from their low quality as food for insects and partly from their production of copious latex, which might limit the intrinsic rate of increase of herbivorous insects to such low levels that no depression in weed abundance is achieved (see above). Food quality had a key
role in the successful control of the water fern *S. molesta* by the weevil *Cyrtobagous salviniae*. Unless nitrogen fertilizer was applied to plants in the initial release cages, the population of beetles did not build up rapidly enough to reduce the abundance of the fern. Insect population growth following fertilization of the plants was spectacular and brought about complete control of the plants over an area much larger than that to which fertilizer was initially applied (189).

**INSECT DEMOGRAPHY** The demographic attributes of successful biocontrol agents have been reviewed elsewhere (38, 40). Small insect body size and high intrinsic rate of increase are associated with both an increased probability of establishment following release and an increased likelihood of significant weed control following successful establishment. Certain traits that were thought to be of possible importance to successful control, such as lack of obligatory diapause and high powers of dispersal, proved not to be of general significance.

In natural communities, large, mobile polyphagous insect herbivores tend to have more impact on plant dynamics than small, sedentary specialist species because the former insects are maintained at higher population densities by the abundance of less preferred, relatively low-quality food plants. Thus these insects tend to affect the population dynamics of less common plants of relatively high palatability, which may be driven locally to extinction (36). Specialist insects, especially sucking species like aphids, can have important effects on community dynamics, not directly by eating their preferred species to extinction, but by reducing the competitive ability of grazed plants relative to their herbivore-free neighbors.

**PLANT LIFE HISTORY** Certain plants appear to be particularly difficult to control using insect herbivores (Table 3). Traits associated with this resistance include (*a*) a long growing period (especially a protracted growing period after a univoltine insect has entered its dormant or nonfeeding stage); (*b*) reserves of carbohydrates and proteins that are inaccessible to the herbivore (as in species with thick underground rhizomes or tough, woody stems); (*c*) high powers of regrowth following defoliation or stem destruction (i.e. growth that is not meristem limited); (*d*) ability to produce replacement crops of fruit following defloration; (*e*) low food quality (e.g. low tissue nitrogen concentration or high tannin content); and (*f*) large seed banks and protracted dormancy.

The duration of the period between insect release and achievement of successful biocontrol differs among plants with different life histories. Weeds of arid lands that are long-lived, achieve large adult size, spread mainly by
vegetative means, possess high powers of regrowth, and represent low-quality food for insects have frequently been controlled, but the insects tend to spread slowly following release. In contrast, successful control of smaller, short-lived perennial weeds of temperate habitats tends to occur more rapidly, with the insects spreading quickly following release. This second group of plants tends to reproduce by seed, to have lower powers of regrowth, and to represent higher-quality food for insects (containing higher tissue nitrogen concentrations and lower concentrations of quantitative defensive chemicals such as tannins and lignin) (38).

CAVEATS Weed biocontrol projects have provided some of the best field data on plant-herbivore dynamics. Releases are carried out on a spatial scale that could never be managed in experiments by individual ecologists. Unfortunately, what biocontrol projects gain in scale, they often lose in rigor. Very few releases are either replicated or randomized. Sometimes releases are made with minimal prerelease study and virtually no postrelease follow-up. Again, the data base is dominated by repeated attempts to control particular plant species: (a) weeds that have been successfully controlled elsewhere in the past (e.g. Opuntia and Lantana species), and (b) weeds that are unsuitable for control by other means (e.g. plants infesting marginal grazing land where cost precludes any other means of control). This taxonomic bias can be seen from the fact that of 627 documented cases up to 1980, 152 involved Lantana camara 117 involved various Opuntia species. Current biocontrol practice is aimed at improving the scientific value of these release experiments by developing protocols that will allow detailed prerelease and followup studies and, where possible, by setting up control plots in addition to replicated release sites, where weed dynamics can be monitored (J. K. Waage, personal communication).

An important question concerns the relevance of weed biocontrol data to an understanding of plant-herbivore dynamics in native vegetation. There are several concerns: (a) The weeds are generally alien plants growing in plant communities that are often quite different from those in which they evolved. (b) The insects are also alien, imported especially for the purposes of control. (c) The insects have been freed from their native natural enemies by careful screening prior to release. (d) The range of genetic variability in both plant and insect populations may be lower than in native communities as a result of the small size of the initial introductions. (e) The habitats in which biocontrol is practiced are often highly disturbed (e.g. overgrazed semiarid rangelands).

Evidence From Insecticide Exclusion Experiments

The best evidence for the impact of insect herbivory on plant population dynamics would come from experiments in which insects were removed from
large, replicated plots using minimally disruptive exclusion techniques (perhaps removal of the insects by hand) and in which the subsequent plant dynamics were compared with other plots that supported normal and enhanced densities of insects. Unfortunately, hand removal of insects is prohibitively labor intensive in most cases, and we must make do with the removal of insects using chemical insecticides or exclusion cages. Both of these techniques have potentially serious shortcomings (discussed below), but they represent better evidence on the importance of insect herbivory in plant dynamics than can ever be obtained from purely observational studies.

