FACTORS AFFECTING THE DISTRIBUTION OF OLD FIELD AND WOODLAND ANNUAL PLANTS: PHYSIOLOGICAL TOLERANCE VS. LIFE HISTORY

By

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ABSTRACT

FACTORS AFFECTING THE DISTRIBUTION OF OLD FIELD AND WOODLAND ANNUAL PLANTS: PHYSIOLOGICAL TOLERANCE VS. LIFE HISTORY

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The relative importance of competition, physiological tolerances and life history characteristics in determining the distribution and abundance of ecologically distinct groups of summer-flowering annual plants was investigated experimentally for natural assemblages of old field and woodland annuals.

In a field experiment, interference from herbaceous vegetation was not responsible for preventing one old field annual (*Chenopodium album*), and one woodland annual (*Pilea pumila*) from establishing in the other's habitat. Only site had a significant effect on survival to flowering time and on seed production, with each species setting seed only in its natural habitat.

In order to ascertain any differences in the physiological response of old field and woodland annuals to the environmental gradient underlying an old field to woodland transect, I monitored seedling emergence, survivorship and reproduction, and measured biomass allocation to reproductive *vs*. vegetative structures, for two old field, *Chenopodium album*, *Polygonum pensylvanicum*, and three woodland species, *Acalypha rhomboidea*, *Pilea pumila* and *Impatiens capensis*, over light and soil moisture gradients in greenhouse experiments. A net replacement rate was calculated for each species, per light x soil moisture treatment combination.

The data suggested that old field annuals cannot replace themselves at low light because they are not able to photosynthesize at high enough rates to allocate biomass to all plant parts, and still allow for seed production to occur at light levels characteristic of disturbed woodland sites. Woodland annuals cannot replace themselves in the old field because their root systems and shoot morphology make them less efficient than old field species at obtaining and conserving water, either in the presence or in the absence of competition. In addition, some woodland annuals, unlike old field annuals, increase biomass allocation to vegetative structures at the expense of reproductive effort, which decreases even further their probability of replacement in old field sites.

These experiments indicate that differences between old field and woodland annuals in light requirements for seed production and in the mechanism varying allocation to reproduction over resource gradients are most important in determining their distribution and hence the type of disturbed habitat in which an annual species can establish.

To Joe -

without whose love, understanding and
moral support my life would have
little meaning

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Chapter 1

INTRODUCTION

A basic problem in ecology is the search for key factors which limit the distribution and abundance of a particular species. It is important to try to answer this question for annual plant species since they are generally absent from habitats where there is a dense cover of perennial species, and are relegated primarily to disturbed and/or resource variable habitats (Pianka, 1974; Schaffer and Gadgil, 1975; Grime, 1979; Hickman, 1979). Theoretical ecologists, in their attempt to develop a unified theory of life history evolution, have generally assumed that annual plants should produce many seeds as quickly as possible, in order to maximize their fitness,even at the expense of future seedling mortality (Pianka, 1974; Grime, 1979; Whittaker and Goodman, 1979). However, although annual plants are expected to have a generalized life history strategy, there are several ecologically distinct groups of annuals associated almost exclusively with particular types of disturbed and/or variable habitats (e.g. dune annuals, desert annuals, old field annuals, woodland annuals, Harper, 1977; Smith, 1983a, Menges and Waller, 1983).

Although annuals are most abundant in disturbed habitats, a short life cycle does not imply that a species can grow in any disturbed habitat. It is obvious that barring disturbance, the base level and availability of resources in a habitat may differ consistently among habitats (e.g. deserts vs. woods). Hickman (1979) and Stearns (1976) argue that it is not just the magnitude of the disturbance but also the distribution of disturbance events and their influence on resource availability that determines which type of plants will live in a habitat. Whereas Grubb (1976,1977) has stressed the importance of differences in the regenerative life history characteristics as the reason for the association of groups of annual species with particular habitats, Bazzaz (1979) has stressed the physiological differences among species in explaining their distributions.

There are three basic explanations of a species absence from a particular habitat: 1) the species is not physiologically able to withstand abiotic conditions in that habitat, even if the surrounding vegetation is removed, 2) the species can establish itself there only if the established species are removed and 3) the suite of life history characteristics (i.e. demographic characteristics) of that species is not adapted to the particular schedule of disturbance in that habitat (so that it cannot utilize the periods favorable for growth), thus it cannot complete its life cycle between disturbance events or cannot survive the disturbance. Are specific groups of annuals prevented from spreading into other disturbed habitats by differences in physiological tolerances and/or differences in life history characteristics? To explore this question I chose two groups of summer-flowering annuals which occurred in distinct habitats: old field annuals and woodland annuals.

Abandoned fields and disturbed woodland areas often border each other. One can find old field annuals at the edge of the woods and woodland annuals growing vigorously at the woodland margin, generally with no further extension of either group's distribution. Very few annual species can thrive in both old fields and in the woods (examples of exceptions are Galium aparine, Stellaria media, Grime, 1979; Turkington, et al, 1980; Rogers, 1982). To explain this pattern, I began an investigation of factors that could help determine the distribution and abundance of old field and woodland annuals.

Newly abandoned fields are characterized by high light intensities of unaltered spectral quality, and wide fluctuations in temperature, humidity and soil moisture near the soil surface. In contrast, the woodland habitat is typified by low light intensities high in far red and low in red wavelengths, with less variable temperature, humidity and soil moisture conditions at the soil surface, due to buffering by the tree canopy (Bazzaz, 1979). The distribution of disturbance events in an old field varies in time, in accordance with the plowing schedule followed, cultivation practices and crop type. In the woods, disturbance consists of infrequent animal disturbance, tree falls and often of predictable yearly flooding (particularly where woodland annuals abound, Menges and Waller, 1983). Since old fields and woods differ in both the harshness of the habitat and in the disturbance schedule one would expect selection for a different set of life history characteristics in old field and woodland annuals. In addition since old field annuals have a center of distribution in dry temperate regions (Lawrence, 1958), and most likely evolved in permanent open areas (Marks, 1983), and woodland annual genera have their center of distribution in moist, tropical areas (Lawrence, 1958), it is possible that evolutionary constraints in each group of annuals may play an important role in defining their current distribution.

The change in the environment observed along any transect extending from the old field into the woods involves a complex gradient of varying light, soil moisture, nutrients and predictability of disturbance. The physiological response of old field annuals along light, moisture and nutrient gradients has been studied in detail with emphasis on which factors allow coexistence of several annual species in the old field (Wieland and Bazzaz, 1975; Pickett and Bazzaz 1976, 1978a,b; Parrish and Bazzaz, 1976). Germination of many old field annuals requires light (Baskin and Baskin, 1977) and is inhibited by light deficient in red wavelengths (Taylorson and Borthwick, 1969). However, old field annuals can adjust their photosynthetic rate's saturation level to the environmental light conditions in which they are grown. Photosynthesis in several old field annuals half-saturates at considerably lower light levels when plants are grown in the shade than if grown in full sunlight (in which case they do not saturate at all, Bazzaz and Carlson, 1982). Old field annual species which have been studied, generally attain larger plant size and have higher survivorship and seed production in high light, moisture and nutrient conditions than under poorer environmental conditions, but can often compensate for deficiencies in any of these resources. Old field annuals diverge in their exploitation of the soil profile and in their response to high temperature and low moisture conditions (Wieland and Bazzaz, 1975; Parrish and Bazzaz, 1976).

Very little experimental information on physiological requirements for light and soil moisture is available for woodland annuals. It is known that woodland annuals have a higher water content than woodland perennials and than both annuals and perennials from open habitats (Struik, 1965). The only data on the effect of these two factors on the distribution of woodland annuals indicate that annuals in floodplain forests segregate along an elevational gradient concentrating in low to medium elevations in openings with the highest irradiance levels (Menges and Waller, 1983). Do old field and woodland annuals respond differently to similar light and soil moisture environmental conditions, and if so, are these differences responsible for their habitat success?

Old field and woodland plants in general are also known to differ in reproductive effort (biomass allocation to reproduction/total plant biomass harvested) in the field and in their allocation of biomass to shoot and roots (Abrahamson and Gadgil, 1973; Newell and Tramer, 1978; Abrahamson, 1979). Many annual plants of open habitats are known to allocate more energy to reproduction and more to roots than annual plants of shaded habitats (Struik, 1965; Abrahamson and Hershey, 1977; Newell and Tramer, 1978; Abrahamson, 1979). Are these differences in life history equally, more, or less important in restricting the distribution of old field and woodland annuals, than differences in the effect of light and soil moisture?

Thesis Organization

This thesis has been written as a series of chapters, each of which deals with different factors which may help determine the distribution and abundance of old field and woodland annuals. Chapter 2 examines the importance of herbaceous vegetation in preventing establishment of old field and woodland annuals in each other's habitat. In Chapter 3, I investigate whether or not physiological requirements for light and soil moisture differ between old field and woodland annuals (as measured by emergence, survivorship and reproduction along the two gradients in the greenhouse) and whether or not purely physiological factors are restricting each group's distribution. Chapter 4 focuses on whether these two groups of annuals differ in their reproductive effort and shoot/root biomass allocation along light and soil moisture gradients in a controlled greenhouse environment, and the effect of such life history response in limiting the distribution and abundance of old field and woodland annuals. Chapter 5 summarizes the results and conclusions of the previous chapters and discusses their implications for future studies on these two groups of annuals and on the evolution of the annual habit.

Species Descriptions

I chose two old field and three woodland annuals for these experiments on the basis of growth form, phenology, reproductive potential, seed size and degree of shade and drought tolerance, in order to represent the extremes in these characteristics for erect, summer-flowering annuals in each habitat. Several authors have studied the importance of these life history (Grubb, 1976,1977; Grime, 1979; Gross and Werner, 1982) and physiological characteristics (Pickett and Bazzaz, 1976, 1978a,b; Bazzaz, 1979; Grime, 1979) on colonization. Thus, it is important to choose species within each group of annuals which would bracket the range of possible responses to experimental environmental conditions. Life history characteristics and adult morphology are summarized for all species in Table 1-1.

All five species chosen have similar phenology, emerging in the spring, flowering in early summer and setting most seed in late summer, although there is considerable overlap among their flowering and fruiting stages. Much variability exists in adult plant height and in the total number of seeds produced per plant in these species. All of them produce

Table 1-1. Life history characteristics of two old field and three woodland annual plants.

	OLD FIELD		WOODLAND		
	Chenopodium album	Polygonum pensylvanicum	Acalypha rhomboidea	Pilea pumila	Impatiens capensis
Morphology					
Adult height	0.05 - 289 cm	5 - 200 cm	4 - 60 cm	4 - 50 cm	25 - 150 cm
Flowers	perfect, wind-pollinated; self-compatible	perfect; insect-pollinated; self-compatible	unisexual (monoecious sp.) wind-pollinated? self-compatible	unisexual (monoecious sp.) wind-pollinated? self-compatible	perfect (chasmogamous + cleistogamous); insect-pollinated self-compatible
Fruit	utricle (lenticular) 1-1.5 mm diameter	achene (lenticular) 2.6-3.4 mm diameter	3-celled capsule 1 seed/cell - 1.5-2.2 mm long x 1.0-1.3 mm wide	achene (ovate) 1.3-2 mm long x 0.7-1.4 mm wide	capsule (1-5 seeds) seed - 4.5 mm long x 3 mm wide
Germination	April-October	April-June	May-July	April-July	April
Flowering	June-October	July-October	July-October	July-September	June-October
Seeds/plant	2 - 72,450	60 - 3,140	1 - 327	2 - 706	1 - 748
Seed weight	0.53 - 0.70 mg	3.6 - 9.4 mg	0.25 - 1.48 mg	0.10 - 0.13 mg	7.01 - 14.50 mg
Dispersal ability	passive; endozoochory	passive; endozoochory hydrochory	passive; myrmechochory?	autochory (seeds ejected up to 1.5m) epizoochory? hydrochory?	autochory (seeds ejected up to 2m) epizoochory? hydrochory
Seed Longevity	up to 1700 years	at least 30 years	?	1 - 2 years	1 year
References	Stevens 1932; Gleason and Cronquist, 1963; Williams, 1963; Odum, 1965; van der Pijl, 1972; Bassett and Crompton, 1978; Cid-Benevento, unpubl.	Stevens, 1932; Toole and Brown, 1946; Gleason and Cronquist, 1963; Raynal and Bazzaz, 1975b; Staniforth and Cavers, 1976, 1977; Cid-Benevento, unpubl.	Gleason and Cronquist, 1963, van der Pijl, 1972; Cid-Benevento, unpubl.	Shelford, 1954; Gleason and Cronquist, 1963; Cappel, 1969; Cid-Benevento, unpubl.	Ridley, 1930; Gleason and Cronquist, 1963; Schemske, 1978; Leck, 1979; Waller, 1982; Cid-Benevento, unpubl.

inflorescences only at the axils. Seed production is thus dependent on plant size, since the larger and more branched the adult plant is, the greater the number of axils per plant. Adult plant height, the degree of branching and leaf size appears to vary with light, moisture and nutrient conditions. Germination of all species is enhanced by moist stratification of seeds at 5°C for 8-10 weeks. However, some germination of unstratified seeds is possible for scarified seeds of the old field annuals and one woodland annual (Pilea pumila), providing that light and alternating temperatures for germination are provided (Struik, 1965; Baskin and Baskin, 1977). Seeds of old field annuals generally have a much thicker seed coat than do those of woodland annuals. The two groups of annuals differ mostly in maximum seed production per plant and in seed longevity. In addition, all five species have been observed growing at the margins of the other group's habitat, the old field annuals either in shaded roadsides (Chenopodium) or in large openings in floodplain forests (Polygonum), and the woodland annuals in the shade of old field species (herbs, bushes or young trees), at the woodland-old field margin. Therefore, each group of annuals is not completely excluded from the other's habitat but rarely occurs there. Dispersal into each other's habitat by animal vectors is possible.

The old field annuals, Chenopodium album L. and Polygonum pensylvanicum L., are well studied species typical of one-year-old fields in the eastern United States. The species bracket the range of erect old field annuals in terms of leaf width, field depth of root system, reproductive output (number of seeds per plant and seed weight) and soil moisture distribution in the field. Both Chenopodium and Polygonum are classified as competitive ruderals (Grime, 1979) because of their potentially large stature and fast growth rate, and thus are more likely to be able to colonize the woodland habitat, an environment traditionally described as competitive. Both species attain greater biomass in moist soil, but Chenopodium appears to perform better than Polygonum with increasing soil dryness.

Chenopodium album L. (Chenopodiaceae), lamb's quarters, is a polymorphic species originating in Eurasia, the United States and southern Canada and widely introduced elsewhere. The family Chenopodiaceae has a worldwide distribution with centers in xerophytic and halophytic areas. In the New World, the centers of distribution are the prairies and plains of North America and the pampas of South America.

Chenopodium album is most abundant in fallow fields in the first year after abandonment from cultivation but is also found in roadsides and waste places. It is found over a broad range of soil moisture and nutrient conditions but usually in well lit areas. Adult size differs greatly among populations, with the tallest, most branched plants developing in areas with moist, rich soil (high in nitrate) and high light intensities (Williams, 1963). Chenopodium seeds germinate early in the spring when average maximum daily temperature is less than 20°C (Baskin and Baskin, 1977; personal observation). Seedlings emerge after a period of heavy rainfall. Germination can occur throughout the growing season. In areas where winters are not severe (parts of India, mean temperature 12-15°C), there are summer-flowering populations which emerge in March-April and spring-flowering populations which emerge in December (Ramakrishnan and Kapoor, 1974).

Flowering in the United States begins in mid-June and continues until late summer. Fruiting overlaps with flowering with seed production starting approximately one month after the first flowers are receptive and continuing throughout the summer. Up to four types of seeds of similar size but differing in degree of dormancy can be produced in a population (Williams, 1963). Flowering can occur relatively soon after emergence and is largely dependent on photoperiod. Flowers are borne in tightly clustered spikes. There is one ovule per flower and the calyx remains attached to the mature seed.

Seed production per plant varies with plant height and degree of branching, and can be very high. Most seeds fall close to the parent plant. Birds and cattle are common long distance dispersers of *Chenopodium album* seeds. *Chenopodium* seeds pass unharmed through their digestive tract (Salisbury, 1961; Bassett and Crompton, 1978). Dispersal in time is aided by differential germination requirements among seeds in the seed pool. Viable seeds have been recovered from 1700-year-old archeological sites (Odum, 1965). However, the period of viability varies with depth of seed burial (Roberts and Feast, 1972).

Polygonum pensylvanicum L. (Polygonaceae), Pennsylvania smartweed, a species indigeneous to the U.S., is found in moist, rich soil in recently abandoned fields, and along riverbanks, in southeastern Canada and throughout the eastern half of the United States. The family Polygonaceae is concentrated in the northern hemisphere with a mostly temperate distribution. The family has its center of distribution in the southwestern U.S.. *Polygonum pensylvanicum* is usually found in the moister areas of old fields, but it is a generalist in its response to a soil moisture gradient (Pickett and Bazzaz, 1976). Its root system penetrates the soil profile to a consistently deeper section than co-occurring old field annuals (Parrish and Bazzaz, 1976).

Polygonum seeds germinate in early spring following substantial rainfall and seedlings continue to emerge until June (Raynal and Bazzaz, 1975b). No seedling emergence has been detected in either summer of fall, in response to mild, moist weather. Seeds are prevented from germinating by the impermeability of the achene wall to water, which is overcome during overwinter stratification (mostly through scarification of seed coat by soil particles and by frost heaving)(Jordan, 1982). Flowering occurs in late summer. Reproductive potential is reduced by increases in mortality with increasing competition from winter annuals (Raynal and Bazzaz, 1975b).

Flowers are borne on racemes in the axils. Only a few flowers are receptive for fertilization at any given time and there is considerable overlap in flower and fruit production. The petal-like calyx is persistent on the fruit, so that an inflorescence mostly in fruit appears similar to a young inflorescence. One seed is produced per flower. The seeds are high in starch content and are preferred by cottontail rabbits (Staniforth and Cavers, 1977).

Seed production can be as high as a few thousand seeds per plant although it is generally around a few hundred seeds per plant. The seeds either drop close to the parent plant or are eaten by birds (off the plant) and rabbits (off the ground). Some seeds can pass intact through the digestive tract of birds but rabbits usually destroy most of the large Polygonum seeds (Ridley, 1930; Staniforth and Cavers, 1977). Long distance seed dispersal in riverbank populations also occurs when water currents move seeds down stream. Seed dispersal in time is possible, since depending on depth of seed burial, the seeds can remain viable for at least three decades (Toole and Brown, 1946).

The woodland annual species are: *Acalypha rhomboidea* Raf., *Pilea pumila* (L.)Gray and *Impatiens capensis* Meerb.. All three species are native to the United States and have similar distributions, occurring throughout southeastern Canada and the entire eastern half of the United States. Of these species, only *Impatiens capensis* has been studied in detail. All three species are found where irradiance is highest in any particular woodland site. In nature, *Acalypha* can be found in drier soils than either *Pilea* or *Impatiens*. *Acalypha* may be seen almost as likely in old fields and open habitats as in the woods (Struik, 1965; Huston, 1983), although only woodland populations were observed in my study area. All three species develop strongly height-structured populations which self-thin very slowly throughout much of the growing season. *Acalypha* and *Pilea*, are similar in appearance in the vegetative state, because of similar leaf shape, stature and leaf pigmentation. Both *Pilea* and *Acalypha*, because of their short stature and slower growth rate, are not as competitively effective as is *I. capensis*, which has been shown to suppress growth of perennials by producing a dense, tall canopy of even-aged individuals early in the spring (Winsor, 1983). Little is known about the life history and physiological requirements of *Acalypha* and *Pilea*; however, the life history of *I. capensis* has been followed in several populations and much has been written about the environmental regulation (effect of light and soil moisture) of chasmogamous and cleistogamous seed production in this species.

Acalypha rhomboidea Raf. (Euphorbiaceae), three-seeded mercury, is common in dry or moist soil of open woods, roadsides and meadows. Its genus is one of the largest (450 species) in the Euphorbiaceae, with its center of distribution located in tropical America. *Acalypha* seeds germinate weeks later than those of other woodland annuals, when the maximum daily temperature reaches 25^{o}C. Most seedlings emerge in one pulse in late May to early June. A few seedlings may emerge in late June and early July, after heavy rainfall. Male and female inflorescences are bound by a broad leafy bract and are produced at the axils, starting late July. There are usually 1-2 female flowers and usually only 1 male inflorescence per leafy bract. The female flowers consist only of a 3-celled ovary with a feathery stigma; the latter may be an adaptation to wind pollination. The male flowers are reduced to just anthers which aggregate into a head-like inflorescence. Flowering and fruiting overlap throughout the summer. Capsules disperse the seeds soon after ripening. Each seed has a fatty caruncle at one end, which presumably attracts ants and allows for long distance dispersal. From one to three seeds mature simultaneously per capsule, and these fall off separately from the floral bract. The bracts remain attached to the axils. There are no data available on the longevity of the seeds in the soil.

Pilea pumila (L.)Gray (Urticaceae), clearweed, is one of 2 species in this genus which are indigenous to the U.S.. The rest of the 200 species in the genus Pilea (the largest genus in the family Urticaceae) occur mostly in South America. Pilea pumila forms dense patches in moist, rich, shaded soil. Most seeds germinate in late April to early May. Some seedlings may emerge as late as July,and flowering begins in mid July. Male flower production begins earlier than female flower production, with a small degree of overlap per plant. Female inflorescences are fully developed by mid August, and most seeds mature in September. Male flowers are borne in separate cymes from those bearing female flowers. Inflorescences of both types are borne at each axil. Male inflorescences are closely gathered to the main axis of the plant whereas female inflorescences extend outward up to 5 cm from the main axis. Both pollen and seeds are forcefully ejected when mature. The seeds are sprung by the action of 3 staminodes found in each female flower. The forceful dissemination of pollen (through the uncoiling of anther sacs) and the presence of a sticky stigma appear to be adaptations for wind pollination (Cappel, 1969). The seeds are among the lightest seeds produced by woodland herbs (Struik, 1965; Bierzychudek, 1983). Long distance seed dispersal probably takes place when seeds get caught in the hair of mammals. The seeds can also float in water and may be carried by flood waters in the spring. Seed longevity appears to be approximately 2 years, at most (for seeds stored close to the soil surface).

Impatiens _capensis_ Meerb. (Balsaminaceae), jewelweed, is one of two species of the genus _Impatiens_, which are native to the United States. There are approximately 500 species in the genus, which evolved in tropical Asia and Africa, and are widespread as well throughout Europe, but absent from South America. _Impatiens_ _capensis_ is most abundant on riverbanks and at pond margins in somewhat shaded areas. It is usually the dominant herb where it is found, forming tall and dense populations.

Both chasmogamous (potentially outcrossing) and cleistogamous (permanently closed, selfing) flowers are produced at the axils. The percent chasmogamy varies with position on the plant (more chasmogamous flowers found towards the top and distal portions of the plant) and increases with increasing sunlight (Waller, 1980). The fruit contains 1-5 seeds (the higher number of seeds is found in chasmogamous capsules), and dehisces elastically when mature, ejecting seeds up to 2 meters from the parent plant. The seeds are among the largest seeds for woodland herbs

(Struik, 1965). Long distance dispersal can occur either by flooding waters (seeds can float for several days) or perhaps by being accidentally carried by birds, stuck to mud in their feet. The seeds are also cached by voles (Winsor, 1983) and these may help in carrying seeds further than 2 meters from place of production. The species does not develop a permanent seed bank. Seeds are viable for at most one year. A decrease in moisture content of the seed is the main reason for seeds becoming inviable (Leck, 1979).

Chapter 2

ROLE OF DISPERSAL AND OF INTERFERENCE BY HERBACEOUS VEGETATION IN LIMITING THE DISTRIBUTION OF OLD FIELD AND WOODLAND ANNUAL PLANTS

INTRODUCTION

This chapter represents the first of three parts of an extensive investigation of certain factors that determine the distribution and abundance of old field and woodland annuals. The distribution of any plant species along an environmental gradient is limited by one of three sets of factors which are: 1) the species' dispersal ability, 2) the species' ability to thrive in a particular habitat into which the species has dispersed while interacting (positively or negatively, directly or indirectly) with other plants and animals in that habitat, and 3) the species ability to tolerate, and complete its life cycle under, the physical and chemical conditions of that habitat it has reached.

Several field and greenhouse experiments have indicated that a plant species' actual range does not necessarily represent the range of environmental conditions in which the species can perform best and can be much smaller than the species' potential range (Ellenberg, 1953; Cavers and Harper, 1967; Austin and Austin, 1980). The role of dispersal on a species' colonizing ability and the effect of the surrounding herbaceous vegetation on a species' emergence, growth, survival and/or reproduction have been studied in the field for a few biennial and perennial herbs (Werner, 1976; Gross, 1980; Gross and Werner,1982), and for some old field annuals in the greenhouse (Pickett and Bazzaz, 1976; 1978 a,b).

As indicated in Chapter 1, old field annuals and woodland annuals can grow at the margin of each other's habitat and have the potential for dispersal into the other's habitat but are restricted to their particular environments. This study addresses two questions: 1) Can an old field and a woodland annual species (with as similar a life history as is possible for these two groups of annuals) become established in each other's habitat if a seed source is provided? and 2) Is herbaceous vegetation preventing these two ecologically distinct groups of annuals from colonizing each other's habitat? In order to answer these questions, I chose one old field annual, Chenopodium album L. and one woodland annual, Pilea pumila (L.) Gray and compared the demographies of each species in its natural habitat with that of populations introduced experimentally into the other species' habitat.

SPECIES

Chenopodium album and Pilea pumila are common species in their particular habitats (one-year-old field and moist woodland openings, respectively) in the eastern United States. They have similar phenology: both species emerge in the spring, start flowering in early summer and set most seed by late summer. Both species produce many seeds (relative to other annuals in their respective habitats) which are small and of similar dimensions. There is much variability in adult plant height and in the total number of seeds produced per plant in both species. Both Chenopodium and Pilea have been classified as ruderals (Grime, 1979; Menges and Waller, 1983), i.e. short-lived species with a fast growth rate and high seed production. Both species are characterized as low resource accumulators when competing with species typical of their native habitats (Struik, 1965; Pickett and Bazzaz, 1978a; Menges and Waller, 1983) and are usually found in the more disturbed or more variable areas of their particular habitats. The species differ mostly in maximum seed production per plant, individual seed weight and seed longevity; generally, these are three consistent differences between old field and woodland annuals as a group (Grime, 1979; Cook, 1980) (see Table 1-1). Chenopodium can be found growing in the shade at the edge of the woods, as in shaded roadsides, whereas Pilea can be found by meadows, at woodland margins. Therefore, seed dispersal can occur into the other species habitat, mostly by animal vectors.