Studies in which insecticides have been applied to natural and seminatural vegetation with the object of measuring the impact of insect herbivory on plant distribution and abundance are listed in Table 4. Studies of insecticide application have not been included if the object was merely to measure the impact of insect feeding on plant performance (e.g. growth, seed yields, or survivorship of individual crop plants). The table shows an approximately equal number of cases in which insect feeding did and did not affect plant populations. However, negative results may well have been underrecorded, especially in the early years.

Cantlon's (26) demonstration of a dramatic increase in the abundance of the hemiparasitic woodland herb *Melampyrum lineare* following the eradication of the katydid *Atalanticus testaceous* using insecticides was for many years the only report suggesting that a native insect population might maintain a natural plant population at low density. It is unfortunate that Waloff & Richards (215) in their classic study on broom (see above) did not monitor the recruitment of young plants on the sprayed and unsprayed plots; instead, seedlings were pulled up to maintain the original plant density. Insect exclusion did, however, significantly increase the longevity of the plants and dramatically increase their fecundity. Studies on the exclusion of insects (mainly flies of the genus *Oscinella*) from grasslands have shown that by reducing the vigor of the pasture grasses on which they feed, the flies allowed the ingress of less competitive, weedy species (30, 92). Thus the quality of sown pasture declined less rapidly when insects were excluded by insecticide application (29). Other studies have shown that varying the cutting frequency of sprayed grasslands can alter the importance of leaf- and planthoppers in reducing grass yields. Plots cut once lost 49% of their dry weight to insect feeding, while plots cut frequently to simulate close grazing lost only 4% (89). Insecticide application led to increases in grass dry weight yields for 12 of 14 cultivars tested by Byers & Jung (25). It is noteworthy that the grass species that produced the greatest yields on the insecticide-treated plots (*Festuca arundinacea* var. Fawn; 2.2 t/ha) ranked only eighth of 14 on the unsprayed plots. The species that ranked first on the unsprayed plots (*Poa pratensis* var. Kenblue) was ranked only fifth on the insecticide-treated plots.
Table 4  Experimental exclusion of insects from plant communities using insecticides

<table>
<thead>
<tr>
<th>Plant</th>
<th>Insect</th>
<th>Exclusion effects</th>
<th>Remarks</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>Wireworms</td>
<td>Y</td>
<td>Reduced weed densities</td>
<td>72</td>
</tr>
<tr>
<td><em>Melampyrum</em> sp.</td>
<td>Katydid</td>
<td>Y</td>
<td>Small scale</td>
<td>26</td>
</tr>
<tr>
<td><em>Convulvus</em> sp.</td>
<td>Various</td>
<td>N</td>
<td>Phytotoxic insecticide</td>
<td>197</td>
</tr>
<tr>
<td><em>Calluna vulgaris</em></td>
<td><em>Strophingia ericae</em></td>
<td>N</td>
<td>Exclusion during a psyllid population peak</td>
<td>98</td>
</tr>
<tr>
<td><em>Lolium perenne</em></td>
<td>Frit fly</td>
<td>Y</td>
<td>Increased competitiveness of dominant grass</td>
<td>30</td>
</tr>
<tr>
<td><em>Cytisus scoparius</em></td>
<td>Various</td>
<td>Y</td>
<td>Reduced plant mortality; recruitment not measured; not replicated</td>
<td>215</td>
</tr>
<tr>
<td>Forage grasses</td>
<td>Various</td>
<td>Y</td>
<td>Insects altered relative performance of 14 taxa</td>
<td>25</td>
</tr>
<tr>
<td><em>Abies balsamea</em></td>
<td>Spruce budworm</td>
<td>Y</td>
<td>Selective mortality</td>
<td>14</td>
</tr>
<tr>
<td><em>Raphanus</em> sp.</td>
<td>Various</td>
<td>Y</td>
<td>Not replicated</td>
<td>21</td>
</tr>
<tr>
<td><em>Haplopappus squarrosus</em></td>
<td>Flower and seed feeders</td>
<td>Y</td>
<td>Seed limited</td>
<td>132</td>
</tr>
<tr>
<td><em>Haplopappus venetus</em></td>
<td>Flower and seed feeders</td>
<td>N</td>
<td>Microsite limited</td>
<td>133</td>
</tr>
<tr>
<td><em>Ceanothus</em> sp., <em>Adenosoma</em> sp.</td>
<td>Various</td>
<td>N</td>
<td>Vertebrate herbivores affected seedling survival</td>
<td>153</td>
</tr>
<tr>
<td><em>Solidago canadensis</em></td>
<td>Three chrysomelids</td>
<td>Y</td>
<td>Maintenance of goldenrod dominance</td>
<td>144</td>
</tr>
<tr>
<td><em>Quercus robur</em></td>
<td>Various</td>
<td>N</td>
<td>More seed but not more seedlings</td>
<td>37</td>
</tr>
<tr>
<td>Annuals of secondary succession</td>
<td>Various</td>
<td>N</td>
<td>Matched experiment in Iowa and England</td>
<td>b</td>
</tr>
<tr>
<td>First year in US</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second year in US</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First year in UK</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second year in UK</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cardamine pratensis</em></td>
<td>Various</td>
<td>N</td>
<td>More seeds but not more seedlings</td>
<td>59</td>
</tr>
<tr>
<td><em>Heracleum sphondylium</em></td>
<td>Ray aphids</td>
<td>Y</td>
<td>Seed limited</td>
<td>196</td>
</tr>
<tr>
<td><em>Calluna vulgaris</em></td>
<td>Various</td>
<td>N</td>
<td>No effect until increase in flowering in third year</td>
<td>c</td>
</tr>
<tr>
<td><em>Holcus/Galium</em> sp.</td>
<td><em>Holcaphis holci</em></td>
<td>Y</td>
<td>Bedstraw declines on uninfested plots</td>
<td>d</td>
</tr>
<tr>
<td><em>Medicago lupulina</em></td>
<td>Weevils</td>
<td>Y</td>
<td>Only on sheep grazed plots</td>
<td>77</td>
</tr>
</tbody>
</table>
Table 4 (Continued)