STUDY SITES

The three study sites, a one-year-old field, a three-year-old field and disturbed woodland, were located within 2 km of each other at the W. K. Kellogg Biological Station, in southwestern Michigan, U.S.A. (Bailey Field holds the old field sites; Kellogg Bird Sanctuary, the woodland site, Figure 2-1). All sites had sandy loam soil. The three sites differed significantly from each other ($p < 0.01$) in mean daily irradiance (photosynthetically active radiation - PAR) and in percent soil moisture both in the spring, at time of seedling emergence, and in the summer, at time of flowering. Site differences in soil moisture and in light incident on the herbaceous layer were less pronounced in the spring than in the summer; available light decreased whereas moisture increased with increasing successional age. The percent organic matter, total nitrogen, calcium, magnesium and potassium content of the soil increased with increasing successional age. Both soil pH and nitrate

Figure 2-1. Locations of the one-year-old field (1), three-year-old field (3) and woodland (W) sites used for species introductions in Spring 1981. Experimental areas were located at the W. K. Kellogg Biological Station, Kalamazoo County, Michigan. Scale: 1 cm = 230 m.

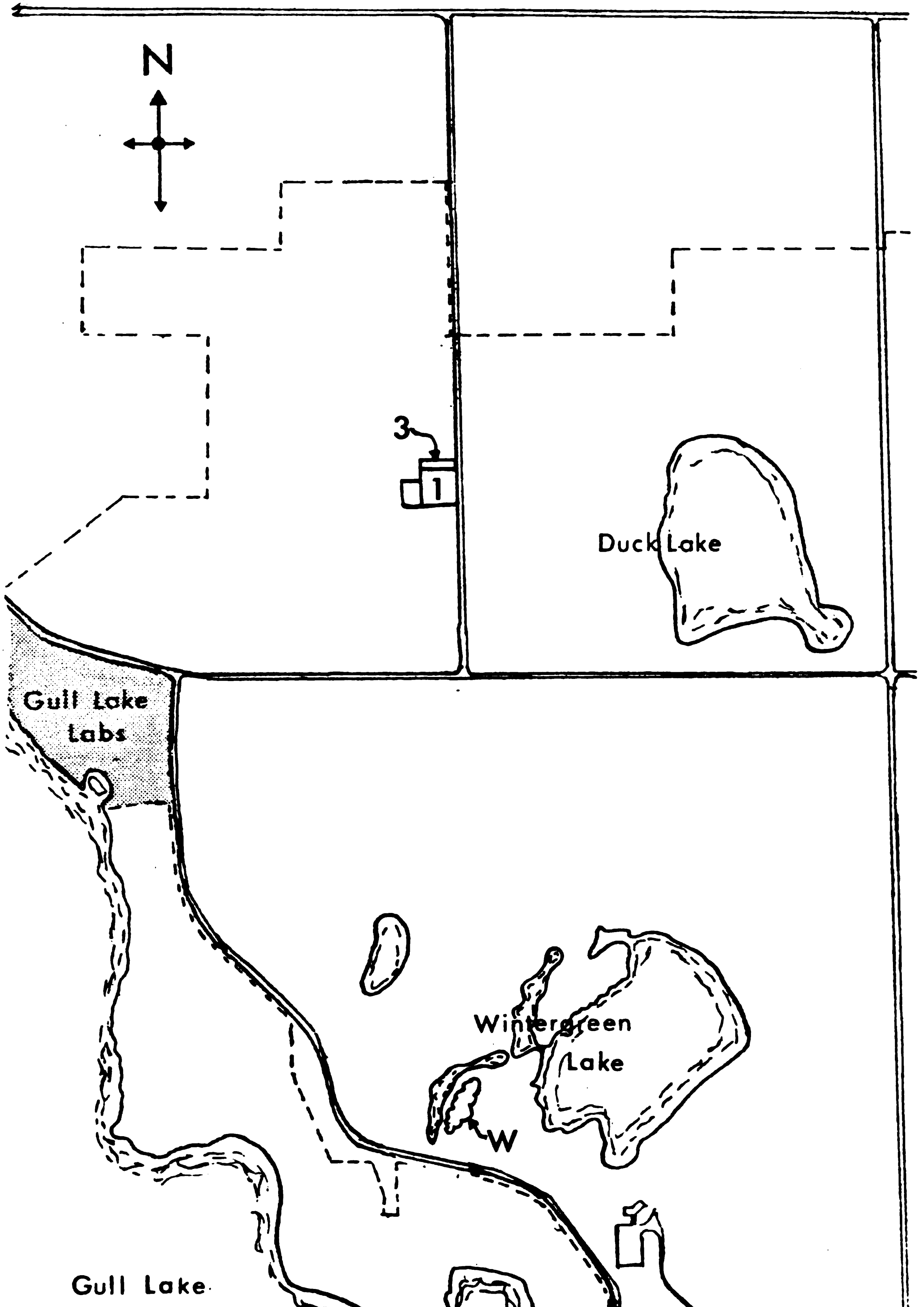

Figure 2-1

content were lower in the one-year-old field than in the other sites (Table 2-1).

The one-year-old field was plowed and herbicided (Roundup, 7 l to the ha) in the autumn prior to the start of this experiment, in October, 1980. In 1981, vegetation was sparse, with grasses (mostly *Agropyron repens* with some *Bromus inermis*), *Ambrosia artemisiifolia* and *Plantago lanceolata* being the most abundant species. The three-year-old field was burned in the summer of 1978, and was located approximately 100 m from the one-year-old field. The dominant species present in 1981 were *Agropyron repens*, *Bromus inermis* and *Arctium minus*. The mesic woodland site was an abandoned path where vegetation was trampled infrequently but on a yearly basis. The herbaceous layer was composed almost entirely of *Pilea pumila*, and was shaded mostly by a mature tree canopy of *Acer negundo*. All canopy shade was due to branches stretching out from trees that bordered the *Pilea* population. Litter accumulation was minimal at all sites, none in the one-year-old field and 1/2 to 1 cm in the three-year-old field and in the woods. Litter in the old field was composed of mostly dead grass whereas in the woods it consisted primarily of broad leaves from deciduous trees. The percentage bare ground decreased with successional age from 44% in the one-year-old field, to 29% in the three-year-old field, to less than 5% in the woodland site.

METHODS

Seeds of the two annuals were collected from each of 50 plants (chosen at random along a transect) in Autumn 1980 from naturally occurring populations, *Chenopodium* seeds from the three-year-old field study area and *Pilea* seeds from the woodland site. Seeds were stored dry

Table 2-1. Description of the light environment and soil characteristics for plots into which *Chenopodium* or *Pilea* seeds were sown in the Spring 1981, in a one-year-old field, three-year-old field and woodland sites. Light was measured at seedling height in the morning, at midday and in the afternoon, in each plot. Samples for soil moisture determination were taken from the top 8 cm of soil adjacent to the same study plots. The "Spring" data were collected in early May 1982. The "Summer" data were collected in early August 1981. Two samples for soil analyses were taken at each study site in late August 1982.

Study Site	Mean Percent Full Sunlight[a] Incident on the Herbaceous Layer		Percent Soil Moisture[b]		Soil pH	Percent Organic Matter	NO_3^- (ppm)	Total N (% dry weight)	$PO_4^{\equiv}$ (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)
	Spring	Summer	Spring	Summer								
one-year-old field	53% (727)	51% (735)	13	3	5.9	1.6	4.2	0.09	14.8	135.5	711.0	85.0
three-year-old field	——	22% (335)	—	4	7.7	4.6	9.8	0.10	172.8	354.0	1632.3	125.0
woods	29% (363)	2% (29)	20	15	6.8	7.7	7.2	0.33	76.3	140.7	1983.0	487.3

a = Percent of maximum available photosynthetically active radiation averaged over the entire day. The value in parentheses is expressed in $\mu E\ m^{-2} s^{-1}$.

b = Percent soil moisture was determined gravimetrically. Soil samples were weighed wet, dried in a 105°C oven for 24 hours and weighed dry. Percent soil moisture was calculated as gH_2O lost/g soil dry weight.

c = Soil pH, organic matter and nutrient content of the soil was measured following standard procedure in the M.S.U. Soil Testing Lab.

at 4°C until the start of the experiment. (Germination of *Chenopodium* and *Pilea* seeds is enhanced by several weeks of cold, moist storage, but seeds of both species can germinate without such pretreatment if scarified or exposed to temperature fluctuations typical of Spring (+ light) (Struik, 1965; Baskin and Baskin, 1977). Seed viability was determined prior to sowing, using the standard tetrazolium chloride test (Bonner, 1974). Viability was high (>80%) for both species.

In April 1981, I established a total of 56, 60 and 60 0.25 m x 0.25 m permanent plots along three transects, at the two old field and woodland sites, respectively. The plots were randomly assigned to each of two-treatment combinations which involved: removal of herbaceous vegetation cover by clipping plants at ground level and sowing a known weight of seeds of one of the two species (Table 2-2).

Sixteen seed lots (0.1161 g each) were weighed for each species; *Chenopodium* seed lots averaged 204 ± 5.13 seeds (± standard error) and *Pilea* seed lots averaged 616 ± 15.07 seeds (± S.E.). Seed lots were hand-sown and misted into the ground in sixteen plots per species, 8 of each vegetation treatment. Seeds were sown on May 3 in the one-year-old field, April 26 in the three-year-old field and May 4 in the woods. Seeds were sown in the Spring (rather than in the Fall) to minimize seed losses due to soil erosion, granivory or fungal attack. If seedlings of the species being introduced had already emerged in any plot, they were clipped at the base prior to sowing. This was done for all vegetation treatment plots for *Chenopodium* in the three-year-old field and for *Pilea* in the woods. Clipping was done approximately every two weeks in an effort to provide a less competitive microhabitat for each species. Litter was removed from clipped plots at the start of the experiment.

Table 2-2. Experimental design showing the treatments (clipping vegetation at ground level and sowing seeds) and the number of 0.0625m^2 plots which were randomly assigned to each treatment in a one-year-old field, three-year-old field and woodland sites.

		Number of Plots per Treatment Combination	
		+ SEEDS	- SEEDS
VEGETATION REMOVED	1-year-old field	8	4
	3-year-old field	8	4
	Woods	8	4
VEGETATION INTACT	1-year-old-field	8	$12^C/8^P$
	3-year-old-field	8	12/8
	Woods	8	8/12

C = Chenopodium plots
P = Pilea plots

Additional plots were established as control plots for monitoring background seed germination and emergence, survival and reproduction of each species in completely undisturbed plots. The percent germination of introduced seeds was calculated from natural seed pool germination by subtracting the mean number of seedlings per plot with no added seed from the mean number of seedlings per plot with added seed. Soil samples taken for soil moisture determination in the two old field sites were subsequently sifted for *Chenopodium* seeds and their volumes measured, in order to compare the size of the seed pool for the the two old field sites. In the three-year-old field there were an average of 17 *Chenopodium* seeds per ml of soil whereas less than one *Chenopodium* seed per ml of soil was found in the one-year-old field.

During the spring germination pulse, from mid-April to mid-June 1981, emergence and survival were followed weekly. Afterwards, both were monitored every two to three weeks. Each seedling was marked with a plastic color-coded toothpick. All seedling cohorts were monitored from April to November 1981. Seedlings of each species were grouped into monthly cohorts and survivorship curves plotted for each cohort at each site. The percent survivors flowering and setting seed was also determined. An analysis of variance was used to determine the effect of site and of herbaceous vegetation removal on total seedling emergence per plot and percent survival to time of flowering. A Tukey test was used for multiple comparisons of treatment means.

Treatment effects were further detailed by considering the relationship of herbaceous vegetation removal to sunlight incident on *Chenopodium* and *Pilea* plants at time of flowering and percent soil moisture per plot at time of flowering, in August 1981.

Photosynthetically active radiation (PAR - as $\mu E\ m^{-2}\ s^{-1}$) was measured in the morning, midday and afternoon, at seedling height for Chenopodium and Pilea, in all plots with added seed. One soil sample was taken from the top 8 cm (where most roots of both species introduced were found) from plots with vegetation removed and adjacent to plots with vegetation intact (for plots with added seed), three days after a saturating rainstorm. The percent soil moisture was determined gravimetrically as gH_2O lost/g soil dry weight. The light and soil moisture were statistically analyzed in the same way as for the demographic data.

The results of a 4-way analysis of variance of mean irradiance indicated that the quantity of light incident on seedlings monitored was significantly affected by the species for which light was being measured (Chenopodium and Pilea plants differed in the stage of development and thus in height, at time of measurement), the field site, presence of herbaceous cover and time of day (Table 2-3). Of the six possible two-factor interactions, only one, species x time of day, was not significant. Of the five possible three- and four-factor interactions, only the species x field site x vegetation removal interaction was significant ($p < 0.05$).

Removing herbaceous cover from a 0.0625 m^2 area provided significantly less light to both species in the three-year-old field than in the one-year-old field, in the morning and/or in the afternoon (Table 2-4). Only at midday, with the sun approximately directly overhead, was a 0.0625 m^2 opening in the vegetation in the three-year-old field equivalent to the same size opening in the one-year-old field. The taller the vegetation surrounding the cleared 0.0625 m^2 plot, the greater the amount of lateral shading in the morning and in the afternoon due to the

Table 2-3. Results of a 4-way analysis of variance of mean irradiance (measured as $\mu E\ m^{-2}\ s^{-1}$ at seedling height in the morning, midday and afternoon in August 1981) for *Chenopodium album* and *Pilea pumila* plots, with species, field site (place), herbaceous vegetation removal (clipping) and time of day as main effects. The data were log-transformed to achieve a normal distribution and homogenous variance.

Source of Variation	Mean Square	F	p	d.f.
Species	28.50	45.74	0.0000	1
Place	1322.42	2122.53	0.0000	2
Clipping	54.53	87.53	0.0000	1
Time of Day	146.43	235.02	0.0000	2
S x P	15.91	25.53	0.0000	2
S x C	5.20	8.34	0.0040	1
P x C	5.02	8.06	0.0003	2
S x T	0.28	0.45	0.6347	2
P x T	23.40	37.56	0.0000	4
C x T	2.47	3.97	0.0193	2
S x P x C	2.74	4.40	0.0126	2
S x P x T	1.18	1.90	0.1090	4
S x C x P	1.39	2.23	0.1079	2
P x C x T	0.85	1.36	0.2474	4
S x P x C x T	1.33	2.14	0.0739	4
Error	0.62			842

Table 2-4. Mean photosynthetically active radiation ($\mu E\ m^{-2} s^{-1} \pm$ standard error) measured at seedling height for *Chenopodium album* and *Pilea pumila* in August 1981 in the presence or in the absence of herbaceous vegetation cover, for a one-year-old field, three-year-old field and disturbed woodland sites (3 measurements per plot per time of day; 8 plots per treatment). Treatment means not sharing a superscript are significantly different from each other, $p < 0.05$.

		Chenopodium		*Pilea*	
Site	Time of day	Vegetation Removed	Vegetation Intact	Vegetation Removed	Vegetation Intact
one-year-old field	morning	$456.4^{a} \pm 43.5$	$298.4^{ad} \pm 36.1$	$388.8^{a} \pm 51.3$	$421.7^{ac} \pm 47.1$
	midday	$1491.3^{b} \pm 83.3$	$1250.0^{bc} \pm 103.7$	$1587.5^{b} \pm 75.3$	$1367.1^{b} \pm 90.5$
	afternoon	$581.3^{ac} \pm 59.4$	$479.6^{a} \pm 58.9$	$631.3^{c} \pm 61.5$	$612.5^{ac} \pm 76.9$
three-year-old field	morning	$185.1^{d} \pm 30.0$	$192.9^{d} \pm 43.5$	$242.1^{a} \pm 47.9$	$150.0^{d} \pm 35.7$
	midday	$1337.1^{b} \pm 81.5$	$522.0^{ac} \pm 95.3$	$1311.9^{b} \pm 111.2$	$853.8^{c} \pm 128.7$
	afternoon	$167.6^{d} \pm 28.2$	$125.4^{d} \pm 20.4$	$249.6^{a} \pm 50.3$	$115.8^{d} \pm 18.6$
woods	morning	$61.1^{g} \pm 27.8$	$4.3^{ef} \pm 0.4$	$66.0^{g} \pm 18.3$	$50.1^{g} \pm 13.7$
	midday	$28.1^{g} \pm 5.0$	$9.8^{e} \pm 2.0$	$77.6^{g} \pm 25.4$	$37.9^{g} \pm 13.6$
	afternoon	$4.1^{ef} \pm 0.2$	$2.7^{f} \pm 0.3$	$8.4^{e} \pm 1.2$	$5.5^{e} \pm 0.2$

lower angle of incidence of sunlight at those times. Seedlings in cleared plots in the one-year-old field, received 389-456 $\mu E\ m^{-2}\ s^{-1}$ in the morning and 480-631 $\mu E\ m^{-2}\ s^{-1}$ in the afternoon, whereas at midday, 1491-1588 $\mu E\ m^{-2}\ s^{-1}$ were incident on those seedlings. However, clearing the same area of herbaceous vegetation in the three-year-old field provided only 185-242 $\mu E\ m^{-2}\ s^{-1}$ in the morning and 168-250 $\mu E\ m^{-2}\ s^{-1}$ in the afternoon, with 1312-1337 $\mu E\ m^{-2}\ s^{-1}$ reaching seedlings at midday. In the woods, light incident on both species in cleared plots was significantly lower than light available to them in the same plots in the old field, since the tree canopy was not disturbed in this experiment.

Removing herbaceous cover significantly increased mean irradiance on at least one species, in the three-year-old field and in the woods, but not in the one-year-old field (Table 2-4). In the three-year-old field, Chenopodium received significantly more light at midday in the absence of herbaceous cover whereas the same was true for Pilea in cleared plots, in the morning, midday and in the afternoon. In the woods, the removal of herbaceous cover resulted in significantly more light incident on Chenopodium but not on Pilea for the three periods when light was measured.

The removal of herbaceous vegetation cover had no significant effect on soil moisture at any site (at least in August, at the driest time of the year) (Table 2-5). Only site had a significant effect on percent soil moisture. The old field sites had an average of 3.3-3.8 percent soil moisture (regardless of vegetation treatment) whereas in the woods, there was a mean of 17.3 percent soil moisture.

Table 2-5. Results of a 3-way analysis of variance for percent soil moisture (determined gravimetrically) for samples taken in early August, 1981 from clipped plots and adjacent to plots not clipped with species, field site (place) and herbaceous vegetation removal (clipping) as main effects. Data are log-transformed to satisfy the assumptions of normality and homogeneity of treatment variances (cf. Appendix, Table A-4).

Source of Variation	Mean Square	F	p	d.f.
Species	0.004	0.03	0.8667	1
Place	23.77	151.13	0.0000	2
Clipping	0.07	0.43	0.5119	1
S x P	0.004	0.03	0.9751	2
C x P	0.45	2.83	0.0644	2
S x C	0.28	1.80	0.1831	1
S x P x C	0.04	0.26	0.7708	2
Error	0.16			84

RESULTS

Seedling emergence was significantly affected by three of the four main factors included in the analysis of variance: site, herbaceous vegetation removal and adding seeds (but not species) (Table 2-6). Of the eleven possible interaction effects in this analysis, only three had no significant effect on seedling emergence (species x site x adding seeds, species x site x herbaceous vegetation removal, vegetation removal x adding seeds). Only site had a significant effect on each species survival to flowering time (Table 2-7). The results of the 4-way analysis of variance indicated no significant interaction effects among the species, site and vegetation removal main effects. Chenopodium flowered and set seed only in the one-year-old field, although some Chenopodium plants survived to flowering time at each site (Figure 2-2). Pilea was less tolerant of environmental change than Chenopodium since the latter survived in all three sites whereas Pilea only survived to flowering time in the woodland site.

Effect of site on emergence, survival and reproduction

Chenopodium had significantly greater emergence in the three-year-old field than in the one-year-old field or woods, for all plots (Table 2-8). Chenopodium had significantly greater emergence in the one-year-old field in undisturbed plots than in the same plots in the woods, but emergence in cleared plots in the one-year-old field did not differ from emergence in cleared plots in the woods (for plots with added seed). Pilea seedling emergence increased significantly with increasing successional age in the presence of herbaceous cover (for plots with added seeds). In clipped plots (with added seed), Pilea seedling emergence was significantly

Table 2-6. Results of a 4-way analysis of variance of Chenopodium album and Pilea pumila seedling emergence with species, field site (place), herbaceous vegetation removal (clipping) and adding seeds as main effects. The data were log-transformed to achieve a normal distribution and homogeneous variance.

Source of Variation	Mean Square	F	p	d.f.
Species	0.11	0.30	0.5868	1
Place	57.43	154.62	0.0000	2
Clipping	3.26	8.77	0.0036	1
Adding seeds	75.00	201.93	0.0000	1
SP	144.08	387.91	0.0000	2
SC	4.30	11.58	0.0009	1
PC	6.56	17.65	0.0000	2
SA	29.03	78.16	0.0000	1
PA	2.20	5.93	0.0034	2
CA	0.94	2.54	0.1134	1
SPC	0.46	1.24	0.2920	2
SPA	12.90	34.72	0.0000	2
SCA	0.16	0.44	0.5085	1
PCA	1.67	4.50	0.0128	2
SPCA	2.42	6.51	0.0020	2
Error	0.37			136

Table 2-7. Results of a 3-way analysis of variance for percent survivorship to flowering time for *Chenopodium album* and *Pilea pumila* with species, field site (place) and herbaceous vegetation removal (clipping) as main effects. The arc-sine tranformation was used to normalize the data and equalize treatment variances.

Source of Variation	Mean Square	F	p	d.f.
Species	3634.44	37.77	0.0000	1
Place	10334.71	107.40	0.0000	2
Clipping	38.04	0.40	0.5312	1
S x P	39493.36	410.42	0.0000	2
S x C	55.23	0.57	0.4508	1
C x P	250.02	2.60	0.0804	2
S x P x C	44.30	0.46	0.6326	2
Error	96.23			84

Figure 2-2. Survivorship curves for Chenopodium album and Pilea pumila in a one-year-old field, three-year-old field and disturbed woodland sites. Data for treated and control plots were combined into monthly cohorts. April cohort = closed circle; May cohort = open cicrcle; June cohort = open square; July cohort = open triangle; August cohort = closed triangle; September cohort = closed square; October cohort = closed diamond. For Chenopodium, n = 8 plots for the April cohort (undisturbed plots); n = 16 plots for the May cohort (all plots with added seed); n = 24 plots (plots with added seed + undisturbed plots) for all other cohorts. For Pilea, n = 24 plots for all cohorts.

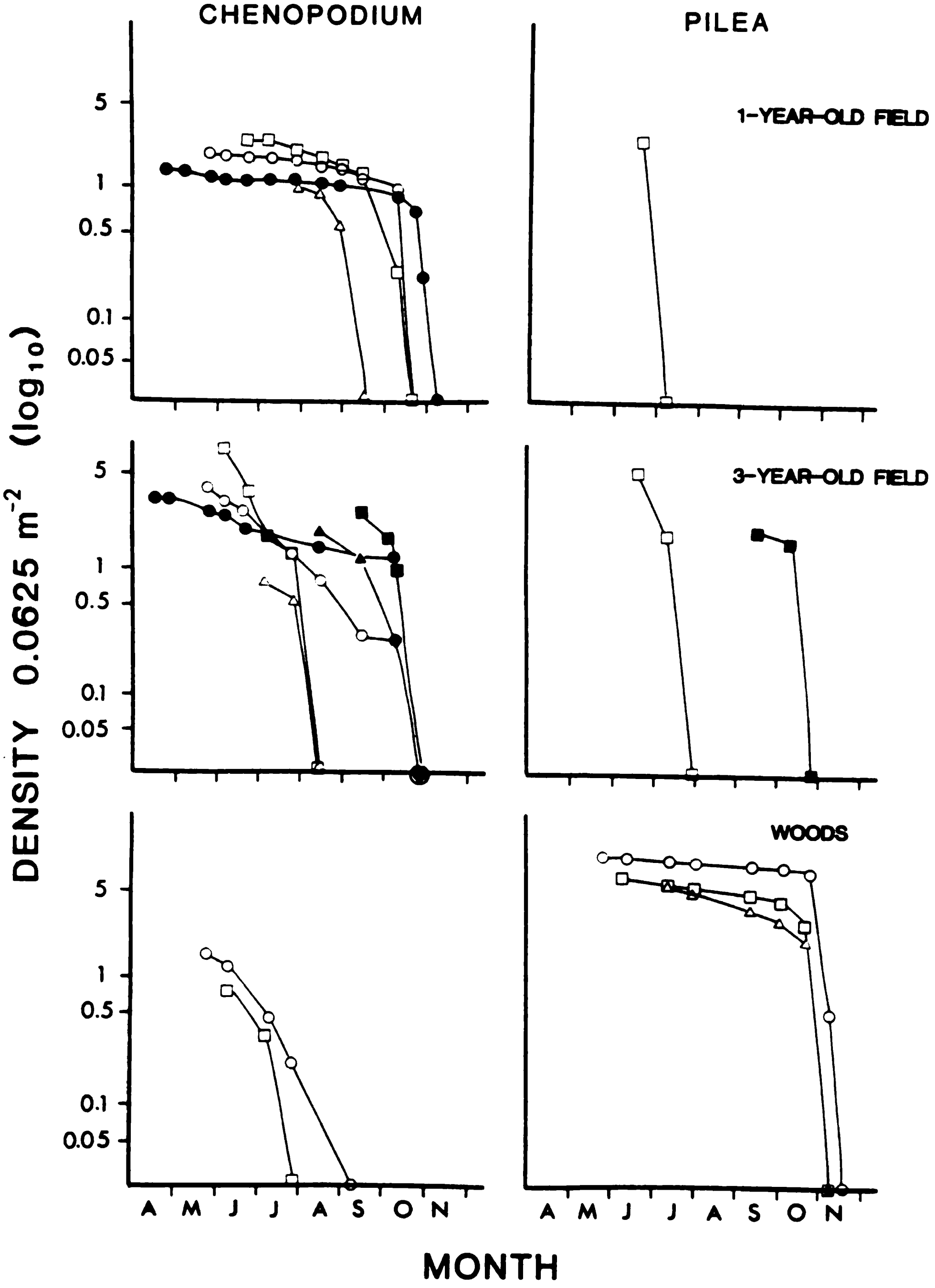
CHENOPODIUM
PILEA
1-YEAR-OLD FIELD
3-YEAR-OLD FIELD
WOODS
DENSITY 0.0625 m^{-2} ($\log_{10}$)
5
1
0.5
0.1
0.05
A M J J A S O N
MONTH

Figure 2-2

greater in the three-year-old field and in the woods than in the one-year-old field. No Pilea seedlings emerged in the old field in plots without added seed.

Chenopodium seedlings emerged over a six-month period in the old field sites and could be grouped into 3 to 6 cohorts, whereas there were two Chenopodium cohorts in the woods (which emerged in May and in the first week in June, the second cohort emerged in cleared plots)(Figure 2-2). Site differences in the number of germination pulses reflected the differences in the size of the Chenopodium background seed pool. There were more Chenopodium seeds in the three-year-old field seed pool than in the one-year-old field, and none in the woods. Pilea seedlings emerged from May to July and could be grouped into three cohorts in the woodland site but only 1 to 2 Pilea seedling cohorts were evident in the old field sites.

Time of emergence affected survivorship to flowering time for Chenopodium but not for Pilea (Figure 2-2). The earliest-emerging Chenopodium cohort in the one-year-old field (April for completely undisturbed plots and May for treated plots) lived considerably longer (1 to 1 1/2 months) than the other 2 cohorts. Although there were more Chenopodium cohorts in the three-year-old field than in the one-year-old field, the earliest-emerging cohort lived the longest (1 1/2 months longer than the others). In the woods, all Chenopodium seedlings emerging in June were dead approximately three months before all of the May cohort had died.

Chenopodium had significantly higher survivorship in the one-year-old field than in the other two sites (Figure 2-3). Seedling mortality was low for the first seedling cohort in the one-year-old field

Figure 2-3. Percent survivorship to time of flowering for *Chenopodium album* and *Pilea pumila* in the presence or in the absence of herbaceous vegetation cover, in a one-year-old field (1), three-year-old field (3), and disturbed woodland (W) sites.

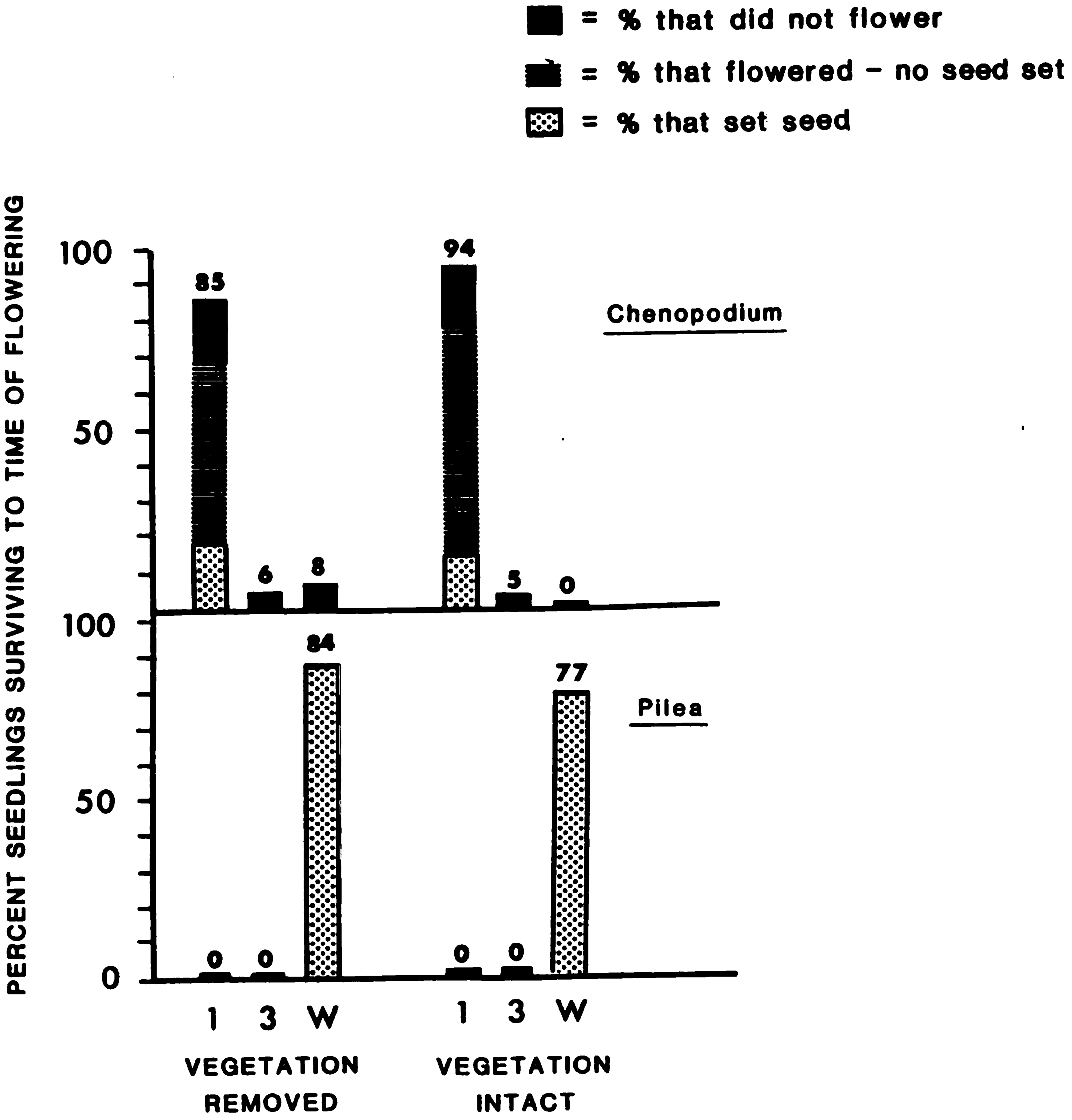
■ = % that did not flower
■ = % that flowered – no seed set
▨ = % that set seed
PERCENT SEEDLINGS SURVIVING TO TIME OF FLOWERING
100
50
100
50
0
85
6
8
94
5
0
Chenopodium
84
77
0
0
0
0
Pilea
1
3
W
1
3
W
VEGETATION REMOVED
VEGETATION INTACT

Figure 2-3

(Deevey Type I survivorship curve, Deevey, 1947) (Figure 2-2). The mortality rate was approximately constant throughout the season for later-emerging cohorts in the one-year-old field and for all cohorts in the three-year-old field and woods (approximately Deevey Type II survivorship). All *Pilea* seedlings died at the old field sites 2-3 weeks after emergence (Deevey Type II survivorship) (Figure 2-2). More than 75% of *Pilea* seedlings survived to flowering time in the woods (Deevey Type I) and all set seed (Figures 2-2,2-3).

Effect of herbaceous vegetation and of seed introduction on emergence

Removal of herbaceous vegetation cover resulted in a significant increase in seedling emergence for *Chenopodium* in the three-year-old field and woods and for *Pilea* in the three-year-old field. In the one-year-old field, Pilea had significantly higher emergence in undisturbed plots than in cleared plots (Table 2-8). Adding seeds had no significant effect on *Chenopodium* seedling emergence in the old field but did in the woods, in the presence of herbaceous cover. Thirty two to fifty six percent of total *Chenopodium* seedling emergence in the one-year-old field came from sown seeds, whereas in the three-year-old field, there was only a twenty one percent contribution from sown seeds to total emergence (only possible to calculate it in plots with herbaceous cover). In the woods, all *Chenopodium* seedlings emerged from sown seeds. Adding seeds increased seedling emergence for *Pilea* in the old field sites (since no Pilea seedlings emerged in plots without added seed), but not in the woods, regardless of vegetation treatment. Removal of herbaceous cover had no significant effect at any site on survival to flowering time (Table 2-7) nor on the percent of plants flowering or

Table 2-8. Mean seedling emergence per $0.0625m^2$ plot ($\pm$ standard error) for *Chenopodium album* and *Pilea pumila* in the presence or in the absence of herbaceous vegetation cover, in plots with or without added seed, in a one-year-old field, three-year-old field and woodland sites. For each species, treatment means with different superscripts are significantly different from each other, $p < 0.05$

		+SEEDS		-SEEDS		Percent Germination of Sown Seeds		Percent of Total Emergence Due to Sown Seeds	
	Site	Chenopodium	Pilea	Chenopodium	Pilea	Chenopodium	Pilea	Chenopodium	Pilea
VEGETATION REMOVED	1-year	$3.4^{a} \pm 0.63$	$2.1^{a} \pm 0.81$	$1.5^{a} \pm 0.29$	$0^{f} \pm 0$	$0.9\%^{a}$	$0.3\%^{a}$	55.9%	100%
	3-year	$154.9^{b} \pm 19.09$	$62.3^{c} \pm 14.13$	$198.0^{b} \pm 18.93$	$0^{f} \pm 0$	?	$10.1\%^{b}$	?	100%
	Woods	$4.6^{a} \pm 1.18$	$83.8^{e} \pm 23.21$	$0^{d} \pm 0$	$22.6^{e} \pm 5.56$	$2.3\%^{c}$	$9.9\%^{b}$	100%	73%
VEGETATION INTACT	1-year	$4.4^{a} \pm 1.15$	$6.5^{b} \pm 1.13$	$3.0^{a} \pm 0.76$	$0^{f} \pm 0$	$0.7\%^{a}$	$1.1\%^{a}$	31.8%	100%
	3-year	$52.4^{c} \pm 9.20$	$24.3^{d} \pm 13.30$	$41.5^{c} \pm 8.53$	$0^{f} \pm 0$	$5.3\%^{b}$	$3.9\%^{c}$	20.8%	100%
	Woods	$0.4^{d} \pm 0.18$	$81.4^{e} \pm 15.01$	$0^{d} \pm 0$	$29.3^{e} \pm 4.61$	$0.2\%^{a}$	$8.5\%^{b}$	100%	64%

setting seed, for either *Chenopodium* or *Pilea* (Figure 2-3).

DISCUSSION

Effect of site on emergence, survival and reproduction

Chenopodium and *Pilea* appear to differ in their physiological tolerances to light and soil moisture and clearly differ in their pattern of emergence throughout the growing season, regardless of the habitat. Whereas *Chenopodium* seeds germinate from early spring to as late as October, only a few weeks prior to a killing frost, *Pilea* seeds are most likely to germinate early in the growing season. The different way in which these species cue their germination to environmental conditions could easily affect their distributions. If *Pilea* had a persistent seed bank and its seeds would germinate soon after any favorable period during the growing season, then it would be possible for its seeds to be present in an old field after disturbance, and in a wet year, it might have higher survivorship than observed in this experiment. The question still remains as to whether *Pilea* could become established on the wetter areas of the old field if its seeds were available and ready to germinate at the appropriate time of the year.

On the other hand, if *Chenopodium* seeds were present in the woods and those seeds germinated before the tree canopy had closed, those seedlings might be able to develop quickly during the period of higher irradiance and begin flowering early in the life cycle. *Chenopodium* plants have been observed to produce flower buds even at low light intensities (Cumming, 1963). Stem growth in *Chenopodium album* is able to respond quickly to sunflecks similar to those observed in the woodland habitat (Morgan and Smith, 1978). Thus, the question arises as to whether *Chenopodium album* could produce enough seeds to replace itself, if sunflecks and early germination (before tree canopy closure) made normal plant development possible, since this species maintains a seed pool with only a small percent of seeds germinating in any given year (Roberts, 1964).

Chenopodium seedlings emerged in several pulses throughout the growing season in both old field sites but only two Chenopodium cohorts were observed in the woods. The greater number of Chenopodium cohorts in the three-year-old field than in the one-year-old field may have resulted from a larger seed pool contribution in the three-year-old field. A previous study has also shown that only a small percentage of Chenopodium seeds will germinate every year in undisturbed soil (Roberts and Feast, 1973). It appears that the lack of a Chenopodium seed pool and of soil disturbance were responsible for the fewer pulses of germination for Chenopodium in the woods than in the old field sites.

In contrast, Pilea seedlings formed 3 cohorts in the woods (early in the growing season) but emerged in only 1 or 2 pulses in the old field sites. Seeds of several woodland annuals germinate in one pulse early in the spring, before canopy closure (Coombe, 1956; Smith, 1983b; Winsor, 1983). Selection for nearly synchronous, early spring germination under more favorable light and moisture conditions may explain the fewer germination pulses for Pilea at all sites.

Chenopodium cohorts differed in mean lifespan, with the earliest emerging cohorts surviving the longest in both old field sites. These results are similar to those obtained from demographic studies of old field annuals and perennials (Black and Wilkinson, 1963; Ross and Harper, 1972; Abul-Fatih and Bazzaz, 1979b; Gross, 1980; Klemow and Raynal, 1983) which showed that the earliest emerging seedlings had a higher probability of survival and of reproductive success than the later cohorts. In contrast, *Pilea* cohorts did not differ in average lifespan and had similar survivorship curves, whereas for *Chenopodium* cohorts in the old field, the later the cohort emerged, the steeper the survivorship curve became. The differences in survivorship between *Chenopodium* and *Pilea* for their natural habitats may have been due to soil moisture and nutrient conditions in these old field sites not being as favorable for *Chenopodium* growth and survival (Williams, 1963; Pickett and Bazzaz, 1978a) as this woodland site's environment was for *Pilea*.

Time of emergence is known to have a significant positive effect on survivorship for *Impatiens capensis*, the only woodland annual species for which such data are available (Howell, 1981; Winsor; 1983). However, *I. capensis* is one of the first annual species to emerge in the woods in the spring. *Pilea* seeds germinate at least 3-4 weeks after *Impatiens* seeds do. *Pilea* also has a slower growth rate than *I. capensis* (personal observation, Struik, 1965). It is possible that since adult *Pilea* plants are shorter (and the difference in emergence time between its few cohorts is small), size of plant does not affect survivorship to flowering as much as in *Impatiens* species (Cid-Benevento, 1979; Howell, 1981).

Effect of herbaceous vegetation on emergence, survival and reproduction

Herbaceous vegetation cover did not prevent *Chenopodium* or *Pilea* seeds from germinating at any site. Herbaceous vegetation cover inhibited *Chenopodium* seedling emergence at two of the three field sites. These results are consistent with previous laboratory and greenhouse studies on the effect of light quantity and spectral quality on *Chenopodium* germination. *Chenopodium* seed germination is under phytochrome control, and vegetation-filtered light (i.e. light high in far red wavelengths and low in red wavelengths) inhibits germination in this species (Cumming, 1963; Williams and Harper, 1965; Taylorson and Borthwick, 1969; Henson, 1970).

It is not surprising that *Chenopodium* seedling emergence was affected little by vegetation removal in the one-year-old field, since on average nearly 50% of intact plots was bare ground. Plots which were not clipped still received close to 50% of full sunlight, averaged over the entire day. In the three-year-old field there was greater herbaceous cover and less light was available, even in clipped plots, than in untreated plots in the one-year-old field. Lateral shading (in the morning and afternoon) probably contributed to increasing the far red/red light ratio in light incident on the soil surface thus increasing the negative effect on *Chenopodium* germination. In the woodland site, removal of herbaceous vegetation increased available light only slightly since shading by trees was still prevalent. Sunlight reaching cleared plots had already been filtered through the tree canopy and thus lacked the red light wavelengths which promote *Chenopodium* germination.

The only clear effect of herbaceous vegetation on *Pilea* was that it inhibited *Pilea* germination in the three-year-old field. *Pilea* is a woodland annual most abundant in open areas of moist woodland (Struik, 1965; Menges and Waller,1983). There are no published studies on the factors that affect *Pilea* germination. However, one would expect its germination requirements to be somewhat similar to those of other spring-emerging woodland annuals (in the same way as several co-occurring old field annuals have similar germination requirements, Pickett and Bazzaz, 1978a).

The only known requirements for the germination of several woodland annuals are that seeds stay fairly moist from time of dispersal to germination time (Leck, 1979) and that they experience a cold period (Struik, 1965). It appears that since removal of herbaceous cover did not increase available soil moisture at any site, differences in soil moisture among plots could not have responsible for higher *Pilea* emergence in cleared plots in the old field. Light incident on seedlings in undisturbed plots in the three-year-old field was significantly lower than in cleared plots at that site but considerably higher than in the woods. It appears that too much or too little light could not have been an inhibitory factor on *Pilea* emergence in the three-year-old field and no data are available on a possible reason for whether germination of *Pilea* seeds is inhibited by vegetation-filtered light. Since undisturbed plots in the three-year-old field were mostly covered with *Agropyron repens* (a species reported to be allelopathic, Rice, 1974) it is possible that such herbaceous cover chemically inhibited (directly or through its effect on fungus-seed interactions) the germination of *Pilea* seeds. In the one-year-old field, removal of herbaceous cover resulted in significantly lower *Pilea* emergence. It is possible that a combination of factors including high light intensities associated with high soil surface temperatures and low soil moisture inhibited *Pilea* emergence in cleared plots in the one-year-old field.

Herbaceous vegetation did not have a negative effect on *Chenopodium* survival in the one-year-old field but may have contributed to the high *Chenopodium* mortality in the three-year-old field and in the woods due to the negative effect of vegetation-filtered light and low light intensities on *Chenopodium* growth (Morgan and Smith, 1976; Holzner, Hayashi and Glainzer, 1982). The two old field sites differed little in moisture and nutrient content of the soil. The woodland site had a higher soil moisture and nutrient content than either old field site, at a level more favorable for Chenopodium survival and growth than found in the old field sites (Williams, 1963; Pickett and Bazzaz, 1978a).

It is highly probable that the change in the light environment with increasing successional age may have been most responsible for the increase in Chenopodium mortality. However, although herbaceous cover can limit the Chenopodium distribution and abundance in the old field (Pickett and Bazzaz, 1978a) it is not the only factor preventing Chenopodium establishment in the woods (since cleared plots did not have flowering Chenopodium plants). Pilea did not survive in either old field site, either in the presence or absence of herbaceous cover. These data suggest that this species' intolerance of the physico-chemical environment in the old field habitat, (including those environmental conditions not directly related to the presence of herbaceous cover), is one factor limiting Pilea to the woods.

The results from this field experiment suggest that interference from herbaceous vegetation alone is not responsible for keeping each species out of the other's habitat. The data suggest that the species differ in their physiological tolerances for light and soil moisture conditions as well as in their life history characteristics.

Chapter 3

ROLE OF PHYSIOLOGICAL TOLERANCES AND DEMOGRAPHY IN LIMITING THE DISTRIBUTION OF OLD FIELD AND WOODLAND ANNUAL PLANTS

INTRODUCTION

The results from the field experiment discussed in Chapter 2 suggested that interference from herbaceous vegetation was not a key factor in restricting the distribution across habitats of the old field and woodland annual species used in that experiment. The data suggested that old field and woodland annuals might differ in their physiological response to the environmental gradient extending from a one-year-old field to disturbed mesic woodland. Changes in the availability of two essential resources, light and soil moisture, were identified along the old field to woods gradient which paralleled the differences between species in their survivorship and reproductive response in old field and woodland sites.

Several characteristics describing the physiological response of plants to light and soil moisture have been associated with plants of old fields and woods (Bazzaz, 1979). However, these classifications involve comparisons of early-successional herbs (usually annuals) and late-successional perennial herbs and tree species. Woodland annuals occupy disturbed areas amidst a late-successional habitat. Thus, it is unlikely that they be considered late-successional species. Thus, there is no *a priori* reason for expecting the same physiological differences between old field and woodland annuals as have been observed between old field annuals and late-successional trees. Grubb (1976) distinguishes among various groups of annuals in terms of the type of disturbed site occupied by each group. He focuses on the suite of life history characteristics necessary to colonize each type of disturbance. Watkinson (1981) also emphasizes the importance of the dispersal strategy in determining the number of different habitats which annual species can occupy in spatially and temporally heterogeneous environments. In addition, several studies have shown that seed dispersal patterns (rather than physiological tolerances) can determine the distribution of annuals and perennials over well-defined environmental gradients (Pemadasa and Lovell, 1974; Rabinowitz, 1978; Keddy, 1982).

Annual plants are usually favored in habitats with large-scale disturbances (Davis and Cantlon, 1969; Schaffer and Gadgil, 1975), in which the effects of light, soil moisture and temperature on species performance are often interrelated. In the old field, differences in vegetative cover are correlated with differences in temperature and humidity at the soil surface and a decrease in percent ground cover is associated not just with an increase in available light but also with an increased drying rate at the top portion of the soil profile (Bazzaz, 1979). In the woodland habitat, variability in incident light due to sunflecks and gaps in the canopy, can cause abrupt changes in leaf temperature of herbs (Young and Smith, 1979, 1980). In this study I tried to simulate the complex environmental gradient observed along a transect from old field to woods by varying availability of these two essential resources.

The comparative experimental approach of growing old field and woodland annuals in a controlled environment over a gradient similar to that in field conditions is the most effective way to discover consistent differences between the two groups of species in their response at one or more stages in the life cycle of these along the old field to woodland environmental gradient (Grime, 1965). In order to determine whether differences in physiological tolerances or differences in the suite of life history characteristics were responsible for habitat restriction in old field and woodland annuals (and thus answer the questions raised by the field experiment in Chapter 2), I conducted a greenhouse experiment to determine if old field and woodland annuals differed in their physiological tolerances of light and soil moisture at any stage of their life cycle in a way that could account for their general absence from each other's habitat.

I tested four hypotheses about the response of these two groups of species to the complex environmental gradient observed from old field to woods. The hypotheses were: 1) Old field annuals are more successful than woodland annuals in replacing themselves with increasing available light, regardless of the soil's water-holding capacity, 2) Woodland annuals are more successful than old field annuals in replacing themselves in a low light environment, regardless of the soil's water holding capacity, 3) Woodland annuals are less drought resistant than are old field annuals at a particular light level, and 4) The water-holding capacity of the soil has a greater effect on the distribution of woodland annuals over a light gradient than on old field annuals.

I monitored two old field annuals, _Chenopodium album_ and _Polygonum pensylvanicum_ and three woodland annuals, _Acalypha rhomboidea_, _Pilea pumila_ and _Impatiens capensis_, from time of seedling emergence to time of reproduction, over the light and soil moisture gradients established in the greenhouse. Both groups of annuals included species that represented the extremes of physiological and morphological response to these gradients (see Chapter 1 for detailed species descriptions) observed within these groups of summer-flowering annuals.

METHODS

Experimental Design and Techniques

Light and soil moisture gradients were established in the greenhouse, in March, 1982. The light gradient consisted of six light levels ranging from 2% to 100% of sunlight coming into the greenhouse. The soil moisture gradient consisted of three sand and potting soil mixtures differing in water-holding capacity and referred to as soils of low, medium and high water-holding capacity.

Each of the six light treatments was established by stapling black polypropylene fabric (Chicopee Manufacturing Co., Cornelia, GA) onto a box-like frame which was placed over a 3.2 m^2 dark green plastic-covered plywood surface (Figure 3-1). The fabric is produced in specific weave densities which allow a certain percent of light through. Light levels of 8% to 53% of incoming sunlight were obtained with a single layer of fabric. A single layer of each of two fabrics, the weave of which allowed 8% and one allowing 75% light penetration were superimposed to create a treatment level of 2% incoming sunlight. No fabric was used in the 100% incoming sunlight treatment but a frame similar to those used in the other light treatments was placed over the greenhouse bench to control for the frame's shading effect.

I characterized the light gradient by measuring photosynthetically

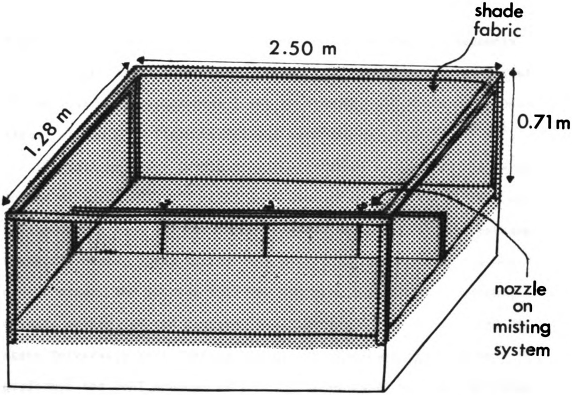

Figure 3-1. Experimental design for each light treatment in the greenhouse, including dimensions of greenhouse bench and position of misting system (scale: 1 cm = 25 cm).

active radiation (as $\mu E\ m^{-2}\ s^{-1}$) incident on plants at each light level, at midday and in the early afternoon (when plants received the most light), throughout the growing season, from late March to September, 1982 (see Appendix, Table A-1). The mean photosynthetic irradiance ($\mu E\ m^{-2}\ s^{-1}$ $\pm$ 95% confidence interval) on plants at each light treatment is shown on Figure 3-2. In addition, spectroradiometric measurements were made at midday in August for each light treatment to compare the spectral energy distribution (in $\mu E\ m^{-2}\ s^{-1}$) among light treatments (see Appendix, Figure A-1). To facilitate comparison of the light conditions at different times of the year among greenhouse light treatments, old field and woodland sites, all data on light conditions were presented as $\mu E\ m^{-2}\ s^{-1}$.

The soil moisture gradient was established by varying the percent per volume of sand (80%, 30%, 15%) in a mixture of sand and potting soil. Medium silica sand and commercially packaged and sterilized potting soil (Meijer's brand, Grand Rapids, MI) were thoroughly mixed in a one yard cement mixer. The potting soil was analyzed for nutrient content, percent organic matter, pH and texture (see Appendix, Table A-2) by the Michigan State University Soil Testing Laboratory. The same analyses were performed for soil samples taken from field sites occupied by natural populations of the five annual species used in this experiment (see Appendix, Table A-3) for comparison to greenhouse soil mixtures. The resulting soil mixtures could be classified as loamy sand, sandy loam and silt loam, respectively.

Differences in water-holding capacity among these soil mixtures have been described in detail by Potvin and Werner, 1984 (see moisture levels 2, 6 and 8 therein; Meijer's potting soil = Vita-Hume brand). The relationship between percent soil moisture and soil water potential is

Figure 3-2. Mean photosynthetic irradiance (± 95 % confidence interval) available to plants at each of six light treatments in the greenhouse (ranging from 2% to 100% of incoming sunlight). Means were obtained by averaging light measurements (in μE m^{-2} s^{-1}) taken under each light treatment at midday and in the early afternoon, throughout the growing season. Measurements made on 29 September were excluded since they were only representative of the light environment at the time most plants were dying (cf. Appendix, Table A-1).