<table>
<thead>
<tr>
<th>Plant</th>
<th>Insect</th>
<th>Exclusion effects</th>
<th>Remarks</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Vicia</em> spp.</td>
<td>Various</td>
<td>Y</td>
<td>Increased seedling densities</td>
<td>22</td>
</tr>
<tr>
<td><em>Trifolium pratense</em></td>
<td>Various</td>
<td>Y</td>
<td>Increased survivorship but no seedling recruitment</td>
<td>e</td>
</tr>
<tr>
<td><em>Senecio jacobaea</em></td>
<td>Cinnabar moth</td>
<td>N</td>
<td>Not seed limited</td>
<td>44</td>
</tr>
<tr>
<td>Grassland seed bank</td>
<td>Various</td>
<td>N</td>
<td>Pronounced effect of rabbit exclusion</td>
<td>42</td>
</tr>
<tr>
<td><em>Poa pratensis</em></td>
<td>Various</td>
<td>N</td>
<td>Build-up of thatch</td>
<td>5</td>
</tr>
</tbody>
</table>

*Y* denotes significant effects of insect exclusion on plant abundance. *N*, no significant effects on plant dynamics reported.

*S. Hendrix & V. K. Brown, personal communication.*

*V. C. Brown & S. McNeill, personal communication.*

*J. Packham, personal communication.*

*A. Gange, personal communication.*

Reanalysis of these data shows that there is no significant rank correlation between the yields of the treated and untreated plots (Spearman’s $r = 0.235; p >> 0.05$), which suggests that insect exclusion had a substantial effect in altering the relative performance of these grasses. The species were grown as monocultures, however, so these results cannot be interpreted as direct evidence of changes in interspecific competitive ability following insect exclusion.

After shrubs of *Haplopappus squarrosus* and *Haplopappus venetus* were sprayed with insecticide, seed production was increased in both species; plant recruitment, however, only increased in *H. squarrosus* (132). Evidently, recruitment was seed limited in *H. squarrosus* but not in *H. venetus*, so insect herbivory had no impact on the population dynamics of *H. venetus* despite its causing substantially reduced fecundity (133).

Some insecticide experiments have shown effects on plant abundance that subsequently turned out to be due to direct phytotoxic effects of the pesticide on the dominant species that allowed competitive release of previously suppressed plants (197). Subsequent workers have been more careful to choose chemicals that have no direct stimulatory or phytotoxic effects (references in Table 4). There are very few reports of stimulatory effects on plant growth, even with systemic organophosphorus insecticides, when insecticides are applied at recommended rates (109).

Long-term insecticide studies aimed at determining the effect of insect exclusion on plant recruitment have only been initiated recently, and few results have been published. Elsewhere (42) I have given details of a number of these studies in progress; here I simply report that exclusion of insects sometimes has no measurable effect on plant recruitment (e.g. in heather,
*Calluna vulgaris*, and in communities of arable weeds), sometimes modifies the competitive balance between different plant species (as when the grass aphid *H. holci* reduced the competitive ability of its host plant *H. mollis* and allowed an increase in the abundance of the herb *G. saxatile*), and occasionally has more pronounced effects on plant community dynamics (references in Table 4). In the few cases in which insect and vertebrate herbivores have been excluded singly and in combination, the vertebrate herbivores have always proved to have the greater impact on plant dynamics (41, 77, 153).