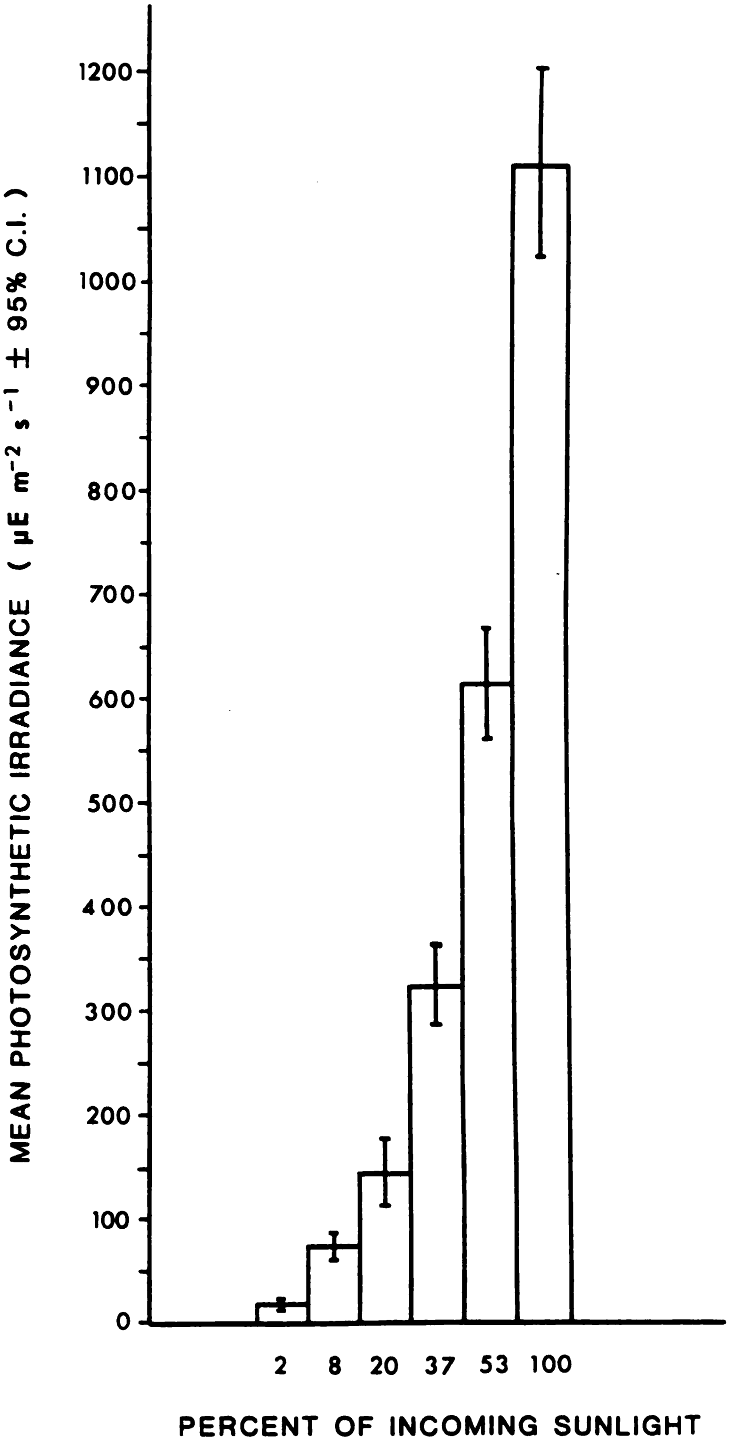
MEAN PHOTOSYNTHETIC IRRADIANCE (μE m⁻² s⁻¹ ± 95% C.I.)
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
2
8
20
37
53
100
PERCENT OF INCOMING SUNLIGHT

Figure 3-2

such that as the proportion of sand in the soil decreases, the percent soil moisture available increases for a given soil water potential. For soil mixtures of low, medium and high water-holding capacity, values of approximately 1%, 11% and 21% soil moisture, respectively, were equivalent to each other in terms of soil water potential at less than -5 bars (Potvin and Werner, 1984).

The percent soil moisture was determined gravimetrically (as g H_2O/g soil dry weight) for each soil mixture throughout the growing season, after intervals of 2-10 days without watering. These values represented the maximum percent soil moisture values for each of the three soil types since most sampling was done from flats or pots without plants (except for 19 August and 7 October samples) (see Appendix, Table A-4). Percent soil moisture for soil mixtures of low, medium and high water-holding capacity are shown for lowest, intermediate and highest light treatments on Figure 3-3.

All flats were kept well watered with a fine mist sprinkling system (Figure 3-1) during the month of April to simulate Spring field moisture conditions. Thereafter, flats or pots were watered to saturation whenever it rained outside the greenhouse (see Appendix, Table A-5, for watering schedule). In order to minimize nutrient differences among soil mixtures, all flats or pots were watered to saturation with a dilute solution of 15:30:15 NPK fertilizer (Miracle Gro) on a biweekly basis. Care was taken to make the time of fertilization coincide with the regular watering schedule to avoid decreasing the osmotic potential of the soil solution to a growth-inhibiting level (Kramer, 1969).

Daily alternating temperature conditions were provided in order to simulate field conditions at time of seedling emergence for the five

Figure 3-3. Mean percent soil moisture (± standard error) for three sand and potting soil mixtures of low (L), medium (M) and high (H) water-holding capacity. Results are shown for greenhouse light treatments of low (<50 μE m^{-2} s^{-1}), intermediate (250–400 μE m^{-2} s^{-1}) and high (>1000 μE m^{-2} s^{-1}) photosynthetic irradiance. The soil samples were taken from flats (n=2 per soil type, April-June) or pots (n=2 per soil type, August-September; n=4-6 for October) filled with one of the three soil mixtures. The number of days without watering is shown in parentheses, under each sampling date (cf. Appendix, Table A-4).

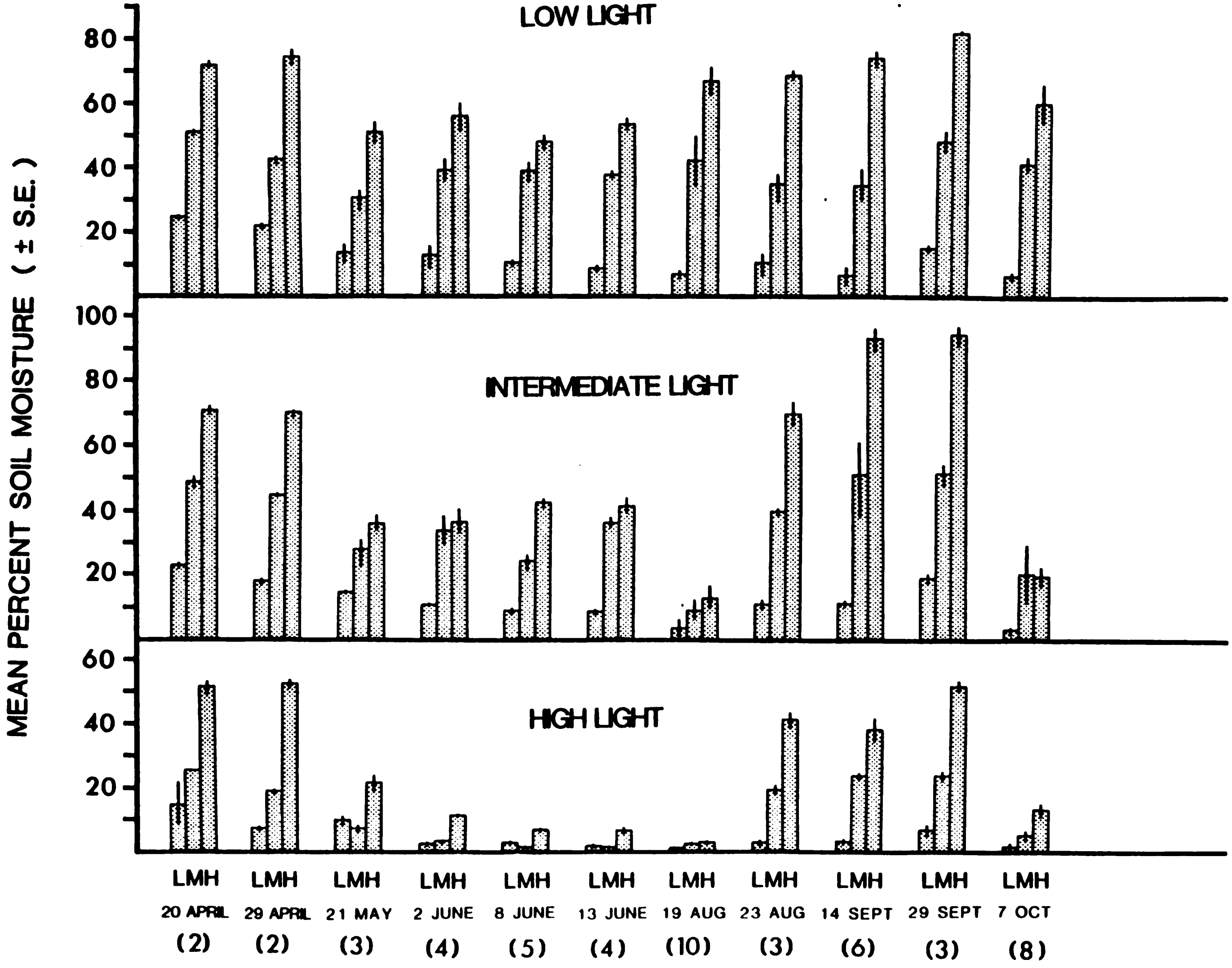
LOW LIGHT
INTERMEDIATE LIGHT
HIGH LIGHT
MEAN PERCENT SOIL MOISTURE (± S.E.)
80
60
40
20
100
80
60
40
20
60
40
20
LMH
20 APRIL
(2)
LMH
29 APRIL
(2)
LMH
21 MAY
(3)
LMH
2 JUNE
(4)
LMH
8 JUNE
(5)
LMH
13 JUNE
(4)
LMH
19 AUG
(10)
LMH
23 AUG
(3)
LMH
14 SEPT
(6)
LMH
29 SEPT
(3)
LMH
7 OCT
(8)

Figure 3-3

species used in this experiment. Greenhouse temperature during April was allowed to rise to between 20°C and 25°C during the day and not allowed to fall below 10°C at night. The daily maximum and minimum air temperatures in the greenhouse were recorded throughout the length of the experiment and compared to field measurements from a weather station located approximately 125 m from the greenhouse. In addition, air temperature was measured under each light treatment in mid and late April, at the time of seedling emergence, and in mid and late August, at the time of reproduction, to determine the effect of the shade fabric on the temperature conditions at each light level.

Description of Environmental Treatment Conditions

Mean photosynthetic irradiance (PAR) on plants differed among light treatments for both midday and early afternoon measurements throughout the year, as indicated by pair-wise comparison of treatment means (Tukey's test modified for heterogeneous variance, see Appendix, Table A-1). Less sunlight was reaching plants in March and September than during the rest of the year. The variance within each light treatment increased with increasing irradiance. The spectral quality of PAR incident on plants did not differ among light treatments and was similar to that of full sunlight at midday for all treatments (Figure A-1).

The percent soil moisture data were analyzed using sampling month, light level and soil type as main effects, in a three-way analysis of variance. The results showed that main effects and all possible interactions were significant (Table 3-1). For any given light level the soil moisture gradient was broader in mid-spring or late summer than in late spring to mid-summer. At low light levels, percent soil moisture for

Table 3-1. Results of a 3-way analysis of variance for percent soil moisture in the greenhouse with month, light treatment and soil mixture as main effects. The arc-sine transformation was used to normalize the data and reduce treatment variance heterogeneity (cf. Appendix, Table A-4).

Source of Variation	Mean Square	F	P	d.f.
Month	3958.48	101.27	0.0000	5
Light	2534.21	64.83	0.0000	5
Soil	19736.55	504.93	0.0000	2
M x L	254.06	6.50	0.0000	25
M x S	590.73	15.11	0.0000	10
L x S	235.11	6.02	0.0000	10
M x L x S	67.28	1.72	0.0031	50
Error	39.09			319

any soil type varied little with time of year. As light increases, soils became drier in mid-summer than they did in spring or late summer. The difference in soil moisture among light treatments was greater at the time of the year with higher temperatures (see Appendix, Table A-6) and with increasing number of waterless days (see Appendix, Table A-5). Although the data were slightly positively skewed even after transformation, the significant values for main effects and interactions were very high and such skewness could be compensated by the robustness of the analysis of variance procedure (Winer, 1971; Underwood, 1981).

The mean maximum and minimum air temperatures in the greenhouse and in the field showed that temperatures in the greenhouse were generally higher than in the field throughout the season (Table A-6). The mean air temperature was generally 3-5°C higher for the 100% incoming sunlight treatment than for the other light treatments. The mean air temperature for the 53% light level was 1-2°C higher than for the other light treatments in the spring but not in the summer. Light levels below 53% incoming sunlight differed little in mean air temperature (Table 3-2).

Description of the Field Environments

To compare the light and soil moisture gradients established in the greenhouse to those observed within sites occupied by the old field and woodland annuals, percent soil moisture and/or light was measured in old field and woodland sites, from May to September,1982 and compared to those in the greenhouse (Tables 3-3 and 3-4). The spectral energy distribution of photosynthetic irradiance was also measured with a spectroradiometer atop the herbaceous layer in the woodland site near midday in mid August, 1982. In the old field, the spectral energy

Table 3-2. Mean air temperature (°C ± standard error) measured in the greenhouse for six light treatments (differing in photosynthetic irradiance - $\mu E\, m^{-2} s^{-1}$), at time of seedling emergence (April - n=4 per treatment) and at time of reproduction (August - n=2-3 per treatment). (The first three sets of temperature readings were done at mid-afternoon on a clear day. The 27 August readings were taken at mid-morning on a partly cloudy day).

	Mean Greenhouse Temperature (°C ± S.E.)					
Date Light Treatment ($\mu E\, m^{-2} s^{-1}$)	<50	50-100	100-200	250-400	550-700	>1000
15 April	22.8 ± 0.1	23.9 ± 0.2	24.4 ± 0.1	25.1 ± 0.1	25.6 ± 0.2	28.1 ± 0.2
24 April	18.9 ± 0.7	20.8 ± 0.1	19.1 ± 0.5	19.7 ± 0.3	22.2 ± 0.2	26.2 ± 0.5
16 August	28.5 ± 0.5	30.0 ± 0.3	29.8 ± 0.2	27.8 ± 2.8	29.0 ± 1.0	33.0 ± 0.5
27 August	21.5 ± 0.0	22.0 ± 0.5	21.5 ± 0.0	24.5 ± 0.5	24.5 ± 0.8	24.8 ± 0.7

Table 3-3. Comparison of the range in photosynthetic irradiance (PAR as $\mu E\ m^{-2} s^{-1}$) on old field and woodland annuals grown over a light gradient in the greenhouse and the mean and range of PAR incident on the same species in field populations, measured at midday, June–September 1982. Mean PAR for the field measurements is shown in parentheses.

	Photosynthetic Irradiance ($\mu E\ s^{-1} m^{-2}$)		
Month	Greenhouse Light Gradient	Old Field	Woods
June	25-1285	474-1900 (1395)	11-300 (52)
July	15-1205	448-1880 (1364)	5-253 (50)
August	7-1138	80-1820 (1195)	5-188 (37)
September	4-880	100-1440 (886)	6-252 (61)

Table 3-4. Comparison of the mean and range in percent soil moisture for greenhouse sand:soil mixtures used to grow old field and woodland annuals, and for soil samples taken from field sites occupied by populations of the same annual species, for June-September 1982. Field sites were sampled in the fourth day after a rainstorm. Greenhouse samples were taken from soil mixtures of low, medium and high water-holding capacity (from each of six light treatments), which had not been watered for approximately the same amount of time as field samples.

Percent Soil Moisture

		Greenhouse Soils			Old Field	Woods
Month		Low	Medium	High		
June	Mean	7.7	21.5	31.0	10.1	26.9
	Range	3.1-11.1[a]	1.3-31.4	7.0-48.3	2.2-33.7	5.2-92.3
August	Mean	9.4	34.9	64.0	8.6	22.4
	Range	3.0-13.1	21.3-39.7	41.5-70.6	2.9-19.9	8.7-35.3
September	Mean	15.4	47.7	80.9	8.0	18.6
	Range	6.4-18.8	23.7-57.8	51.5-94.5	3.0-18.8	10.7-30.0

a = range of mean percent soil moisture over the light gradient distribution atop the herbaceous layer was assumed to be the same as for full sunlight, given no canopy coverage. The woodland spectroradiometric scan was plotted with the scans done for each greenhouse light treatment (Figure A-1). A detailed characterization of light and soil moisture resource levels in the field sites is shown in Figures A-2 through A-4 for a one-year-old field, two-year-old field and disturbed woodland sites.

I measured light reaching both top and base of plants at each site in order to determine the light profile for a particular plant and to describe the light environment that would be experienced by later emerging seedlings at each of the three sites. Six light readings were taken at each of 21 0.25 m^2 plots located along three parallel transects extending diagonally across a 900 m^2 rectangular area. Three readings were taken in each plot at random points atop the surface of the vegetation and three readings were taken per plot at three random points at the base of the vegetation. The percent soil moisture for the same set of plots was determined gravimetrically (as g H_2O/g soil dry weight) for one soil sample per plot taken once a month to a 10 cm depth, four days after a rainstorm.

In the old field, mean photosynthetic irradiance atop of herbaceous vegetation did not vary much throughout the growing season, being somewhat lower in late September than in the previous months. In the woods, light incident on the herbaceous layer decreased considerably from May to June, with canopy closure, and remained relatively low through the rest of the growing season. In contrast, mean photosynthetic irradiance measured at the base of the vegetation in the old field decreased gradually throughout the growing season. In the woods, mean photosynthetic irradiance measured near ground level decreased markedly following canopy closure and increased or decreased each month similarly to light incident on the herbaceous layer (Figure A-2).

Mean photosynthetic irradiance at the top or at the base of the herbaceous layer in the old field was considerably higher than measured for herbaceous vegetation in the woods. There was much more variation about the mean photosynthetic irradiance in the woods than in the old field for light incident on the top of the herbaceous layer, but generally less variation about the mean irradiance values at the base of the vegetation in the woods than in the old field. In the old field, the light environment for plants near ground level is very similar to the woodland light environment at both top and base of the herbaceous vegetation.

The light (Figure A-3) and soil moisture (Figure A-4) conditions experienced by natural populations of the two old field and three woodland annuals were also measured for 0.25 m^2 plots established in Spring 1982 in natural populations of each of the old field and woodland species used in this experiment. If the population had a height structure three light readings were taken at random points atop the tallest vegetation and three readings taken atop the shortest vegetation in each plot.

Mean photosynthetic irradiance was higher for old field annuals than for woodland plants, for measurements taken atop the herbaceous layer. Flowering Chenopodium plants were found over a much broader range of irradiance values than Polygonum plants. Woodland annuals received approximately one third to one half of the mean photosynthetic irradiance on old field annuals. From June to the end of the growing season, only about two fifths of the sunlight incident on old field annuals was available to woodland annuals. The three woodland annuals occurred and flowered at similarly low light levels, over a much smaller range of values than for the old field annuals.

Mean percent soil moisture in the old field was lower than in the woods for all months sampled. In the one-year-old field, percent soil moisture did not change much from June to September, unlike soil moisture in the two-year-old field and in all the woodland sites. The range of soil moisture values for the *Impatiens* site and woods in general was broader than in all old field sites. *Chenopodium* occurred over a broader soil moisture gradient than did *Polygonum*. *Acalypha* and *Pilea* were found in somewhat drier soil conditions than did *Impatiens*, but all three species overlapped in their soil moisture ranges.

Correspondence of Environments in the Field and Greenhouse

The low light treatments in the greenhouse, 2% and 8% of incoming sunlight, corresponded to the low and intermediate portions of the light gradient in the woods (<100 $\mu E\ m^{-2}\ s^{-1}$). The intermediate light treatments, 20% and 37% of incoming sunlight, represented the low end of the light gradient in the old field and the high end of the light gradient in the woods (100 to 400 $\mu E\ m^{-2}\ s^{-1}$). The high light treatments, 53% and 100% of incoming sunlight, corresponded to the middle of the light gradient in the old field and provided more light than was available in the woods, except before canopy closure, in the spring (>550 $\mu E\ m^{-2}\ s^{-1}$). The two low light treatments in the greenhouse corresponded to the light environment at ground level in the woods. Total photosynthetic irradiance incident on the herbaceous layer in the woods was equal to the quantity of light available to plants in intermediate and medium high light treatments in the greenhouse. In the old field, light measured atop herbaceous vegetation was equal to or greater than light incident on plants in the unshaded treatment in the greenhouse. Light energy reaching the base of herbaceous plants in the old field was equal to light available in intermediate or high light treatments in the greenhouse.

Plants received consistently less sunlight at the lowest greenhouse light level than the sunlight that was available to annuals in the old field, but the same or slightly more sunlight than the irradiance in natural populations of woodland annuals. Plants received three to four times more sunlight at the highest light level than was observed for woodland annuals throughout the year, in natural populations (Table 3-3) Woodland herbs received more far red light than red light than was measured for any of the six light treatments in the greenhouse. The red light/far red light ratio in the woods was equal to 0.5 which is typical of vegetation-filtered light (filtered there by the tree canopy) whereas all greenhouse light treatments had a R/FR ratio of approximately 1.2, which is characteristic of full sunlight at midday (Holmes and Smith, 1975).

The soil moisture gradient in the greenhouse was broader than that observed between old field and woodland sites (Table 3-4) during June through September. The soil moisture comparison of old field and woods is for soil samples taken after approximately the same number of days without watering, at the same time of the month and of the year (see Appendix, Table A-3). The low moisture level in the greenhouse was generally lower than the mean percent soil moisture in both the old field and woodland sites. The soil of medium water holding capacity in the greenhouse had a moisture level greater than the mean percent soil moisture in the old field but less than or equal to the moisture available in the woods. The soil of high water holding capacity in the greenhouse on average had a greater moisture content than soils in the old field and in the woods. The differences in moisture content among the three soil types were not stable throughout the year, being greater in mid spring to mid summer. The magnitude of the difference in percent soil moisture among the three soil mixtures decreased as the weather became warmer (Figure 3-3). The change in the difference in moisture content of greenhouse soil mixtures paralleled the change in the range of percent soil moisture from the old field to woodland gradient throughout the year.

Greenhouse Plants

In late March, 1982, after the greenhouse light and soil moisture gradients had been established and temperature conditions had stabilized, six flats (16.8 cm long x 12.5 cm wide x 6 cm deep) were filled with one of each soil mixture for each of the five species and randomly distributed over each of the six greenhouse benches. For each of the five species, there were a total of eighteen light x soil treatment combinations each replicated 6 times for a total of 108 flats per species.

Seeds of the two old field and three woodland annuals had been collected from each of 50 plants (chosen at random along a transect) from natural populations early the previous autumn (1981). *Impatiens* seeds were stored moist in Petri plates from time of collection to time of sowing, in a growth chamber, at 5 °C, with 13 hours of continuous daylight per day (see Leck, 1979; Winsor, 1983 for this species' special germination requirements). Seeds of the other species were stored dry at room temperature in the laboratory until January 1982 and then put in Petri plates and stored moist along with the *Impatiens* seeds until time of sowing. The radicles had ruptured *Impatiens* seed coats in mid- March and had formed the 8-pronged roots characteristic of the genus, but no further growth occurred until the seeds were planted. The same pattern has been observed in the field for seeds stored in mesh bags at the soil surface, throughout the winter (Cid-Benevento, unpublished data). The radicles of *Impatiens* seeds rupture seed coats in March, under heavy snow cover and remain in that state until temperatures get warmer, in mid-April (for southwestern Michigan), when cotyledons emerge and expand rapidly.

The soil surface of each flat was smoothed over and a frame of the same dimensions was placed over the flat prior to sowing seeds, in order to minimize seed lodging at the edges. All seeds were rinsed with tap water, spread out evenly over the soil and hand-misted onto the saturated soil. Seventeen *Impatiens* seeds were sown per flat (70% of the seeds were derived from chasmogamous flowers, with chasmogamous and cleistogamous seeds distributed equally over all flats). For *Acalypha*, fifty seeds were sown per flat. One hundred seeds were sown per flat for each of the other three species.

Seeds were sown over a six-day period between 31 March 1981 and 6 April 1981(Table 3-5). Seedling emergence was monitored every 3-4 days during the month of April and on a weekly basis thereafter. Flats of all species were thinned as needed over the first three weeks in May to

Table 3-5. Seed-sowing schedule and period of seedling emergence for two old field and three woodland annuals in the greenhouse, in Spring 1982.

	Species	Dates Seeds Sown	Seedling Emergence Period
OLD	*Chenopodium*	2 April-4 April	6 April-11 June
FIELD	*Polygonum*	5 April-6 April	12 April- 8 May
	Acalypha	1 April-2 April	14 April- 3 June
WOODS	*Pilea*	5 April	14 April- 9 June
	Impatiens	31 March-1 April	3 April- 2 May

prevent self-shading and minimize intraspecific competition. Each seedling was allowed a circular area with a diameter equal to twice the length of its expanded cotyledons. A grid was placed over each flat to insure randomness in seedling removal. In late June 1982, fourteen seedlings (or fewer, depending on the number of survivors) were chosen at random from each light x soil treatment combination with survivors, for each species, and transplanted individually into 10 cm diameter pots (10 cm deep) filled with the appropriate soil mixture. The pots were then distributed randomly under each light treatment.

Demography

Seedlings were censused every 3-4 days during April and weekly thereafter until time of harvest in mid-October 1982. Two measures of survivorship were obtained: survival of seedlings to time of transplanting and survival of transplants to time of flowering. Both Polygonum and Impatiens seeds and seedlings suffered heavy predation (most likely by rodents) in the 37% incoming sunlight treatment, but sufficient Impatiens seedlings remained to be used as transplants for monitoring reproduction. Polygonum seedlings which had been germinated in a growth chamber were transplanted into the greenhouse flats for this light level to coincide with the May-emerging cohort in the other light treatments. Data for seedling emergence and survival to time of transplanting for Polygonum and Impatiens were excluded from data analysis.

Reproduction was monitored starting with flowering from June to September 1982. Although flower and seed production overlap in all five species, both Chenopodium and Polygonum retain all unfertilized flowers, developing and mature fruits throughout the entire reproductive season whereas Acalypha and Impatiens disperse their seeds as each of these mature. Pilea retains mature seeds for a longer period than do the other woodland annuals but its seeds are dispersed over a longer period than those of Chenopodium and Polygonum. The total number of seeds produced by Chenopodium for the 8%, 20% and 100% incoming sunlight treatments and by Polygonum for 8% - 53% incoming sunlight was obtained by separating and counting seeds from harvested adults. Total Chenopodium seed production per plant for the 37% and 53% incoming sunlight treatments was determined by estimating the number of seeds per gram of reproductive dry weight. Thirty lots of reproductive parts (flower and seeds, only) were weighed for each light x soil treatment combination. The mean number of seeds per gram dry reproductive weight was used to estimate total seed production per Chenopodium plants for these light levels.

For Acalypha, Pilea and Impatiens, flowers, developing fruits and mature fruits were counted on a monthly basis from June to September, 1982. The developing fruits were classified into early-, mid-, late-developing and almost mature categories, and counted on a per axil basis, in order to monitor the dispersal of mature fruits and development of new fruits. The maturation of a fruit was noted in Acalypha by the empty locus left within the floral bract. In Pilea, maturing fruits changed from green to purplish brown, with an empty calyx being a sign of fruit dispersal. For Impatiens, dispersal of mature fruits was recorded by counting the number of remaining pedicels which had a thickened tip at the point of fruit attachment.

A final fruit count was done for only six of the fourteen transplants per treatment combinations for Acalypha and for Pilea at the 20%, 37% and

53% light treatments. Acalypha and Pilea produced a large number of fruits at these light levels which imposed phenological time constraints on the fruit counts. For Acalypha, the total number of seeds produced per plant counted was regressed onto the total dry weight of floral bracts (which remained attached to the stem and branches along with dry immature fruits) in order to estimate seed production for the Acalypha plants not counted. Since the regression did not differ among the three light treatments mentioned, the data from the three light levels was combined for the linear regression ($y = 1864.5\ x + 113.7$, $r=0.94$). For Pilea, the same type of linear regression was done to estimate total seed production for plants not counted in the 20%, 37% and 53% light levels, using total female inflorescence weight per plant (dry weight) as the independent variable in the linear regression. The square root transformation was used to normalize the data distribution. The slope of the regression did differ significantly among light levels ($p < 0.01$) and a separate regression was used for the 20% ($y = 89.6\ x + 21.9$, $r=0.74$), 37% ($y = 35.7\ x + 26.6$, $r=0.66$) and 53% ($y = 32.7\ x + 13.7$, $r=0.68$) light levels to estimate seed production for Pilea plants not counted.

The emergence, survival and seed production data were combined in order to calculate the net replacement rate (R_0) for each species and treatment combination, where R_0 = percent of dispersed seeds which germinate and survive to produce seeds x mean number of seeds produced per transplant.

An analysis of variance was used to detect any significant differences among species, light and soil moisture treatment combinations in seedling emergence, survival of transplants to flowering time and net replacement rate. The data were transformed where necessary to obtain a normal distribution and homogeneous treatment variance. A Tukey test was used for multiple comparisons of treatment means. A modified Tukey test (Gill, 1978) was used to analyze data with substantial treatment variance heterogeneity (instead of an analysis of variance), which included seedling emergence (for woodland annuals), survival to time of transplanting and seed production per transplant.

Transplants were harvested as they died (plants which had dried up and showed signs of chlorophyll loss), with the final harvest occurring in mid-October 1982. All harvested plants were dried in a forced-air oven at 65°C for three days, and stored in newspaper folders inside plastic bags, in order to determine total seed production for plants not counted. Seeds were collected from harvested transplants from each light x soil treatment combination before drying. The number of seeds removed per plant prior to drying was recorded for each transplant to be included in the total seed production for that plant. The standard tetrazolium chloride test (Bonner, 1974) was used to determine seed viability per treatment combination for each species. Twenty or fewer seeds per plant (if a plant did not produce 20 seeds) were collected from four of the five species at all possible treatment combinations. For *Impatiens*, as many seeds as possible were collected (up to 20 seeds per plant) for the viability test, since this species' naturally low seed production per plant and explosive seed dispersal system (which requires bagging all flowers in order to retain all the seeds produced per plant) made it very difficult to collect as many seeds as was done for the other species.

RESULTS

There were no consistent differences between old field and woodland annuals in their seedling emergence, survivorship and onset of flowering responses over both light and soil moisture gradients. Differences within each group in seedling emergence over the gradients were as great as differences between groups of annuals (Figure 3-4). For both old field and woodland annuals, survivorship was generally high at intermediate light levels, regardless of soil type and low at the extremes of the light gradient, particularly in soils of medium and high water-holding capacity (Figure 3-5). In addition, in both groups, flowering started later at low light treatments than at intermediate or high light treatments (Table 3-6).

The only consistent difference between old field and woodland annuals in response to the experimental gradients was observed at the reproductive phase. Old field annuals produced few or no seeds at light levels below 250 $\mu E\ m^{-2}\ s^{-1}$. In general, woodland annuals produced significantly more seeds than old field annuals at low and intermediate light levels. At least one of the three woodland annuals (Acalypha) was able to produce seeds over the entire light gradient (Figure 3-6).

Seedling emergence

Light treatment and soil type had a significant effect on percent seedling emergence (Table 3-7). There were no significant interactions between light treatment and soil type on the emergence response nor a three-way interaction among species, light and soil moisture treatment. Approximately 80% or more of all seedlings emerged in April, except for Chenopodium and Acalypha. Chenopodium, Polygonum and Acalypha had higher

Figure 3-4. Seedling emergence of two old field (at top of figure) and three woodland annuals (at bottom of figure) over light and soil moisture gradients in the greenhouse. Percent seedling emergence is plotted for each species for soil mixtures of low (L, closed circle and dotted line), medium (M, open triangle and dashed line) and high (H, closed square and solid line) water-holding capacity over a photosynthetic irradiance gradient of <50 to >1000 $\mu E\ m^{-2}\ s^{-1}$. The values for Polygonum and Impatiens at the 250-400 $\mu E\ m^{-2}\ s^{-1}$ light level (indicated with an *) are the values for percent seedling emergence, including losses due to heavy predation of both seeds and April-emerging seedlings.

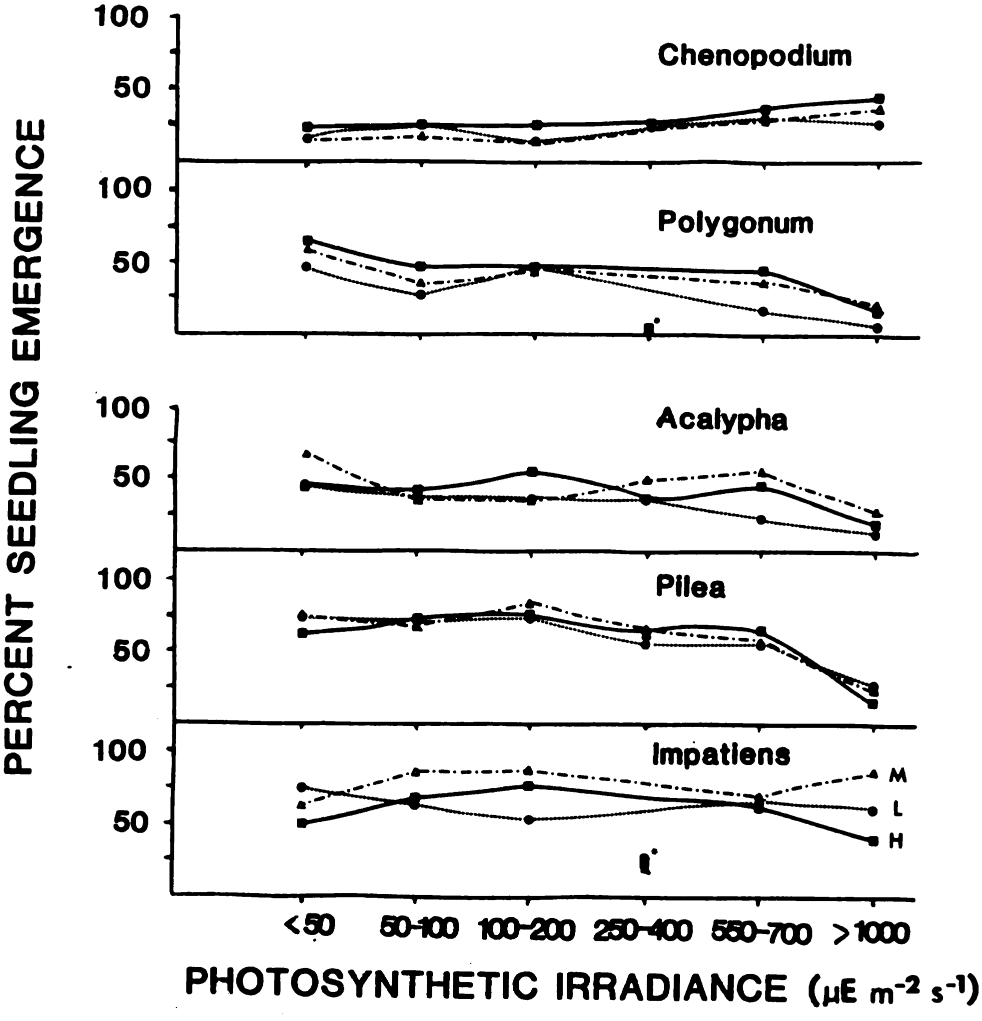
PERCENT SEEDLING EMERGENCE
100
50
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
M
L
H
<50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE (µE m-2 s-1)

Figure 3-4

Figure 3-5. Seedling survivorship to flowering time for two old field (at top of figure) and three woodland annuals (at bottom of figure) over light and soil moisture gradients in the greenhouse. Two measures of survivorship, percent survival of seedlings to transplanting time and percent survival of transplants to flowering time, were combined and plotted for each species, for soil mixtures of low (L, solid circle and dotted line), medium (M, open triangle and dashed line) and high (H, closed square and solid line) water-holding capacity, over a photosynthetic irradiance gradient <50 - >1000 $\mu E\ m^{-2}\ s^{-1}$. Survivorship values for Polygonum and Impatiens for the 250-400 $\mu E\ m^{-2}\ s^{-1}$ light level may be lower than expected due to heavy predation losses of both seeds and April-emerging seedlings of these species.

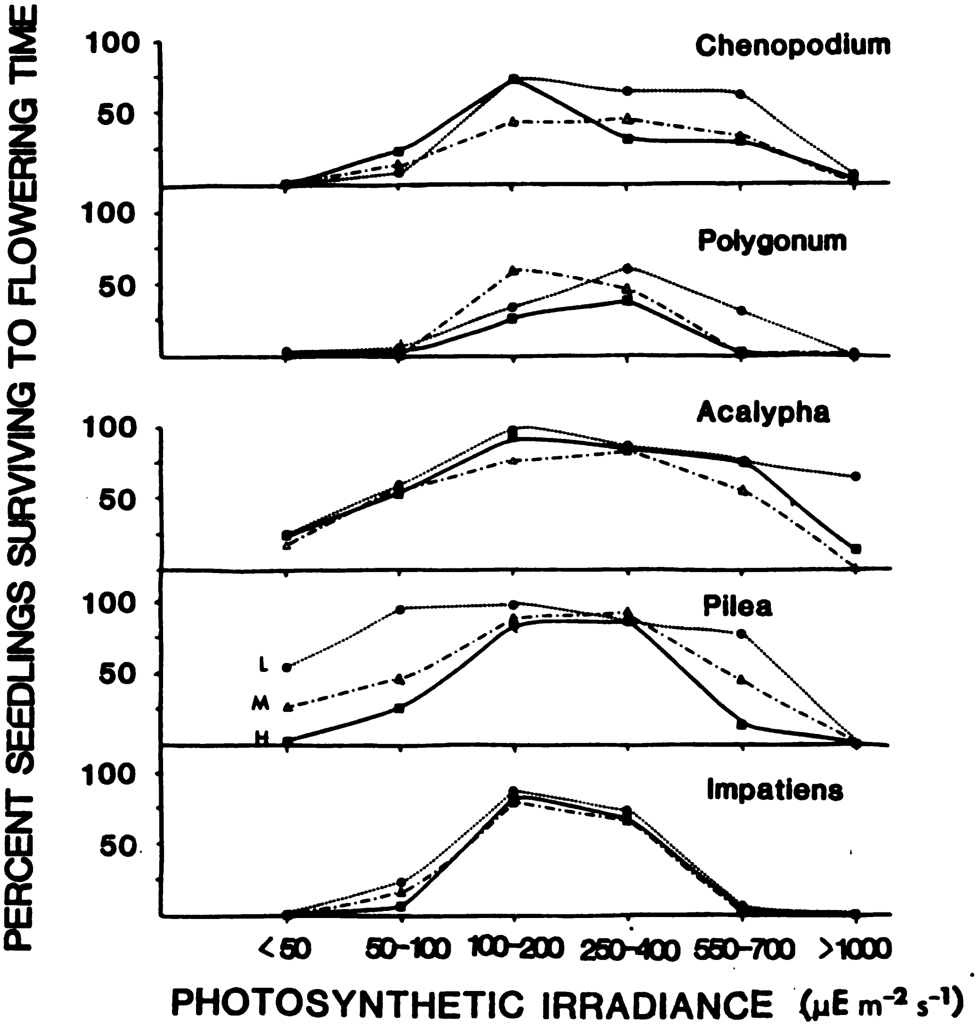
PERCENT SEEDLINGS SURVIVING TO FLOWERING TIME
100
50
Chenopodium
100
50
Polygonum
100
50
Acalypha
100
50
Pilea
L
M
H
100
50
Impatiens
<50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE (µE m-2 s-1)

Figure 3-5

Table 3-6. Flowering phenology of two old field and three woodland annuals over a light gradient (in $\mu E\ m^{-2} s^{-1}$) in the greenhouse.

			Time of Year Most Plants Started to Flower					
	Light Treatment ($\mu E\ m^{-2} s^{-1}$)		<50	50-100	100-200	250-400	550-700	>1000
	Species							
OLD FIELD	Chenopodium		no survivors	late Sept.	early Sept.	late August	late August	late August
	Polygonum		no survivors	late Sept.	early Sept.	late August	late August	no survivors
WOODS	Acalypha		mid-Sept.	mid-August	early July	mid-July	mid-July	late July
	Pilea		mid-August mid-Sept.	mid-August early Sept.	mid-July late August	mid-July mid-August	mid-July mid-August	no survivors
	Impatiens	Ch	no survivors	no ch flowers	late August	mid-August	no survivors	no survivors
		Cl		late August	mid-July	early August	early August	

Ch = chasmogamous flowers
Cl = cleistogamous flowers

Figure 3-6. Mean seed production per transplant for two old field (at top of figure) and three woodland annuals (at bottom of figure) over light and soil moisture gradients in the greenhouse. Seed production values are plotted for each species for three soil mixtures of low (L, solid circle and dotted line), medium (M, open triangle and dashed line) and high (H, closed square and solid line) water-holding capacity, over a photosynthetic irradiance gradient of <50 to >1000 $\mu E\ m^{-2}\ s^{-1}$.

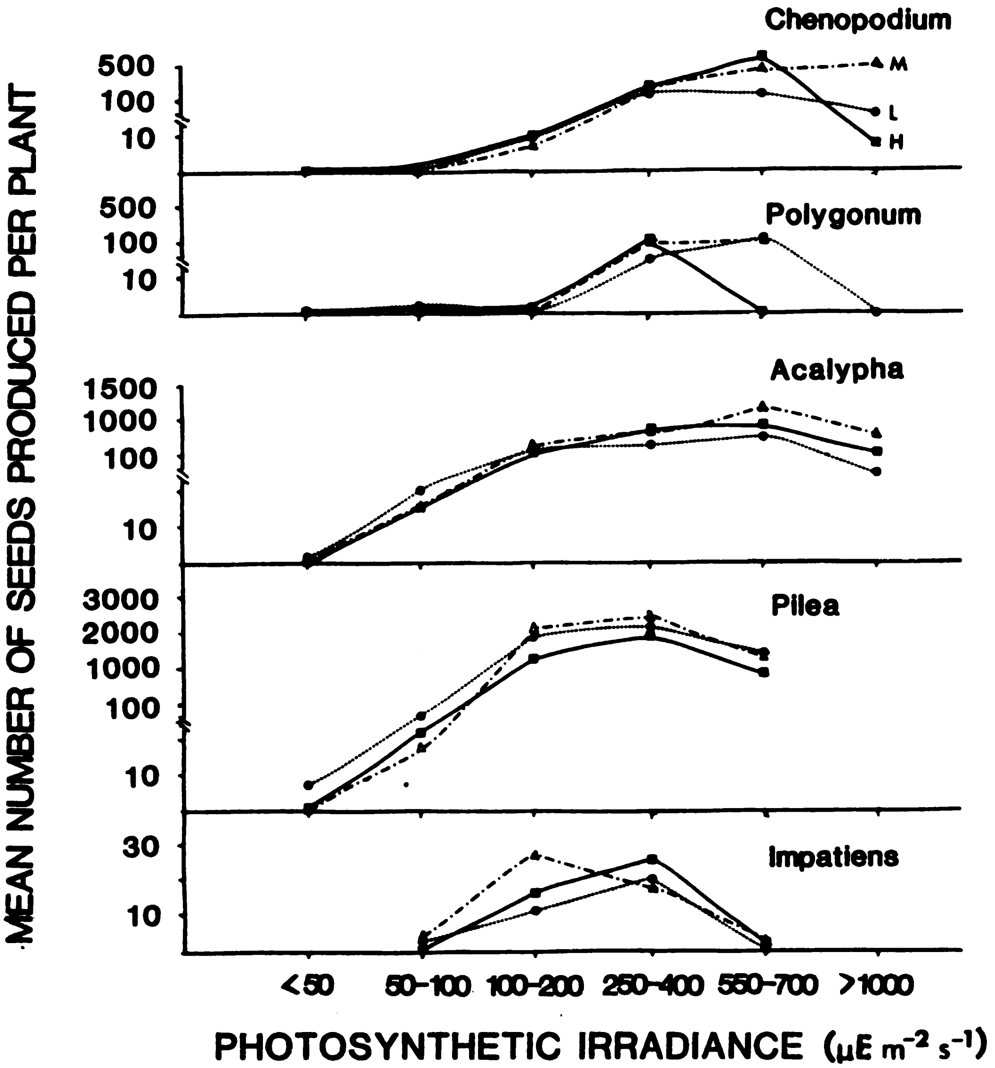
Chenopodium
500
100
10
M
L
H
500
Polygonum
100
10
Acalypha
1500
1000
100
10
3000
2000
1000
100
10
Pilea
30
10
Impatiens
<50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE (µE m⁻² s⁻¹)
MEAN NUMBER OF SEEDS PRODUCED PER PLANT

Figure 3-6

Table 3-7. Results of a 3-way analysis of variance for percent seedling emergence of two old field and three woodland annuals in the greenhouse, with species, light treatment and soil mixture as main effects. The arc sine transformation was used to normalize the data distribution and equalize treatment variances.

Source of Variation	Mean Square	F	p	d.f.
Species (K)	11792.24	63.61	0.0000	4
Light	3145.14	16.97	0.0000	4
Soil	1565.63	8.45	0.0003	2
K x L	1172.17	6.32	0.0000	16
K x S	444.90	2.40	0.0156	8
L x S	275.11	1.48	0.1612	8
K x L x S	193.21	1.04	0.4080	32
Error	185.38			375

emergence in May than the other two species (Table 3-8).

The two old field annuals had completely opposite seedling emergence responses to the light gradient but similar although not equal responses to the soil moisture gradient (Figure 3-4). For Chenopodium, the lowest seedling emergence values were observed at light levels of <200 μE m^{-2} s^{-1} in soils of low and medium water-holding capacity. The highest emergence values were observed at light levels >550 μE m^{-2} s^{-1} in soils of medium and high water-holding capacity. No significant differences in seedling emergence were observed among soil mixtures (Table 3-9). However, a trend of increasing emergence with increasing water-holding capacity of the soil mixture was observed at low and at high light but not at intermediate light levels.

Polygonum had its lowest emergence values at light levels >550 μE m^{-2} s^{-1} in the sandiest soil mixture and its highest emergence values at light levels <200 μE m^{-2} s^{-1}. Polygonum had significantly lower emergence in the sandiest soil than in the other soil mixtures at high light treatments (Table 3-9). Higher emergence values were observed in soils of medium and high water-holding capacity.

The woodland annuals had a similar seedling emergence response to the light gradient, with very low emergence observed only at the highest light level. The three species differed somewhat in their response to the soil mixtures although they generally had higher emergence in soils of medium or high water-holding capacity (Figure 3-4).

Emergence of Acalypha at the highest light level in the sandiest soil was significantly lower than at either the lowest light level or at the next to highest light level in soils of medium water-holding capacity. There was no significant effect of soil type on seedling emergence.

Table 3-8. Percent of all seedlings which emerged each month, prior to transplanting, for old field and woodland annuals, over light and soil moisture gradients in the greenhouse. The light gradient ranged from <50 to >1000 $\mu E\ m^{-2}\ s^{-1}$. The soil moisture gradient consisted of three sand:soil mixtures of low (L), medium (M), and high (H) water-holding capacity.

			Percent of All Seedlings																	
		Light Treatment ($\mu E\ m^{-2}\ s^{-1}$)	<50 Soil Mixture			50–100 Soil Mixture			100–200 Soil Mixture			250–400 Soil Mixture			550–700 Soil Mixture			>1000 Soil Mixture		
	Species	Month	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
OLD FIELD	Chenopodium	April	37	73	82	69	92	67	80	91	92	98	85	94	80	94	94	75	79	85
		May	61	25	15	29	6	32	20	9	8	2	15	5	20	6	6	22	14	13
		June	2	2	3	2	2	1	0	0	0	0	0	1	0	0	0	3	7	2
	Polygonum	April	79	85	79	93	96	95	88	79	78	—	—	—	90	98	94	85	89	82
		May	20	14	21	7	3	5	12	21	21	—	—	—	10	2	6	15	11	17
		June	1	1	0	0	1	0	0	0	1	—	—	—	0	0	0	0	0	1
WOODS	Acalypha	April	73	88	89	63	62	78	58	80	75	46	65	53	58	59	71	61	56	57
		May	27	10	11	37	38	22	42	20	25	45	33	47	42	40	29	39	42	42
		June	0	1	0	0	0	0	0	0	0	9	2	0	0	1	0	0	2	1
	Pilea	April	96	100	99	91	97	94	93	97	99	81	92	97	87	95	94	94	100	98
		May	3	0	0	9	3	5	7	3	1	18	6	3	13	5	6	6	0	2
		June	1	0	1	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0
	Impatiens	April	100	100	100	100	10	100	96	100	100	100	100	100	100	100	100	100	100	100
		May	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
		June	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3-9. Results of Tukey's test for pair-wise comparisons of treatment means for percent seedling emergence of two old field and three woodland annuals, which were grown over light and soil moisture gradients in the greenhouse. Results are shown for six light treatments, ranging from <50 to >1000 $\mu E\ m^{-2} s^{-1}$, and for three soil mixtures of low (L), medium (M) and high (H) water holding capacity. The test was performed separately for each species and modified for heterogeneous treatment variance, for the woodland annuals. Means not sharing a superscript are significantly different from each other with $p<0.05$. ($n=6$ flats per treatment combination)

		Light Treatment ($\mu E m^{-2} s^{-1}$)	Mean Percent Seedling Emergence					
	Species	Soil Mixture	<50	50-100	100-200	250-400	550-700	>1000
OLD FIELD	*Chenopodium*	L	17.5^{a}	25.5^{ab}	14.3^{a}	22.0^{ab}	29.5^{abc}	26.8^{abc}
		M	17.2^{a}	18.2^{a}	15.2^{a}	21.3^{ab}	29.8^{abc}	35.8^{bc}
		H	21.2^{ab}	24.0^{ab}	25.0^{ab}	25.2^{ab}	35.7^{bc}	41.7^{c}
	Polygonum	L	48.8^{de}	28.8^{bc}	45.3^{d}	-*-	18.7^{b}	4.8^{a}
		M	59.3^{e}	36.3^{cd}	43.8^{d}	-*-	34.5^{c}	20.0^{b}
		H	61.7^{e}	48.7^{de}	47.7^{d}	-*-	42.2^{cd}	17.5^{b}
WOODS	*Acalypha*	L	43.7^{ab}	36.7^{ab}	35.3^{ab}	33.0^{ab}	21.0^{ab}	11.3^{a}
		M	67.0^{b}	32.7^{ab}	33.0^{ab}	49.3^{ab}	53.3^{b}	26.7^{ab}
		H	42.7^{ab}	42.3^{ab}	52.3^{ab}	33.3^{ab}	46.3^{ab}	18.7^{ab}
	Pilea	L	71.3^{bc}	70.8^{bc}	71.5^{bc}	55.8^{b}	54.8^{b}	12.5^{a}
		M	75.2^{bc}	68.3^{bc}	81.7^{c}	65.0^{bc}	58.0^{bc}	22.2^{abc}
		H	61.2^{bc}	72.3^{bc}	77.2^{bc}	63.0^{bc}	64.5^{bc}	26.5^{abc}
	Impatiens	L	77.0^{ab}	61.8^{ab}	51.5^{ab}	-*-	64.5^{ab}	59.8^{ab}
		M	60.8^{ab}	84.9^{b}	88.2^{b}	-*-	68.6^{ab}	86.3^{b}
		H	50.0^{ab}	65.6^{ab}	78.3^{ab}	-*-	63.7^{ab}	39.5^{a}

* = data values not included in the analysis due to heavy seed predation.

However, in four out of six light treatments, emergence was higher in the soil of medium water-holding capacity than in the other soil mixtures (Table 3-9).

Pilea emergence was low only at the highest light level. Emergence at the highest light level in the sandiest soil was significantly lower than for all other light levels, regardless of soil type. Highest emergence for each light treatment was observed in soils of medium or high water-holding capacity, but no significant differences in emergence were observed among soil types for any particular light treatment (Table 3-9).