**CAVEATS** There are several potential pitfalls in insecticide application experiments: (a) The chemical may be phytotoxic, perhaps differentially so, giving the erroneous impression of competitor release following insect exclusion. (b) The chemical may have some stimulatory effect on plant growth, either through hormonal action or fertilizer effects. (c) The chemical may actually increase the abundance of herbivorous insects if predatory insects suffer differentially high rates of mortality under insecticide treatment (4, 5). (d) The chemical may deter herbivorous animals other than insects (e.g. mollusks or small mammals) so that responses in plant abundance cannot be attributed directly to a reduction in insect herbivory. (e) The effects on the soil fauna and microflora are generally unknown (e.g. the chemical may kill mycorrhiza-feeding insects, thereby increasing the efficiency of mineral uptake). (f) Because the hypothesis being tested is that insect herbivores influence plant dynamics, responses due to these other processes might be attributed erroneously to insect herbivory.

Despite all these shortcomings, the technique holds tremendous potential for demonstrating the impact of insect feeding on plant population dynamics under field conditions. The more precisely the insecticide can be targeted to eliminate selected species of insects on particular species of plants (e.g. by applying the insecticide to individual leaves of the target plant species with a fine brush, with minimal disturbance to neighboring plants), the more intelligible the results will be. When all the plants in a community are sprayed, it is impossible to tease apart the direct negative effects of herbivory and the indirect negative effects of competitor release of a plant’s neighbors. Similarly, improved insecticide controls need to be employed to convince skeptics that the observed effects really are due to reduced insect herbivory rather than to one or more of the potential side effects listed above. For example, hand picking of insects from plants can provide a useful control when associated with insecticide-spray and blank-spray controls. Although the technique is extremely laborious, work on ragwort (44) and oak (43) has affirmed that hand picking gives results that are indistinguishable from those obtained using insecticide treatment. More such studies are required.
CONCLUSIONS

Insect herbivores can affect every aspect of plant performance, and there is a massive literature from pest control showing effects on plant growth, form, seed production, development rate, and survivorship. In contrast, there is an almost complete dearth of information on the role of insects in plant population dynamics.

Our knowledge of the effects of insect herbivores in natural vegetation is restricted to a small (but growing) number of studies using insecticidal exclusion in natural vegetation. These studies suggest that insects do influence plant population dynamics in some cases, but their effects are often subtle and are typically less pronounced than the effects of other kinds of herbivores [notably vertebrate herbivores (42)]. In several cases no effect on plant population dynamics has been observed despite substantial reductions in the numbers of herbivorous insects feeding on the plants (Table 4).

The different kinds of insect herbivory affect plant population dynamics in different ways. For example, postdispersal seed-feeding insects like ants can reduce plant recruitment in years or in places where recruitment is seed limited (e.g. in deserts or semiarid open woodland). However, following mast crops of seed or in habitats where plant recruitment is microsite limited, seed-feeding insects typically have no effect on the numbers of plants that become established. Predispersal seed predators have been used with considerable success in biological weed control (e.g. the weevil *Rhinocyllus conicus* against nodding thistle *Carduus nutans*). They have also been shown to limit plant recruitment in some natural communities (132) but not in others (133). Certain foliage-feeding and bark-dwelling forest insects can cause the premature death of trees over large areas, with profound effects on forest succession (14, 210a). Other forest insects have no measurable effect on tree seedling recruitment, despite substantial effects on tree growth or seed production. Insect feeding is much more likely to increase the death rate of established plants when these plants are growing in dense stands and are subject to intense inter- or intraspecific competition. We know virtually nothing about the effect of root- and mycorrhiza-feeding insects. Sucking insects can reduce seed production, seed size, and seedling recruitment. Perhaps the most important effect of sucking insects is in reducing vegetative growth rate, and hence in reducing competitive ability. Since the majority of aphids and hoppers are highly specific in their choice of food plants, this kind of insect herbivory provides a possible mechanism for the maintenance of plant species richness, prohibiting competitive exclusion by selectively reducing the competitive ability of the dominant plant species.

While we know what kind of manipulative field experiments need to be
carried out to understand the effects of insect herbivory on plant population dynamics, there are only a handful of published studies that address this question directly. Many more studies are currently under way, but the number of habitats investigated and the replication of studies within given habitats need to be increased before we can begin to generalize about the importance of insect herbivores in the population dynamics of plants. On present evidence, it appears that insect herbivores have a measurable impact on plant abundance in about half the cases studied. In contrast, exclusion experiments have almost always suggested a significant role for vertebrate herbivory in plant dynamics. In short, it appears that plants have substantially more effect on herbivore population dynamics than insect herbivores have on plant population dynamics.

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