Impatiens emergence was lowest at the highest light level in the soil of high water-holding capacity. Emergence was high at light levels <200 $\mu E\ m^{-2}\ s^{-1}$ and at the highest light level, in soils of medium water-holding capacity. In five of six light treatments, emergence was higher in the soil of medium water-holding capacity than in the other mixtures, although not resulting in a significant difference among soil mixtures except at the highest light level (Table 3-9).

Survivorship

Most of the mortality occurred before late June, prior to the time of transplanting. Most seedlings died during hot, dry periods except for Polygonum and Impatiens seedlings. Polygonum seedlings suffered fungal attack at all light levels but especially at lower light levels ($< 250\ \mu E\ m^{-2}\ s^{-1}$). Impatiens seedlings at the lowest light level were severely etiolated and died primarily due to lodging.

A trend for higher survivorship in the sandiest soil was noted for both groups of annuals. However, soil type had no significant effect on survivorship to time of transplanting at any light level for old field annuals. In woodland annuals, the only significant difference in seedling survivorship among soil types were observed for Pilea and Impatiens at the second highest light level and for Impatiens at the second lowest light level (Table 3-10).

Chenopodium survivorship to transplanting time was highest at light levels of 100-700 $\mu E\ m^{-2}\ s^{-1}$ in the sandiest soil, and in the soil of highest water-holding capacity for the 100-200 $\mu E\ m^{-2}\ s^{-1}$ light treatment (Table 3-10).

Polygonum survivorship was highest at intermediate light levels in soils of low and medium water-holding capacity. For any given light level, survivorship was highest in the sandiest soil, except at the 100-200 $\mu E\ m^{-2}\ s^{-1}$ light treatment where highest survivorship was observed in the soil of medium water-holding capacity. Polygonum survivorship decreased with increasing water-holding capacity of the soil for all light treatments except the 100-200 $\mu E\ m^{-2}\ s^{-1}$ light level, whereas for Chenopodium such a trend was evident only for light levels $>200\ \mu E\ m^{-2}\ s^{-1}$ (Table 3-10).

For woodland annuals, Acalypha had seedlings surviving to transplanting time for all light treatments and soil types. Pilea had no survivors at the highest level whereas no Impatiens plants survived to transplanting time at either extreme of the light gradient (Figure 3-5).

Acalypha had significantly higher survivorship at light levels ranging from 100 to 400 $\mu E\ m^{-2}\ s^{-1}$, regardless of soil type, than at the highest light level, in soils of medium and high water-holding capacity. Pilea had significantly higher survivorship for light levels ranging from 50 to 700 $\mu E\ m^{-2}\ s^{-1}$, particularly in the sandiest soil, than at the extremes of the light gradient. For Impatiens, survivorship was highest

Table 3-10. **Results of Tukey's test for pair-wise comparisons of treatment means for seedling survivorship to time of transplanting, for two old field and three woodland annuals, which were grown over light and soil moisture gradients in the greenhouse. Results are shown for six light treatments, ranging from <50 to >1000 $\mu E\ m^{-2} s^{-1}$, and for three soil mixtures of low (L), medium (M) and high (H) water-holding capacity. The test was performed separately for each species and modified for heterogeneous treatment variance. Means not sharing a superscript are significantly different from each other with $p<0.05$. ($n=6$ flats per treatment combination)**

			Mean Percent Seedling Survivorship					
		Light Treatment ($\mu E\ m^{-2} s^{-1}$)	<50	50-100	100-200	250-400	550-700	>1000
	Species	**Soil Mixture**						
OLD FIELD	*Chenopodium*	L	16.7^{ab}	33.5^{ab}	79.0^{b}	62.5^{b}	63.4^{b}	3.2^{a}
		M	0^{a}	37.0^{ab}	42.6^{ab}	44.3^{ab}	31.5^{ab}	0.6^{a}
		H	16.1^{a}	39.8^{ab}	79.3^{b}	32.3^{ab}	29.2^{ab}	0.5^{a}
	Polygonum	L	1.0^{a}	7.9^{ab}	53.8^{ab}	59.9^{ab}	31.9^{ab}	6.3^{a}
		M	0^{a}	2.9^{a}	74.8^{b}	44.9^{ab}	0.8^{a}	0^{a}
		H	0.5^{a}	0.5^{a}	45.9^{ab}	37.4^{ab}	0^{a}	0^{a}
WOODS	*Acalypha*	L	64.3^{ac}	72.0^{bc}	99.4^{b}	88.1^{b}	76.4^{bc}	64.7^{abc}
		M	39.7^{ac}	75.0^{bc}	75.3^{bc}	81.2^{b}	65.3^{ac}	9.0^{a}
		H	28.9^{ac}	79.1^{b}	93.7^{b}	85.0^{b}	75.8^{ac}	12.5^{ac}
	Pilea	L	60.0^{bc}	99.4^{c}	98.8^{c}	92.1^{c}	75.9^{c}	0^{a}
		M	6.6^{ab}	52.8^{bc}	90.5^{c}	91.3^{c}	42.5^{bc}	0^{a}
		H	12.9^{ab}	35.2^{bc}	72.0^{bc}	85.5^{c}	10.7^{ab}	0^{a}
	Impatiens	L	0^{a}	49.3^{bc}	93.9^{b}	81.9^{ab}	44.3^{bc}	0^{a}
		M	0^{a}	20.5^{ac}	85.3^{b}	63.9^{ab}	0.5^{a}	0^{a}
		H	0^{a}	5.3^{a}	93.0^{b}	68.3^{ab}	14.5^{ac}	0^{a}

at intermediate light levels especially at the 100-200 E m^{-2} s^{-1} light level (Table 3-10).

A 2-way analysis of variance for survivorship of transplants to flowering time for each species, using light treatment and soil type as main effects, indicated that light had a significant effect on survivorship of transplants for all five species and soil type did not (Table 3-11). Survivorship was lower at the extremes of the light gradient than for light levels ranging from approximately 100 to 700 μE m^{-2} s^{1} (Table 3-12).

Reproduction

Flowering phenology

Old field annuals flowered 1-3 weeks later at light levels <250 μE m^{-2} s^{-1} than at the other light levels. In woodland annuals, an even greater delay was observed in the onset of flowering (up to 9 weeks) than in old field annuals, with decreasing photosynthetic irradiance, (particularly at light levels <100 μE m^{-2} s^{-1}). Phenological differences among soil mixtures were not noticeable using a weekly time scale (Table 3-6).

Acalypha started to flower first at the 100-200 μE m^{-2} s^{-1} light level (male and female flower production starts at the same time). Plants in light levels > 200 μE m^{-2} s^{-1} began to flower 1-2 weeks later whereas plants growing at <100 μE m^{-2} s^{-1} did not start to flower until 5-9 weeks later.

For Pilea, male flower production began in mid-July at light levels >100 μE m^{-2} s^{-1} and four weeks later at lower light levels. Female flowers were first clearly noticeable in mid-August at light levels > 250 μE m^{-2}

Table 3-11. Results of a 2-way analysis of variance for mean percent survivorship of transplants to flowering time for two old field and three woodland annuals, with light treatment and soil mixture as main effects.

	OLD FIELD								WOODS											
Source of Variation	Mean Square	F	p	df	Mean Square	F	p	df	Mean Square	F	p	df	Mean Square	F	p	df	Mean Square	F	p	df
Light	5096.20	11.55	0.00	5	5066.89	6.84	0.01	5	994.67	9.95	0.00	5	1429.92	6.89	0.01	4	3883.22	19.30	0.00	3
Soil	230.68	0.52	0.61	2	1283.55	1.73	0.23	2	143.13	1.43	0.28	2	356.86	1.72	0.24	2	575.62	2.86	0.13	2
Error	441.30			10	740.93			10	99.98			10	207.63			8	201.25			6

Table 3-12. Survivorship of two old field and three woodland annuals to the time of flowering for individuals transplanted from flats into pots in late June, 1982, and grown over light and soil moisture gradients in the greenhouse. Results are shown for six light levels ranging from <50 to >1000 $\mu E\ m^{-2}\ s^{-1}$ and three soil mixtures of low (L), medium (M) and high (H) water-holding capacity. (n=14 transplants per treatment combination except where indicated differently in parentheses)

			Percent Survivorship of Transplants to Flowering Time					
		Light Treatment ($\mu E\ m^{-2}\ s^{-1}$)	<50	50-100	100-200	250-400	550-700	>1000
	Species	Soil Mixture						
OLD FIELD	*Chenopodium*	L	0	28.6	92.9	100	100	92.9
		M	—*	28.6	100	100	100	57.1
		H	0	50.0	92.9	100	100	54.5 (11)
	Polygonum	L	0 (7)	66.7 (3)	57.1	100	100	0 (2)
		M	—	0 (7)	78.6	100	100 (1)	—
		H	0 (3)	0 (1)	57.1	100	—	—
WOODS	*Acalypha*	L	42.9	78.6	100	100	100	100
		M	42.9	78.6	100	100	100	100 (2)
		H	78.6	78.6	100	100	100	100 (7)
	Pilea	L	85.7	92.9	100	100	100	—
		M	35.7	85.7	100	100	100	—
		H	28.6	71.4	100	100	100	—
	Impatiens	L	—	42.9	92.9	85.7	14.3	—
		M	—	70.0 (10)	92.9	100	33.3 (3)	—
		H	—	0 (2)	92.9	100	40.0 (5)	—

* = dashed line indicates that no seedlings survived to time of transplanting.

s^{-1} and 1-4 weeks later at lower light levels.

For Impatiens, both the onset of flowering and the type of flower produced responded to changes in photosynthetic irradiance. Cleistogamous flowering started 1-5 weeks earlier than chasmogamous flower production for light levels at which both flower types where produced. Cleistogamous flowering started in mid-July for the 100-200 $\mu E\ m^{-2}\ s^{-1}$ light level and 3-5 weeks later at the other light levels. No plants survived to produce chasmogamous flowers at the next to highest light treatment and none of the survivors produced chasmogamous flowers at the next to lowest light treatment. Chasmogamous flowers were produced only at the two intermediate light levels starting in mid-August at the higher of the two light levels and one week later at the lower light level.

Seed production

Chenopodium produced a significantly higher number of seeds per plant at the 550-700 $\mu E\ m^{-2}\ s^{-1}$ light level in soils of medium and high water-holding capacity and in the intermediate moisture level for the unshaded light treatment, than in all other treatment combinations (Table 3-13).

In contrast, Polygonum flowered but did not set seed at the 550-700 $\mu E\ m^{-2}\ s^{-1}$ light level in the soil of high water-holding capacity and did not survive to flowering time at the highest light level. For Polygonum, mean seed production per transplant was significantly higher at light levels between 250 and 700 $\mu E\ m^{-2}\ s^{-1}$ than for any other light treatment (Table 3-13).

In general, woodland annuals produced a significantly lower mean number of seeds per plant at the extremes of the light gradient (except for Acalypha plants at the highest light treatment in the soil of medium

Table 3-13. Results of Tukey's test for pair-wise comparisons of treatment means for seed production of two old field and three woodland annuals, which were grown over light and soil moisture gradients in the greenhouse. Results are shown for six light treatments ranging from <50 to >1000 $\mu E\ m^{-2} s^{-1}$, and for three soil mixtures of low (L), medium (M) and high (H) water holding capacity. The test was performed separately for each species and modified for heterogeneous treatment variance. Means not sharing a superscript are significantly different from each other with $p<0.05$. (n=1-14 plants per treatment combination)

			Mean Seed Production per Transplant					
		Light Treatment ($\mu E\ m^{-2} s^{-1}$)	<50	50-100	100-200	250-400	550-700	>1000
	Species	Soil Mixture						
OLD FIELD	**Chenopodium**	L	0^{a}	0.1^{a}	9.9^{a}	157.5^{b}	155.6^{b}	52.6^{b}
		M	*	0^{a}	7.5^{a}	216.5^{b}	468.1^{c}	492.0^{c}
		H	0^{a}	0^{a}	13.2^{a}	206.2^{b}	569.6^{c}	7.3^{a}
	Polygonum	L	0^{a}	2.3^{a}	0^{a}	53.1^{b}	173.3^{b}	0^{a}
		M	0^{a}	0^{a}	1.1^{a}	100.1^{b}	109.0^{b}	—
		H	0^{a}	0^{a}	1.3^{a}	105.6^{b}	0^{a}	—
WOODS	**Acalypha**	L	0.5^{a}	23.8^{a}	161.3^{b}	417.7^{b}	535.0^{c}	54.6^{abd}
		M	0.2^{a}	15.8^{a}	281.5^{b}	704.1^{c}	1041.3^{c}	539.5^{cd}
		H	1.2^{a}	14.5^{a}	271.2^{b}	684.5^{c}	909.7^{c}	183.3^{abd}
	Pilea	L	7.9^{ab}	75.7^{b}	1447.2^{c}	1533.3^{c}	887.9^{c}	—
		M	0.2^{a}	17.7^{b}	2347.1^{c}	2316.9^{c}	1602.6^{c}	—
		H	0.5^{a}	35.9^{b}	2297.8^{c}	2248.1^{c}	1364.0^{c}	—
	Impatiens	L	—	3.2^{a}	11.5^{ab}	20.7^{ab}	0.7^{a}	—
		M	—	4.7^{a}	27.1^{b}	17.4^{ab}	3.7^{ab}	—
		H	—	0^{a}	16.4^{ab}	25.8^{ab}	2.0^{ab}	—

* = dashed line indicates that no seedlings survived to time of transplanting.

water-holding capacity), than at intermediate light levels (Figure 3-6). Pilea and Acalypha had high mean seed production per plant at light levels ranging (respectively) from 100 and 200 (respectively) to 700 μE m^{-2} s^{-1}. Impatiens had its highest mean seed production per plant only at intermediate light levels (Figure 3-6).

Soil moisture had a significant effect on seed production only for Acalypha of the three woodland annuals at one intermediate light level (250-400 μE m^{-2} s^{-1}) (Table 3-13). Acalypha produced significantly fewer seeds in the sandiest soil than in the two other soil mixtures for that light treatment.

Approximately 80% or more of the seeds produced by both old field and woodland annuals were viable, among all possible treatment combinations (Table 3-14). In general, there were no significant differences in seed viability among treatment combinations for any species. Only Acalypha had <95% viable seeds (78.8%) at a given treatment combination and only at the highest light level and soil of high water-holding capacity. This was due to plants dispersing many immature seeds during dry periods. Generally, for all five species, only seeds that were not completely filled were not viable, and they constituted a very small portion of the seed crop.

Net Replacement Rate (R_0)

Light had a significant effect on the net replacement rate of all species whereas soil moisture significantly affected the net replacement rate of only Acalypha out of the five species (Table 3-15). Net replacement rate for old field annuals at the low light levels was most affected by a delay in the onset of flowering and by the inability to

Table 3-14. Percent seed viability for seeds collected from two old field and three woodland annuals, grown over light and soil moisture gradients in the greenhouse. Mean percent viable seeds is shown for six light treatments, ranging from <50 to >1000 $\mu E\ m^{-2}\ s^{-1}$, and three soil mixtures of low (L), medium (M) and high (H) water-holding capacity. (n=number of seeds tested per treatment combination)

		Light Treatment ($\mu E\ m^{-2}\ s^{-1}$)	Mean Percent Seeds Viable					
			<50	50-100	100-200	250-400	550-700	>1000
	Species	Soil Mixture						
OLD FIELD	Chenopodium	L	—*	100 (1)	100 (97)	100 (280)	100 (140)	100 (58)
		M	—	—	100 (112)	100 (280)	100 (280)	100 (100)
		H	—	—	100 (112)	100 (280)	100 (280)	100 (20)
	Polygonum	L	—	100 (7)	—	100 (254)	100 (242)	—
		M	—	—	100 (16)	100 (230)	100 (20)	—
		H	—	—	100 (18)	99.6 (268)	—	—
WOODS	Acalypha	L	100 (9)	100 (163)	100 (280)	100 (280)	100 (280)	98.3 (143)
		M	100 (4)	100 (178)	100 (280)	100 (280)	96.4 (280)	100 (40)
		H	100 (20)	100 (167)	98.1 (280)	97.6 (280)	97.5 (280)	78.8 (80)
	Pilea	L	100 (86)	99.1 (240)	100 (280)	100 (280)	99.3 (280)	—
		M	100 (4)	100 (255)	100 (280)	100 (280)	99.6 (280)	—
		H	100 (7)	100 (176)	99.7 (280)	100 (280)	100 (280)	—
	Impatiens	L	—	100 (27)	100 (84)	100 (141)	100 (5)	—
		M	—	100 (25)	100 (180)	100 (110)	100 (5)	—
		H	—	—	100 (106)	100 (144)	100 (4)	—

* = dashed line indicates that no seeds were produced at this light x soil moisture treatment combination.

Table 3-15. Results of a 2-way analysis of variance for net replacement rate (R_0) in the greenhouse for each of two old field and three woodland annuals, with light treatment and soil mixture as main effects. The natural log transformation (ln [R_0 + 0.5]) was used to normalize the data and eliminate heterogeneity of treatment variances.

	OLD FIELD						WOODS									
Source of	*Chenopodium*			*Polygonum*			*Acalypha*			*Pilea*			*Impatiens*			d.f.
Variation	Mean Square	F	p	Mean Square	F	p	Mean Square	F	p	Mean Square	F	p	Mean Square	F	p	
Light	11.11	78.52	0.00	4.94	10.13	0.00	17.05	108.53	0.00	36.19	79.31	0.00	4.95	46.54	0.00	5
Soil	0.07	0.47	0.64	0.30	0.61	0.56	0.77	4.88	0.03	0.88	1.94	0.19	0.05	0.49	0.63	2
Error	0.14			0.49			0.16			0.46			0.11			10

produce enough seeds whereas at the highest light level R_0 was most affected by low seedling survival. In woodland annuals the net reproductive rate was most affected by either or both low survival and low seed production at the extremes of the light gradient.

For old field annuals, Chenopodium replaced itself (attained $R_0 \geq 1$) at light levels between 100 and 700 $\mu E\ m^{-2}\ s^{-1}$, although at the 100-200 $\mu E\ m^{-2}\ s^{-1}$ light level it attained $R_0 \geq 1$ only in the soil of high water-holding capacity (Figure 3-7). Polygonum replaced itself over an even narrower section of the light gradient, from 250-700 $\mu E\ m^{-2}\ s^{-1}$, and attained $R_0 \geq 1$ only in the sandiest soil at the next to highest light level.

For woodland annuals, Acalypha was able to replace itself at all light levels except at $< 50\ \mu E\ m^{-2}\ s^{-1}$, where it had very low seed production. Pilea replaced itself at all light levels except at $> 1000\ \mu E\ m^{-2}\ s^{-1}$, where no seedlings survived to flowering time. Impatiens could replace itself only at intermediate light levels due to low survivorship and low seed reproduction at low or high light treatments (Figure 3-7).

DISCUSSION

The results of this greenhouse experiment suggest that old field annuals are generally absent from disturbed woodland for mostly physiological reasons: they cannot produce seeds at the low light levels typical of disturbed woodland. Woodland annuals were indeed more succesful than old field annuals in replacing themselves at low light, regardless of soil type. However, it appears that other factors in addition to physiological intolerance of light and soil moisture conditions of some areas in the old field, can prevent colonization of

Figure 3-7. Net replacement rate (R_0) per species for two old field (at top of figure) and three woodland annuals (at bottom of figure) over light and soil moisture gradients in the greenhouse. R_0 values are shown for each species for three soil mixtures of low (L), medium (M) and high (H) water-holding capacity, over a photosynthetic irradiance gradient of <50 to >1000 µE m^{-2} s^{-1}. R_0 = 1 is the minimum value required in order for a species to replace itself at a point in the two gradients. Values for *Polygonum* and *Impatiens* at the [illegible] µE m^{-2} s^{-1} light level are averages between the R_0 values for that species at points directly below and above that light level in the gradient.

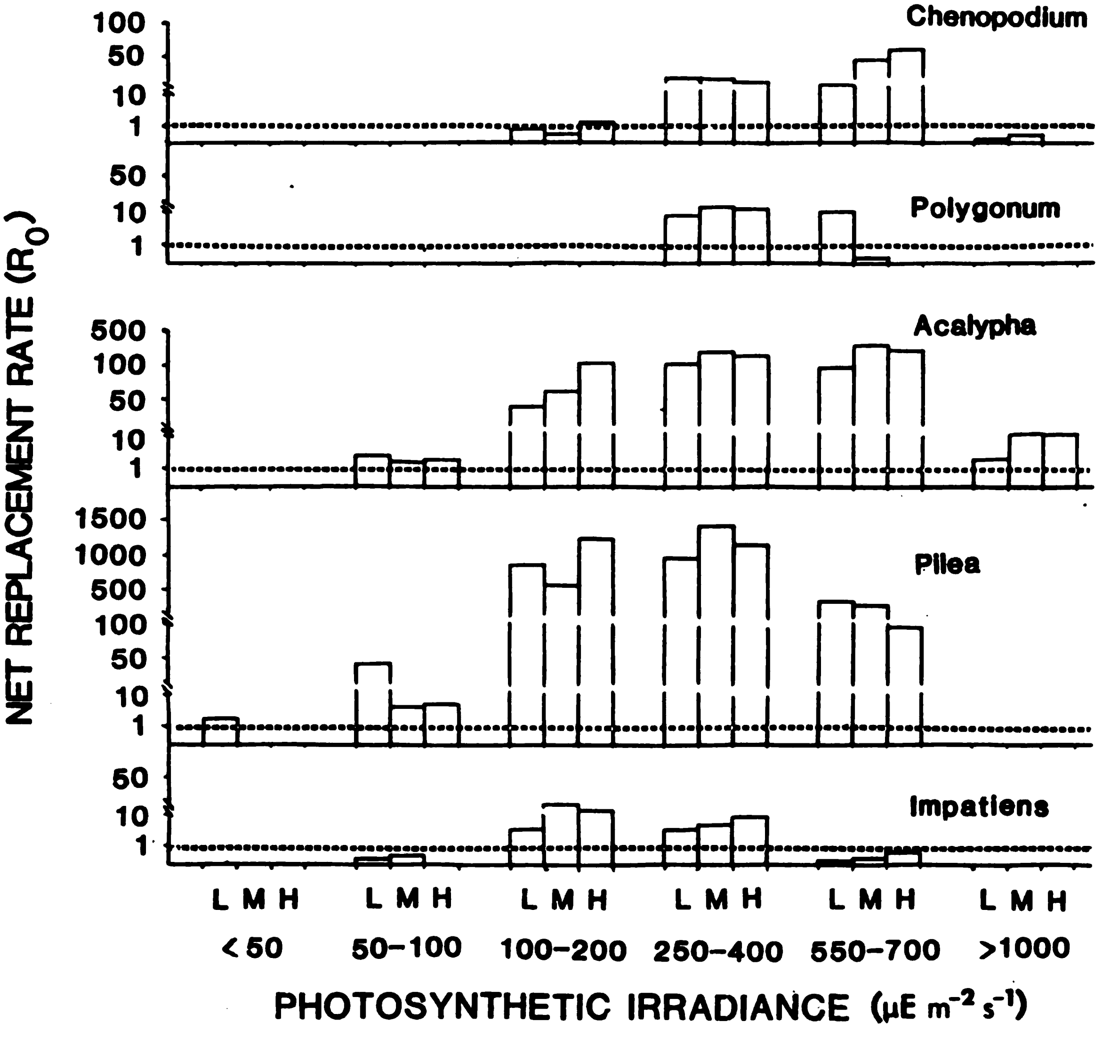
Chenopodium
100
50
10
1
Polygonum
50
10
1
Acalypha
500
100
50
10
1
Pilea
1500
1000
500
100
50
10
1
Impatiens
50
10
1
NET REPLACEMENT RATE (R_0)
L M H
<50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE (μE m^{-2} s^{-1})

Figure 3-7

old fields by annuals common in disturbed woodland.

It was evident from this experiment that inspite of the general lack of woodland annuals in the old field, at least one of the annual species common in the woods could replace itself in full sunlight, in the absence of competitors, under the moisture conditions typical of one-year-old fields. In addition, all three woodland annuals were able to replace themselves in light and soil moisture conditions found in some areas in the old field, as in the shade of other herbaceous species (see Figures A-2 - A-4).

Two of the three woodland annual species (Pilea, Impatiens) could not replace themselves in full sunlight, at any soil moisture level in environmental conditions typical of a one-year-old field, which was in agreement with the results from the field experiment. However, purely physiological factors are not preventing woodland annuals from establishing in fields abandoned more than one year from cultivation, from which the harsh microclimatic conditions associated with bare ground would be absent (Stoller and Wax, 1973; Raynal and Bazzaz, 1975a). The spectral quality of light under the shade of old field species is not different from that in the sites where woodland annuals are commonly found (Holmes and Smith, 1975), but in the old field, soil moisture content at the uppermost portion of the soil profile is usually much lower than in woodland sites, except in early spring (Figure A-4, Appendix, Table 2-1, Chapter 2).

Woodland annuals may not be able to compete effectively for soil moisture in the old field due to their usually shallow root systems and dependence on turgor pressure for mechanical support (Struik, 1965). Old field annual species with few or no xeromorphic morphological or physiological characters usually compensate for their poor drought resistance by investing more energy into developing larger rooting systems, which can in turn reach water available deeper in the soil profile, as the uppermost soil region becomes increasingly drier (e.g. *Polygonum pensylvanicum* and to some extent, *Chenopodium album*, Wieland and Bazzaz, 1975; Parrish and Bazzaz, 1976). In fact, in this greenhouse experiment, *Polygonum pensylvanicum*, which had its roots confined to pots, was not able to survive in any soil mixture in full sunlight in the greenhouse. Only two species, *Chenopodium album* and *Acalypha rhomboidea*, which had relatively more woody stem tissue than other members of their group, were able to survive and reproduce at the highest light level and in all three soil mixtures. Only *Acalypha* replaced itself at the highest light level. Thus it is likely that unless woodland annuals can produce large root systems in the old field, or they can generate a greater water potential gradient between plant and soil than that of neighboring species, when rooted near the soil surface, that they could not be effective competitors for soil moisture in the old field.

Other factors which could prevent woodland annuals from colonizing old fields might be allelopathy, seed predation or their lack of a persistent seed bank as insurance against catastrophic events (fire, trampling, grazing) or, a very dry year. Of these three factors, the general lack of a persistent seed bank in woodland annuals may be most critical in preventing their establishment in old fields, since recolonization of such unpredictably disturbed habitats after disturbance, is known to rely heavily on buried seed (Raynal and Bazzaz, 1973; Gross and Werner, 1982; Gartner, et al, 1983). Allelopathic species would not preferentially inhibit establishment of woodland annuals over old field annuals at all old field sites so it is unlikely to expect that chemical inhibition is responsible for woodland annuals regularly being absent from old fields. Several old field annuals lose a large portion of their seed crop to predators (Raynal and Bazzaz, 1975a; Staniforth and Cavers, 1977; Abul-Fatih and Bazzaz, 1979). Little is known about predation of woodland annuals seeds in any habitat, but barring any large immigration of seeds, given that most seeds produced in the fall in the woods appear to germinate in the spring, and seed production is relatively low, there seems to be little seed predation on woodland annuals studied (Warner, 1963; Winsor, 1981; Smith, 1983b).

Having no persistent seed bank can lead to woodland annuals having a higher germination fraction than old field annuals given similar environmental conditions at time of emergence. In order to maintain a persistent seed bank, seeds of old field annuals have to either respond differently to a given set of environmental conditions, or be buried at different depths so that they experience different environmental conditions (Williams, 1963). Theoretical and empirical studies have indicated that a way in which old field annuals adapt to their environment is by having a small germination fraction even in years favorable for high germination so that some seeds are always left in the seed pool to help avoid local extinction in unfavorable years (Roberts, 1964; Cohen, 1966; Weiss, 1981; Klemow and Raynal, 1984).

Seeds of woodland annuals are not buried deep below the soil surface after dispersal, and often have nearly synchronous germination (Grime,1979; Winsor, 1983; personal observation). In two woodland annuals, (*Impatiens glandulifera*, Grime, 1979 and *Impatiens capensis*, Winsor, 1983) such a strategy appears effective in suppressing the growth of perennial herbs. These woodland annuals tend to occupy environments that are disturbed but in a predictable fashion, unlike old fields, where disturbance is unpredictable, both in time and in space. Disturbance for woodland annuals is predictable in time (on a yearly basis) and often in space as well, as in the case of widespread flooding or herbivory (Menges and Waller, 1983; Schemske, 1984).

The comparative experimental approach, besides indicating the life cycle stage at which these two groups of annuals are most susceptible along these experimental gradients, also indicates the combination of light and soil moisture conditions under which both groups of annuals would most likely co-occur. In addition, any similarities between groups in their response to essential resources as light and soil moisture, can suggest a general explanation for patterns of distribution of summer-flowering annual species.

For both groups of annuals, mortality was higher at the extremes of the light gradient than at intermediate light levels, regardless of soil type, although all species tended to have higher survivorship in the sandiest soil than in the other soil mixtures at each light level. Seed size (another factor which can affect survivorship over light and soil moisture gradients, Baker, 1972; Gross and Werner, 1982; Gross, 1984) did not appear to be of consequence in this experiment. Large-seeded species did not have greater survivorship than small-seeded species over the gradients but had just as high or a lower probability of survival than small-seeded species, in comparisons within or between groups of annuals.

Poor plant performance at high light levels for both groups of annuals may have resulted from higher drying rates near the soil surface than evident for low light treatments, which in turn would have led to heat stress. Although sandy soils dry faster at the surface than soils higher in organic matter (Kramer, 1969), the darker soil can store heat longer (Larcher, 1975), when both soil types are dry. Soil mixtures were contained in flats or pots, (thus there was no capillary connection to ground water, which is usually maintained in more highly organic soil), and probably causing those soils to reach higher soil temperatures than the sandiest soil. Too high soil temperatures could have resulted in higher drying rates for the darker soils, which would have had adverse effects on the growth of all species, but particularly on that of woodland annuals. Annual plants of shaded habitats can rely heavily on evapotranspiration for regulating leaf temperature which leads to a higher demand for water from the soil (Rackham, 1966).

At low light levels, the soils with higher water-holding capacity may have been too wet for all five species, given that soil mixtures took longer to dry out under low light conditions. High moisture and low light levels favor fungal growth. Etiolated seedlings at low light levels can be more susceptible to fungal attack due to thin, elongated cell walls (Grime and Jeffrey, 1965). Of the five species in this experiment, at least one (Polygonum pensylvanicum) is known to be highly susceptible to attack by various species of fungi (Kirkpatrick and Bazzaz, 1979). Large-seeded species tend to produce taller etiolated seedlings (Grime and Jeffrey, 1965) which are more susceptible to mechanical collapse. Etiolated woodland annual seedlings from large-seeded species (as is Impatiens capensis) would be even more likely to collapse since these species have very little support tissue.

Both groups responded to a decrease in light by delaying the start of flowering and by decreased seed production. Reproduction appeared to be limited by soil moisture only in high light. Flowering of both old field and woodland annuals was delayed at the low end of the light gradient. However, the onset of flowering in old field annuals was delayed at higher light levels than was noted for woodland annuals.

The lowest light level at which both old field annuals were able to produce seeds corresponds to the light level at which these particular species half saturate in photosynthesis, when grown in low light (Bazzaz and Carlson, 1982). These results suggest that reproduction is light-limited in all five species, regardless of the habitat in which they abound. Such a delay in flowering leads to a significant delay in fruiting and since it takes at least one month for a fruit to mature in any of the five species (personal observation) used in this experiment, any delay in fruiting wil lead to many fruits not reaching maturity before the first fall frost, when all plants die.

Delay in flowering at low light levels might have been related to a need for accumulating a certain amount of photosynthate or nutrients prior to flowering which would then be relocated from leaves into reproductive structures. A delay in the start of flowering has been observed in several old field annuals when these were grown over a soil moisture gradient in the greenhouse, in competition with one or several naturally co-occurring annual species (Pickett and Bazzaz, 1976; 1978a). Photosynthetic rates of these two old field annuals may not have been high enough to provide energy for the development of reproductive structures, as well as for maintenance. Flowering has been related to size in several monocarpic perennials (Werner, 1975; Gross, 1981; Gross, 1983) and in one annual (Waller, 1980). It appears that there is a light energy threshold below which photosynthate can only be used for maintenance and none is available to develop reproductive structures, given that as available light decreased, there was a greater delay in the onset of flowering. Photoperiod did not vary across the light gradient and that is the only factor known to affect onset of flowering in at least two of these species (Chenopodium album, Ramakrishnan and Kapoor, 1974, and Pilea pumila, Cappel, 1969).

For Impatiens capensis, light limitation appeared to affect not only the onset of flowering but also the type of flower produced. Waller (1980) found that in Impatiens capensis, cleistogamy increased as available light and soil moisture decreased. Chasmogamous flowers are more costly than cleistogamous flowers in this species (Schemske, 1978; Waller, 1979). There seems to be a threshold in the photosynthetic irradiance level required to produce cleistogamous vs. chasmogamous fowers with lower photosynthate levels needed to start cleistogamous flower production than for chasmogamous flowering. As light increases, more energy is readily available and both flower types can be produced. Chasmogamous flowering in Impatiens capensis is dependent on plant size (Waller, 1980) with a certain number of nodes necessary to be produced before chasmogamous flowering occurs (same as for Impatiens parviflora, Evans, 1972). The number of chasmogamous flowers produced is also positively correlated with available light (Waller, 1980).

It seems that old field and woodland annuals would be most likely to co-occur at intermediate light levels, regardless of soil type. Old field annuals can grow at intermediate or high light levels, regardless of soil moisture conditions. Woodland annuals should be found in wet areas of old fields, regardless of light or at intermediate light levels, regardless of soil type, under low levels of competition. Both groups of annuals could also coexist in one site if woodland annuals occurred in the shade of old field annuals, providing that soil moisture levels did not drop below those observed in this greenhouse experiment. The results of this greenhouse experiment suggest that the distribution of both old field and woodland annual plants within their particular habitats may depend primarily on their competitive ability for light. They are secondarily differentiating over a moisture gradient which is often associated with the light gradient (e.g. high light and low moisture, or low light and high moisture).

The comparative experimental approach can also be effective in suggesting which factors regulate the abundance of these five species within their particular habitats. Similarities among species of each group can suggest which of these two resources is less limiting in each environment for these two groups of annual plants. Differences within each group of annuals in their response to resource gradients can help rank the species in each group as to their potential competitive ability over the resource gradients.

Seedling emergence

Germination of old field annuals is generally lower in low light environments because germination of their seeds is under phytochrome control and those environments often have vegetation-filtered light, which is high in far red light wavelengths and can inhibit germination (and low in red wavelengths, which promote germination). However, the ratio of red to far red light wavelengths did not vary among light treatments (Figure A-1). Thus any decrease in emergence with a decrease in light would not have been due to a lower R/FR ratio but might have been a response to reduced photosynthetic irradiance. Lower germination in shaded conditions (without a change in spectral quality of light) than in full sunlight has been recorded for Chenopodium album (Grime and Jarvis, 1975).

It is possible that the different emergence response of both old field annuals to the light gradient was actually a differential response to a soil moisture or to a temperature gradient or a response to a combination of those three factors. All soil mixtures had higher soil moisture contents at low light levels than at intermediate or high light levels (Figure 3-3). Soil surface temperature was higher in high light treatments, with a 5-7°C temperature difference between the lowest and the highest light treatment (Table 3-1). Temperature at the highest light treatment during the month of greatest emergence (April) probably was not higher than the optimal of 30 °C (alternating with 15°C at night) reported for Chenopodium album (Baskin and Baskin, 1977) but may have been higher than optimal for Polygonum germination (Abul-Fatih and Bazzaz, 1979).

Chenopodium has been observed to have higher emergence in moderately moist soils (Raynal and Bazzaz, 1973; Pickett and Bazzaz, 1978b) and its germination is lower in wet, highly organic soil than in sandy soil(Raynal and Bazzaz, 1973). Higher Polygonum emergence has been observed in rich, organic soil than in sandy soil. For Polygonum, the role of soil moisture in emergence appeared to be more critical at the extremes of the light gradient than at intermediate light levels. Thus Polygonum may have had highest seedling emergence at low light levels in response to the higher moisture content of all soil mixtures at low light levels in the greenhouse. Chenopodium may have had greater emergence at intermediate and high light levels than at low light because soils at intermediate and especially at high light treatments were more likely to be moderately moist than at low light levels, regardless of sand content. In the field, *Polygonum* seedlings often emerge from more deeply buried seeds than do *Chenopodium* seedlings (Abul-Fatih and Bazzaz, 1979). Such seeds would be exposed to low light levels and higher moisture conditions similar to those when *Polygonum* had highest emergence in this greenhouse experiment.

Woodland annuals had moderate to high seedling emergence at all light levels, regardless of soil type except at the highest light level. Negative responses to high light might have been the result of high temperature and fast-drying rate of the soil surface under high light. Two of the three woodland annuals (not *Impatiens*) had greater emergence at light levels <250 μE m^{-2} s^{-1} than at higher light levels. This may also be a response to the more moderate temperature and moisture conditions at the lower light levels. *Impatiens* germinates very early in the spring, under the snow (<10°C), before most other woodland herbs, whereas *Pilea* does not emerge until the first week in May (20°C) and *Acalypha* does not emerge until mid- to late May (when temperatures reach 25°C), in southwestern Michigan. These differences in time of emergence due to different temperature cues for germination provides *Impatiens* with a competitive edge over other woodland herbs (Winsor, 1983) and may make *Pilea* and *Acalypha* poorer competitors in the woodland environment.

Survivorship

Although all species had greater survivorship at intermediate light levels and in the sandiest soil mixture, regardless of habitat of origin, species in each group differed as to the relative survival ability at each light level. For old field annuals, Chenopodium had higher survivorship than Polygonum at both ends of the light gradient. Chenopodium was more tolerant of the high temperatures and low moisture conditions in high light treatments, and less susceptible to fungal attack in low light than was Polygonum.

The woodland annuals differed in their survivorship response to the light gradient. Acalypha survived over the entire light gradient, even at the hotter and drier conditions found in the unshaded treatment. Pilea did not survive at the highest light level but had high survivorship at all other light levels. Impatiens did not survive at either extreme of the light gradient. Differences among the three woodland species in their survivorship response over the light gradient (given that these species have all been categorized as high light specialists, Struik, 1965; Menges and Waller, 1983) may help explain how they can co-occur in the woodland environment. Impatiens has the largest seeds of these three woodland species and has a faster growth rate than the other two species. It could readily shade out Pilea in a habitat of intermediate light. Acalypha emerges much later in the spring than Impatiens does, and even later than Pilea. Acalypha could avoid competition with the other two species by occupying areas of low soil moisture, regardless of light conditions.

Reproduction

Seed production

For old field annuals, a delay in the onset of flowering and the small number of flowers produced resulted in little or no seed production at light levels of $<250\ \mu E\ m^{-2}\ s^{-1}$. Soil moisture had no effect on seed production of old field annuals except at the highest light level. This is similar to what is encountered in the field, where seed production in old field annuals under full sunlight, increases with increasing moisture (except it is low at saturated conditions) (Pickett and Bazzaz, 1976; Pickett and Bazzaz, 1978a). Thus for old field annuals, light is the main limiting factor; once that requirement is satisfied, then moisture is the limiting factor for reproduction, which could possibly be combined with nutrient limitation, similar to that seen in *Ambrosia artemisiifolia* (Raynal and Bazzaz, 1975a).

Seed production in woodland annuals was likewise affected most strongly by light than by soil moisture, but differently than for old field annuals. The species seemed to sort themselves out over a light gradient with increasingly narrower niche breadths over the light gradient, for *Acalypha*, *Pilea* and *Impatiens*, respectively. Soil moisture affected seed production only for *Acalypha* at one intermediate light level where the sandiest soil favored seed production over the other soil types. However, it is possible that the differences among the three woodland annuals in their survivorship and reproduction response over the light gradient are in response to the better combination of light, soil moisture and temperature conditions at certain points along the measurable light gradient.

Net replacement rate

Woodland annuals are equally as succesful as old field annuals in replacing themselves with increasing photosynthetic irradiance, except in full sunlight, in the greenhouse. Although in the field, in full sunlight, old field annuals may generally be more succesful than woodland annuals, the latter can replace themselves as well or better than old field annuals at lower light levels also found in old fields.

Woodland annuals differed as to the range of light conditions in which they could replace themselves. The net reproductive rate was affected by light at the establishment phase for Pilea and Impatiens and at the reproductive phase for Acalypha and also for Impatiens.

Woodland annuals can replace themselves in low light more consistently than old field annuals. Even if the emergence value and seedling survivorship to transplanting time value for a higher light level was used in calculating R_0 for the old field annuals at the low light treatments, one would still get $R_0 < 1$ at light levels $<100\ \mu E\ m^{-2}\ s^{-1}$, for Chenopodium and at light levels $< 250\ \mu E\ m^{-2}\ s^{-1}$ for Polygonum. Old field annuals which maintain a large viable seed pool in the soil must produce many seeds to be able to maintain that seed bank and still attain $R_0 \geq 1$. In low light, seed production is low for both old field and woodland annuals. It is possible that species with germination adaptations to maintain a viable seed bank cannot produce enough seeds to replace themselves in the woods even if their seedlings have high survivorship.

Old field and woodland annuals differ in the relative role of physiological tolerance of light and soil moisture and of life history characteristics, in limiting the distribution of each group to one type of habitat. However, within each group the mechanisms allowing coexistence of several species in one habitat are very similar. All species in this experiment, regardless of habitat of origin, had similar emergence, survivorship and reproduction responses to soil moisture, within each light level. In each habitat, there are some species which have a narrower range of light levels at which they can replace themselves, and which in nature are more competitively effective than co-occurring species under those environmental conditions. Those species which have characteristics associated with good competitive ability (fast growth rate, large seeds) (e.g. *Polygonum* in the old field, Pickett and Bazzaz, 1976; *Impatiens* in woodland areas, Winsor, 1983) are usually associated with the more mesic, less variable areas of their respective habitats. The other species are tolerant of a wider range of light conditions but are usually found (in terms of either light and moisture levels) in the more variable, less productive areas of their respective habitats (Pickett and Bazzaz, 1978a; Menges and Waller, 1983). Both old field and woodland summer-flowering annuals occur in the disturbed areas of their particular habitats. Differences in the timing and nature of disturbance are probably most responsible for creating the heterogeneity in constancy and supply level of resources within each habitat.

Chapter 4

IMPORTANCE OF RESOURCE ALLOCATION PATTERN IN LIMITING THE DISTRIBUTION OF OLD FIELD AND WOODLAND ANNUAL PLANTS

INTRODUCTION

The results of the greenhouse experiment discussed in Chapter 3 indicate that two old field annuals (*Chenopodium album* and *Polygonum pensylvanicum*) set few or no seeds at low light levels whereas two of the three woodland annuals (*Acalypha rhomboidea*, *Pilea pumila*, but not *Impatiens capensis*) set seed over a broader range of light and moisture conditions than do the old field annuals. Within each group of annuals, species differ in the range of light and soil moisture conditions over which they can replace themselves.

One would expect these annual plants found in old fields or woods to differ in their resource allocation pattern because of the differences between the two habitats in light and water availability. Light incident on plants decreases and soil moisture increases along a transect extending from old fields to open woodland. There is much information on how resource allocation to shoot vs. roots is influenced by light and soil moisture availability (Leonard, 1962). Much research has also focused on the effect of environmental change on reproductive effort. The data indicate that among annuals, biennials and perennials, some species vary reproductive effort over environmental gradients and some species allocate the same proportion of their total resources to reproduction over the entire range of habitats they occupy (see Soule and Werner, 1981 for a review of the literature).

The purpose of this study was to determine if the biomass allocation pattern of these two old field and three woodland annuals could provide a mechanism for explaining differences between groups in the probability of population replacement over the light and soil moisture gradients. I also examined how individuals of these old field and woodland species regulate reproductive effort and thus ascertain if reproductive effort is increased by increasing reproductive yield or through alterations between the fraction of total biomass allocated to reproduction and the absolute weight of aerial vegetative and/or root tissue.

METHODS

Biomass allocation to aerial vegetative tissue, roots and reproduction was measured under controlled conditions for two old field and three woodland annuals grown over light and soil moisture gradients (for the adult plants harvested in the experiment described in Chapter 3). The light gradient consisted of six light treatments that ranged from $<50\ \mu E\ m^{-2}\ s^{-1}$ to $>1000\ \mu E\ m^{-2}\ s^{-1}$ (the latter being the unshaded treatment). Treatments differed only in the total amount of photosynthetic radiation incident on plants. The soil moisture gradient was established by decreasing the percent sand per volume in a sand and potting soil mixture, and consisted of three moisture levels. The mixtures were characterized by low, medium, and high water-holding capacity (see Chapter 3 for a detailed description of how these gradients were established and of the overall greenhouse environment).

Seeds of two old field and three woodland annuals were sown onto flats over the experimental gradients in April, 1982. Fourteen of the surviving seedlings (or any remaining survivors) were transplanted from flats into 10 cm diameter pots in late June, 1982, for each light x soil treatment combination. The old field annuals had no seedlings surviving to time of transplanting at the lowest light level in the soil of medium water-holding capacity. *Polygonum pensylvanicum* had no transplants for the soil of high water-holding capacity at the two high light treatments, nor for the soil of medium water-holding capacity, at either the highest or the lowest light level. Of the three woodland annuals, only *Acalypha* had seedlings available for transplanting at the highest light level. In addition, Impatiens did not have any survivors to time of transplanting at the lowest light level.

I censused the transplants once a week and harvested plants that appeared dead (plants which had dried up and showed chlorophyll loss), until the final harvest in mid-October, 1982. I collected any dry leaves which fell from the plants to include them in the determination of total aerial vegetative biomass. All harvested plants and plant parts were dried in an oven for three days, at 65°C and stored in newspaper folders or in paper bags, inside closed plastic bags. I separated any remaining reproductive structures from all transplants, and weighed reproductive and vegetative shoot biomass, and roots separately for each plant.

For *Chenopodium* and *Polygonum*, both of which retained all flowers and fruits until death, total biomass allocation to reproduction was obtained directly from harvested plants. For the three woodland annuals, *Acalypha*, *Pilea* and *Impatiens*, all of which drop most of their reproductive tissue before they die, samples of both mature and developing flowers and fruits were collected (where applicable). For *Acalypha* and *Pilea*, twenty (or fewer if a plant did not make 20 seeds) seeds were collected per plant and weighed to the nearest 10,000th of a milligram for each treatment combination. For Impatiens, as many seeds as possible were collected (up to 20 seeds per plant) for weighing. This species produces few seeds per plant (relative to other annuals) and the seeds are dispersed by explosive dehiscence of the capsules, which requires bagging all flowers in order to retain all the seeds produced per plant. Both features made it very difficult to collect as many Impatiens seeds as was done for the other species (see Chapter 3, Table 3-14 for sample sizes for seeds collected from the three woodland annuals).

Mean weights were obtained per reproductive part per species for each treatment combination. All types of flowers produced (male, female, chasmogamous and cleistogamous), early-, late-developing and mature fruits were counted for each woodland annual plant on a monthly basis from July to September, 1982 (see Methods, Chapter 3 for details on the counting of reproductive parts). The number of each part produced was multiplied by the mean dry weight for that part, and the weights of all yield components added together in order to obtain total biomass allocation to reproduction Seeds to be weighed for determining mean seed weight per species per treatment combination were air-dried (these seeds were also used to determine seed viability at each treatment combination); all other parts were oven-dried.

Floral bracts of Acalypha were removed (permanently attached to axils) and any fruits, female flowers and male inflorescences, still remaining on the dried, harvested plant, and weighed them. For Acalypha, which disperses each seed separately from its papery, pericarp enclosure, a sample of such pericarp portions (n=4-42 per treatment combination) was collected from the surface of the soil from each pot, dried and weighed separately.

I had collected two male inflorescences from each Acalypha plant for each treatment combination (n=4-28 inflorescences per treatment combination), except at the two low light levels, where the low number of male inflorescences produced precluded collection until after pollen had been dispersed. For the lowest light level, all male inflorescences were collected after pollen dispersal (n=4-13); for the next to lowest light level, five male inflorescences were collected per treatment combination. There was no significant difference among treatments for mean male inflorescence weight.

The mean weights for male inflorescences and seeds of Acalypha plants were multiplied by the total number of male inflorescences and seeds produced per plant (seee Chapter 3 for the procedure used to estimate total seed production). Male inflorescence production began in July and continued until September. In September, only six plants per treatment combination were counted for the 20%, 37% and 53% incoming sunlight treatments. A linear regression of the total number of axils per plant in August to the total number of male inflorescences produced in September ($y = 2.32x + 3.86$; $r=0.88$) was used to estimate the last count of male inflorescences for plants not counted.

I removed Pilea female flowers and all inflorescence parts from dried, harvested, plants. I collected three male flowers per plant per treatment combination (n=30-42 per treatment combination), except at the lowest light level, where the extremely low production of male flowers precluded collection until after pollen had been dispersed (n=2-27). There was no significant difference among treatments in mean male flower weight.

I multiplied the mean male flower weight per Pilea treatment combination by the total number of male flowers produced per plant (obtained from the August flower count) to obtain the total dry weight of biomass allocated to male flowers, per plant. The total dry weight of biomass allocated to reproduction was obtained by adding the three reproductive weights mentioned above for each plant.

For Impatiens, I separated all remaining floral buds, pedicels (from flowers and fruits) and developing fruits and flowers remaining on dried, harvested plants, and weighed them (all pedicels from mature or developing fruits and from flowers usually remain on the plant throughout its life). I collected up to three chasmogamous flowers from each plant after they had dropped off (n=12-24 chasmogamous flowers per treatment combination with chasmogamous flower production). In addition, I collected up to three per plant of each of the following reproductive yield components: dried up early-developing cleistogamous capsules, mature chasmogamous and mature cleistogamous capsules (valves only)(n=1-39, n=1-21, n=3-39, respectively, per treatment combination). Mean weights were obtained from each floral part and multiplied by the number of parts produced per plant to obtain the total dry weight of biomass allocated to each reproductive structure. Mean weights for these reproductive yield components did not differ significantly among treatments. All weights were added together to obtain the total dry weight of biomass allocated to reproduction per plant, per treatment combination.

Total plant dry weight, the ratio of shoot to root biomass, and the fraction of total plant dry weight allocated to aerial vegetative biomass, roots, and to reproduction were determined for each species per treatment combination. The mean percent of total biomass allocated to each plant component by each species was obtained by averaging relative biomass allocation to reproduction, aerial vegetative tissue and roots over all light x soil moisture treatment combinations in which each species set seed. The Mann-Whitney test was used for between-group comparisons of means. Tukey's test (modified when necessary for data with heterogeneous treatment variance, Gill, 1978) was used for pair-wise comparisons among species and among treatment combinations for each species. Product-moment correlation coefficients were calculated separately for individual reproductive effort with reproductive, aerial vegetative and root weights. The data presented and analyzed here were obtained only from plants which produced $\geq$ 1 seed (some plants flowered but did not produce seeds).

RESULTS

Old field and woodland annuals differed most strikingly in the relationship between reproductive effort and weight of reproductive tissue, of aerial vegetative tissue and of roots. The results suggest that old field annuals increased reproductive effort by increasing the size of all parts of the plant body. In contrast, woodland annuals seemed to increase reproductive effort by either increasing reproductive yield (*Acalypha*, *Impatiens*) or by decreasing absolute weight of root or aerial vegetative tissue (*Pilea*, *Impatiens*). An increase in root and/or aerial vegetative tissue with increasing photosynthetic irradiance resulted in a decrease in reproductive effort in two of the three woodland annuals, but not for old field annuals.

Averaged over both light and soil moisture gradients, old field annuals had significantly lower allocation to reproduction and significantly higher allocation to vegetative shoot tissue than was observed for woodland annuals ($p < 0.01$). Woodland annuals allocated an equal or slightly larger fraction of total biomass to roots than did old field annuals over the experimental gradients ($p > 0.05$). All five species allocated the largest fraction of total biomass to aerial vegetative tissue at most light x soil moisture treatment combinations and the smallest fraction to roots over both experimental gradients (Table 4-1).

For old field annuals, *Polygonum* allocated a significantly greater proportion of total biomass on average to vegetative shoot tissue and to roots (and thus less to reproduction) than did *Chenopodium*. For woodland annuals, *Impatiens* allocated a significantly greater fraction of its total biomass to vegetative shoot tissue on average than did *Pilea*, and both species had significantly greater mean allocation to vegetative shoot tissue than was observed for *Acalypha*. The reverse pattern was observed for biomass allocation to reproduction. *Pilea* had significantly higher root allocation, averaged over the gradients, that did the other two woodland annuals.

Plant size and shoot:root ratio

For both old field and woodland annuals, total plant weight increased with increasing light. Plants were generally largest at the next to highest light level, except for *Impatiens*, which had greatest total biomass in intermediate light (Table 4-2).

For both groups of annuals, plants growing at >250 $\mu E\ m^{-2}\ s^{-1}$ were significantly larger than plants at lower light levels. Plant weight of

Table 4-1. Mean percent of total plant dry weight allocated to reproduction, to aerial vegetative tissue and to roots (± standard error), for two old field and three woodland annuals grown over light and soil moisture gradients in the greenhouse. Means were averaged over all treatment combinations in which plants set seed. For each category, means with different superscripts are significantly different from each other with $p < 0.05$.

		Mean Percent of Total Biomass (± S.E.)		
	Species	Reproduction	Aerial Vegetative	Roots
OLD FIELD	*Chenopodium*	$33^{b} \pm 1.5$	$57^{b} \pm 1.7$	$10^{a} \pm 0.4$
	Polygonum	$22^{a} \pm 1.4$	$64^{c} \pm 1.6$	$15^{b} \pm 0.7$
WOODS	*Acalypha*	$41^{d} \pm 0.9$	$48^{a} \pm 0.8$	$11^{a} \pm 0.4$
	Pilea	$28^{c} \pm 1.0$	$56^{b} \pm 0.9$	$16^{b} \pm 0.6$
	Impatiens	$25^{c} \pm 1.6$	$64^{c} \pm 1.5$	$11^{a} \pm 0.7$

Table 4-2. Total dry weight (mean ± standard error, in g) of transplants producing ≥ 1 seed, for two old field and three woodland annuals which were grown over light and soil moisture gradients in the greenhouse. The light gradient consisted of six light treatments and ranged from <50 $\mu E\ m^{-2}\ s^{-1}$ to 1000 $\mu E\ m^{-2}\ s^{-1}$. The soil moisture gradient consisted of three sand and soil mixtures of low (L), medium (M) and high (H) water-holding capacity. Sample size is shown in parentheses. Means not sharing a superscript (each row taken separately) differ significantly from each other, with $p<0.05$.

		Light ($\mu E\ m^{-2}\ s^{-1}$)	Mean Total Biomass (g ± S.E.)					
	Species	Soil Mixture	50	50-100	100-200	250-400	550-700	1000
OLD FIELD	**Chenopodium**	L	---*	0.01^{a} ± 0.0 (1)	0.05^{a} ± 0.0 (10)	1.75^{b} ± 0.2 (14)	2.64^{bcd} ± 0.3 (7)	1.44^{bcd} ± 0.5 (3)
		M	---	---	0.07^{a} ± 0.0 (13)	2.53^{bc} ± 0.4 (14)	4.06^{cd} ± 0.4 (14)	2.74^{bcd} ± 0.5 (5)
		H	---	---	0.11^{a} ± 0.0 (8)	2.01^{b} ± 0.3 (14)	4.51^{d} ± 0.2 (14)	1.91^{bcd} ± 0.0 (1)
	Polygonum	L	---	0.01^{a} ± 0.0 (2)	---	1.37^{ab} ± 0.2 (14)	3.33^{bc} ± 0.2 (13)	---
		M	---	---	0.39^{a} ± 0.1 (3)	2.41^{bc} ± 0.2 (14)	4.95^{c} ± 0.0 (1)	---
		H	---	---	0.19^{a} ± 0.0 (3)	2.27^{bc} ± 0.2 (14)	---	---
WOODS	**Acalypha**	L	0.006^{a} ± 0.0 (3)	0.07^{b} ± 0.0 (11)	0.46^{c} ± 0.0 (14)	1.37^{d} ± 0.2 (14)	1.87^{def} ± 0.1 (14)	0.82^{ce} ± 0.1 (11)
		M	0.003^{a} ± 0.0 (3)	0.04^{b} ± 0.0 (11)	0.94^{cde} ± 0.1 (14)	2.56^{ef} ± 0.2 (14)	3.06^{f} ± 0.3 (14)	2.29^{cd} ± 0.0 (2)
		H	0.007^{a} ± 0.0 (8)	0.05 ± 0.0 (11)	0.93^{cde} ± 0.1 (14)	2.27^{de} ± 0.2 (14)	2.65^{ef} ± 0.1 (14)	1.52^{def} ± 0.2 (4)
	Pilea	L	0.01^{a} ± 0.0 (12)	0.10^{c} ± 0.0 (13)	1.80^{d} ± 0.2 (14)	2.36^{de} ± 0.2 (14)	2.65^{de} ± 0.2 (14)	---
		M	0.001^{a} ± 0.0 (2)	0.03^{b} ± 0.0 (12)	2.64^{de} ± 0.3 (14)	4.02^{e} ± 0.2 (14)	4.23^{e} ± 0.4 (14)	---
		H	0.003^{a} ± 0.0 (3)	0.04^{b} ± 0.0 (10)	2.62^{de} ± 0.2 (14)	3.44^{de} ± 0.2 (14)	4.16^{e} ± 0.2 (14)	---
	Impatiens	L	---	0.26^{a} ± 0.1 (5)	0.79^{b} ± 0.1 (13)	1.45^{cd} ± 0.1 (11)	0.63^{b} ± 0.2 (2)	---
		M	---	0.13^{a} ± 0.0 (7)	1.28^{bd} ± 0.1 (13)	2.22^{d} ± 0.2 (10)	1.56^{bd} ± 0.0 (1)	---
		H	---	---	1.08^{bc} ± 0.1 (13)	1.89^{d} ± 0.2 (13)	1.22^{bd} ± 0.2 (2)	---

* = dashed line indicates no plants produced seeds

woodland annuals was more sensitive to an increase in photosynthetic irradiance at low light levels (<250 $\mu E\ m^{-2}\ s^{-1}$) than was observed for old field annuals. Woodland annuals may have been more photosynthetically efficient than old field annuals at light levels <250 $\mu E\ m^{-2}\ s^{-1}$. Woodland annual plants were 2 to 38 times larger than old field annual plants in species comparisons for the same soil mixture at each light treatment <250 $\mu E\ m^{-2}\ s^{-1}$. At light levels $\geq$ 200 $\mu E\ m^{-2}\ s^{-1}$, woodland annuals were as efficient or slightly less so than old field annuals in converting available resources into biomass. Plants of the two species which produced seeds in the unshaded treatment (Chenopodium and Acalypha) were approximately half the size of plants at the next to highest light level.

For all five species, plants were generally smallest in the sandiest soil at light levels >100 $\mu E\ m^{-2}\ s^{-1}$ but the opposite was true in low light treatments. Plants grown in the soil of medium water-holding capacity were of equal size or larger than plants in the soil of high water-holding capacity, over the entire light gradient.

Both groups of annuals allocated more biomass to shoot than to roots at all light treatments. Woodland annuals had higher shoot:root ratios at light levels <100 $\mu E\ m^{-2}\ s^{-1}$ than did old field annuals, but both groups had similar values at higher light levels. Old field annuals generally had higher shoot:root ratios at light levels < 250 $\mu E\ m^{-2}\ s^{-1}$, and woodland annuals at light levels < 100 $\mu E\ m^{-2}\ s^{-1}$, than at higher light levels (Figure 4-1).

Both Chenopodium and Polygonum had higher shoot:root ratios at 100-200 $\mu E\ m^{-2}\ s^{-1}$ than at most light x soil moisture treatment combinations at higher irradiance. Acalypha had significantly higher

Figure 4-1. Ratio of shoot to root biomass for two old field (top of figure) and three woodland annuals (bottom of figure) which were grown over light and soil moisture gradients in the greenhouse. The light gradient consisted of six light treatments ranging from <50 μE m^{-2} s^{-1} to >1000 μE m^{-2} s^{-1}. The soil moisture gradient consisted of three sand and soil mixtures of low (L), medium (M) and high (H) water-holding capacity. For each species, means per treatment combination not sharing a superscript are significantly different from each other with $p < 0.05$.

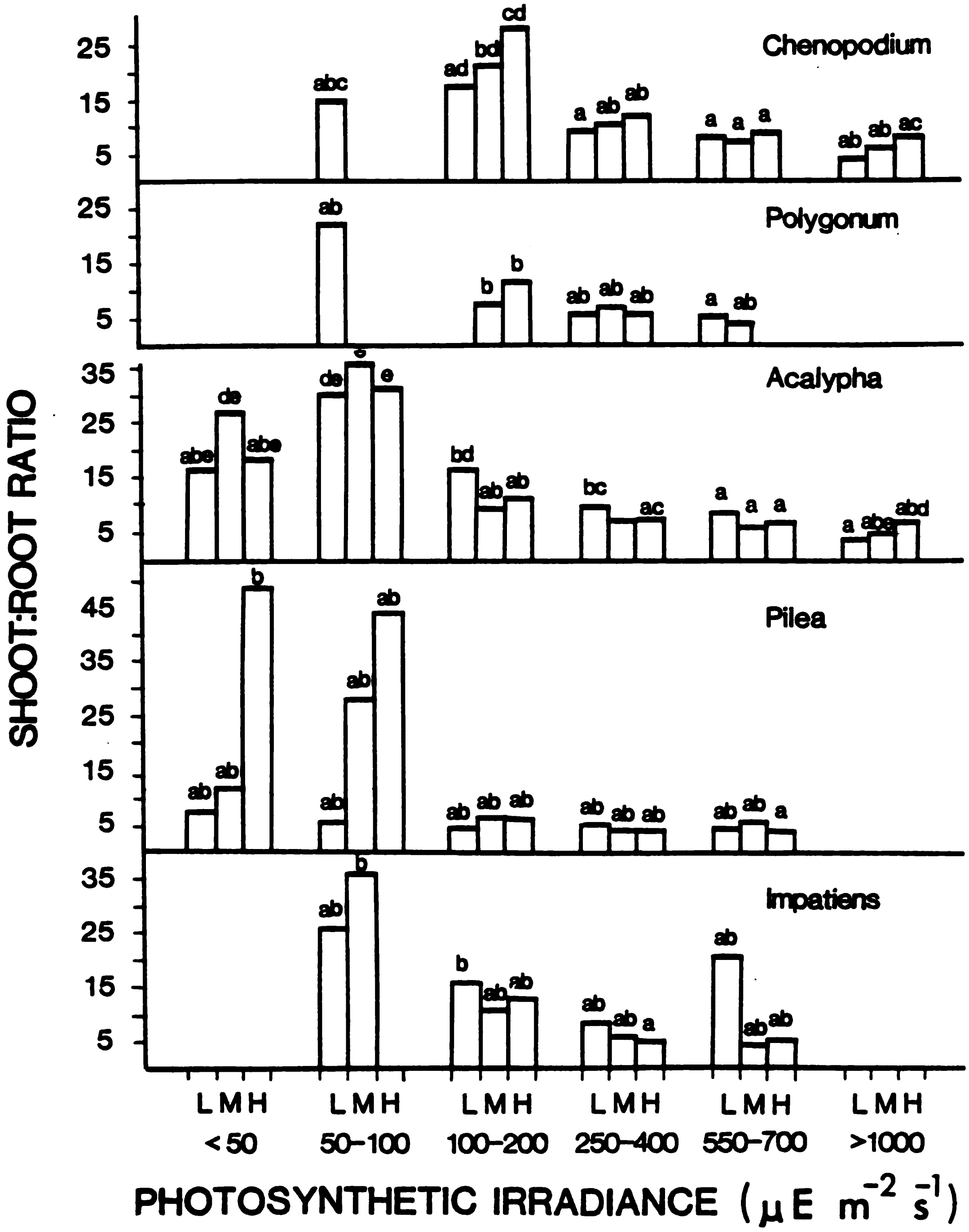
SHOOT:ROOT RATIO
Chenopodium
25
15
5
abc
ad
bd
cd
a
ab
ab
a
a
a
ab
ab
ac
Polygonum
25
15
5
ab
b
b
ab
ab
ab
a
ab
Acalypha
35
25
15
5
abe
de
abe
de
e
e
bd
ab
ab
bc
ac
a
a
a
a
abe
abd
Pilea
45
35
25
15
5
ab
ab
b
ab
ab
ab
ab
ab
ab
ab
ab
ab
ab
ab
a
Impatiens
35
25
15
5
ab
b
b
ab
ab
ab
ab
a
ab
ab
ab
L M H
L M H
L M H
L M H
L M H
L M H
<50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE (μE m-2 s-1)

Figure 4-1

shoot:root ratios at the 50-100 μE m^{-2} s^{-1} light level than at most treatment combinations at higher light levels. Shoot:root ratios for Pilea at the lowest light level in the soil of highest water-holding capacity were significantly higher than shoot:root ratios at the next to highest light level for the same soil type. At low light, Pilea showed a trend for increasing shoot:root ratio with increasing water holding capacity of the soil. Impatiens plants at the 250-400 μE m^{-2} s^{-1} light level, growing in the soil of high water-holding capacity, had significantly lower shoot:root ratio than plants at low light, in the soil of medium water-holding capacity, or in the sandiest soil at the 100-200μE m^{-2} s^{-1} light level.

Relative biomass allocation to aerial vegetative tissue

Light had a significant effect on relative biomass allocation to aerial vegetative tissue on four of the five species (except Impatiens). Old field annuals allocated a greater fraction of total biomass to aerial vegetative tissue at light levels <250μE m^{-2} s^{-1} than did woodland annuals, but the two groups did not differ consistently in relative biomass allocation to aerial vegetative tissue at higher light levels (Figure 4-2). For old field annuals, plants growing at 100-200 μE m^{-2} s^{-1} allocated a greater fraction of their total biomass to aerial vegetative tissue than plants at some of the treatment combinations at higher light levels. Chenopodium plants at the 100-200 μE m^{-2} s^{-1} light level allocated a greater percentage of total biomass to aerial vegetative tissue than plants at higher light levels (except for soils of low and high water-holding capacity at the highest light levels). Polygonum plants at the 100-200 μE m^{-2} s^{-1} light level allocated a greater

Figure 4-2. Percent of total biomass allocated to aerial vegetative tissue by two old field (top of figure) and three woodland annuals (bottom of figure) which were grown over light and soil moisture gradients in the greenhouse. The light gradient consisted of six light treatments ranging from <50 μE m^{-2} s^{-1} to >1000 μE m^{-2} s^{-1}. The soil moisture gradient consisted of three sand and soil mixtures of low (L), medium (M) and high (H) water-holding capacity. For each species means per treatment combination not sharing a superscript are significantly different from each other with $p<0.05$.

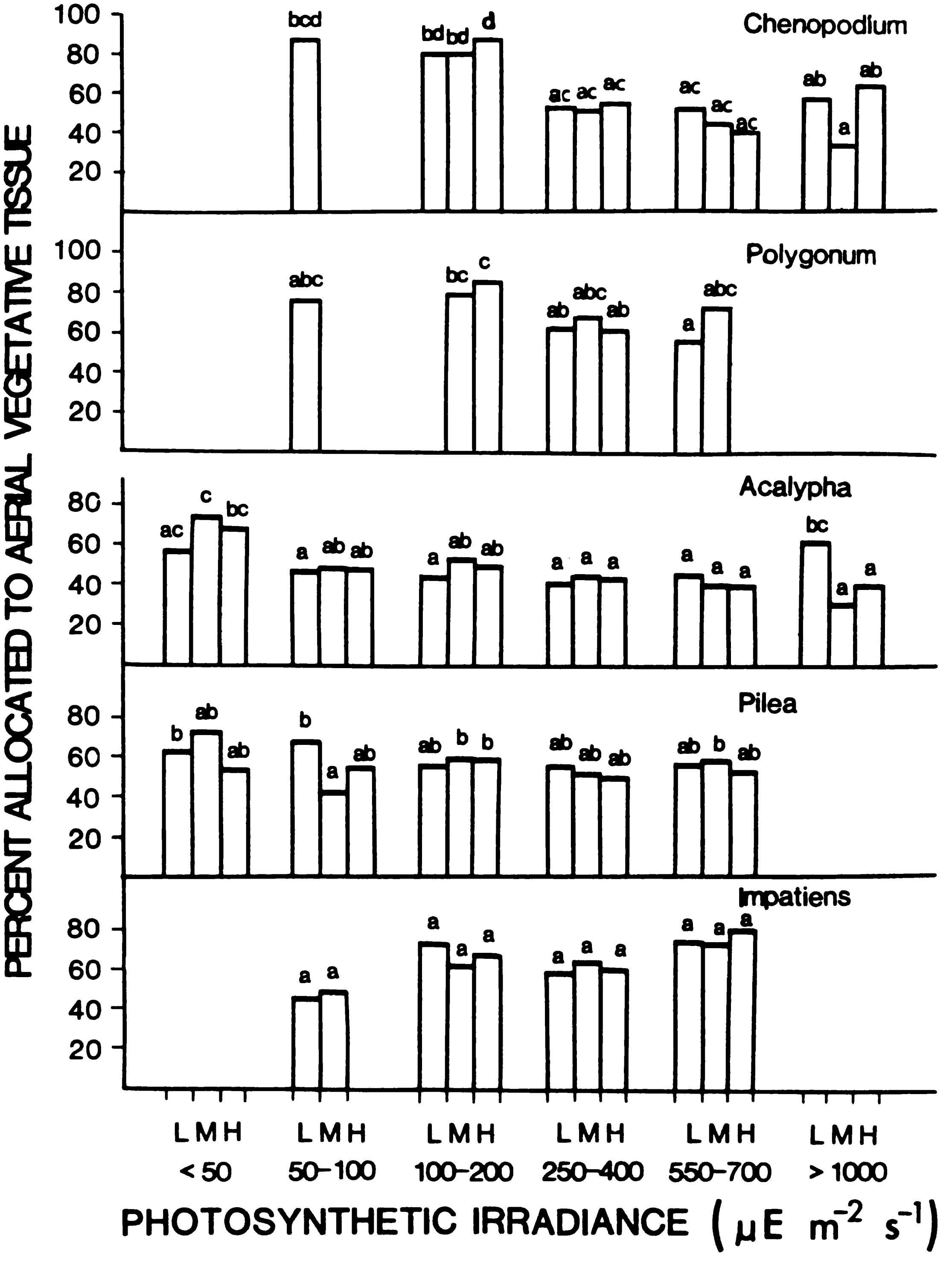
PERCENT ALLOCATED TO AERIAL VEGETATIVE TISSUE
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
100
80
60
40
20
LMH
< 50
50–100
100–200
250–400
550–700
> 1000
PHOTOSYNTHETIC IRRADIANCE (μE m-2 s-1)

Figure 4-2

proportion of total biomass to aerial vegetative tissue in the soil of high water-holding capacity than at higher light levels.

Woodland annuals did not exhibit a consistent trend in the percent of total plant weight allocated to aerial vegetative tissue over the light gradient (Figure 4-2). Acalypha plants at the lowest light level in soils of medium and high water-holding capacity allocated a higher proportion of total biomass to aerial vegetative tissue than did most plants at higher light levels, regardless of soil type. Pilea plants at the 50-100 $\mu E\ m^{-2}\ s^{-1}$ light level, in the soil of medium water-holding capacity, allocated a smaller fraction of their total biomass to aerial vegetative tissue than plants at some of the light x soil treatment combinations at lower or higher light levels. Impatiens plants did not differ significantly in the fraction of total biomass allocated to aerial vegetative tissue over the light and soil moisture gradients. However, there was a slight trend towards an increase in the aerial vegetative tissue fraction with increasing light.

Relative biomass allocation to roots

Both groups of annuals in general tended to allocate a greater proportion of biomass to roots with increasing light (Figure 4-3). Significant differences among light levels in relative biomass allocation to roots were observed for Chenopodium, Acalypha and Pilea. Although Polygonum and Impatiens tended to increase the proportion of biomass allocated to roots with increasing photosynthetic irradiance, the sample sizes for these species at the extremes of the light gradient were too small to allow for significant differences among light levels in the relative biomass allocation to roots.

Figure 4-3. Percent of total biomass allocated to roots by two old field (top of figure) and three woodland annuals (bottom of figure) which were grown over light and soil moisture gradients in the greenhouse. The light gradient consisted of six light treatments ranging from <50 μE m^{-2} s^{-1} to >1000 E m^{-2} s^{-1} . The soil moisture gradient consisted of three sand and soil mixtures of low (L), medium (M) and high (H) water-holding capacity. For each species, means per treatment combination not sharing a superscript are significantly different from each other with $p<0.05$.

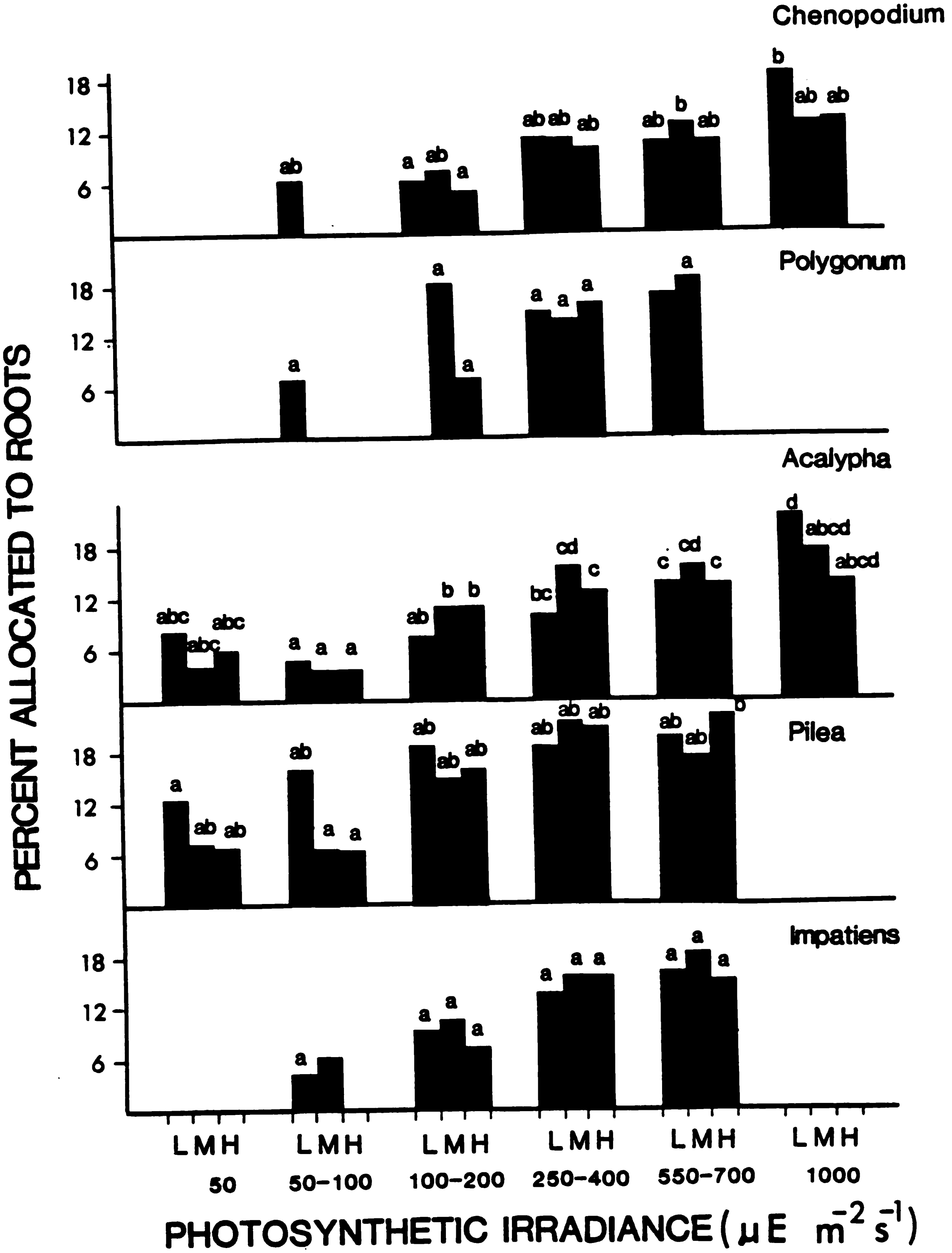
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
PERCENT ALLOCATED TO ROOTS
18
12
6
L M H
50
50–100
100–200
250–400
550–700
1000
PHOTOSYNTHETIC IRRADIANCE (µE m^{-2} s^{-1})
a
ab
b
abc
bc
c
cd
d
abcd

Figure 4-3

For Chenopodium, the relative biomass allocation to roots at the 100-200 μE m^{-2} s^{-1} light level in soils of low or high water-holding capacity was significantly lower than allocation to roots in high light treatments in soils of medium (550-700 μE m^{-2} s^{-1}) or low water-holding capacity (unshaded treatment). Acalypha plants growing at <250 μE m^{-2} s^{-1} allocated a smaller fraction of total biomass to roots than plants at higher light levels. For Acalypha, the highest root fraction was observed in plants growing in the sandiest soil at the highest light level. For Pilea, plants growing in the sandiest soil and at the lowest light level and in soils of medium and high water-holding capacity at the 50-100 μE m^{-2} s^{-1} light level, allocated a smaller portion of their total weight to roots than plants in the soil of high water-holding capacity at the next to highest light level.

Relative biomass allocation to reproductive tissue

Reproductive effort (i.e. the proportion of total biomass allocated to reproductive tissue) of old field annuals was lower than that of woodland annuals at light levels <250 μE m^{-2} s^{-1}, but there were no consistent differences in reproductive effort between groups of annuals at higher light levels. Old field annuals had equal, lower or higher reproductive effort than woodland annuals at intermediate and high light treatments (Figure 4-4).

For old field annuals, reproductive effort increased significantly with increasing light but for woodland annuals it remained about the same or showed a decreasing trend with increasing light (Figure 4-4). For each habitat, the broader the range of environmental conditions over which a species set seeds (Figure 4-4), the higher its overall mean reproductive

Figure 4-4. Percent of total biomass allocated to reproductive tissue by two old field (top of figure) and three woodland annuals (bottom of figure) which were grown over light and soil moisture gradients in the greenhouse. The light gradient consisted of six light treatments ranging from <50 $\mu E\ m^{-2}\ s^{-1}$ to >1000 $\mu E\ m^{-2}\ s^{-1}$. The soil moisture gradient consisted of three sand and soil mixtures of low (L), medium (M) and high (H) water-holding capacity. For each species, means per treatment combination not sharing a superscript are significantly different from each other with $p<0.05$.

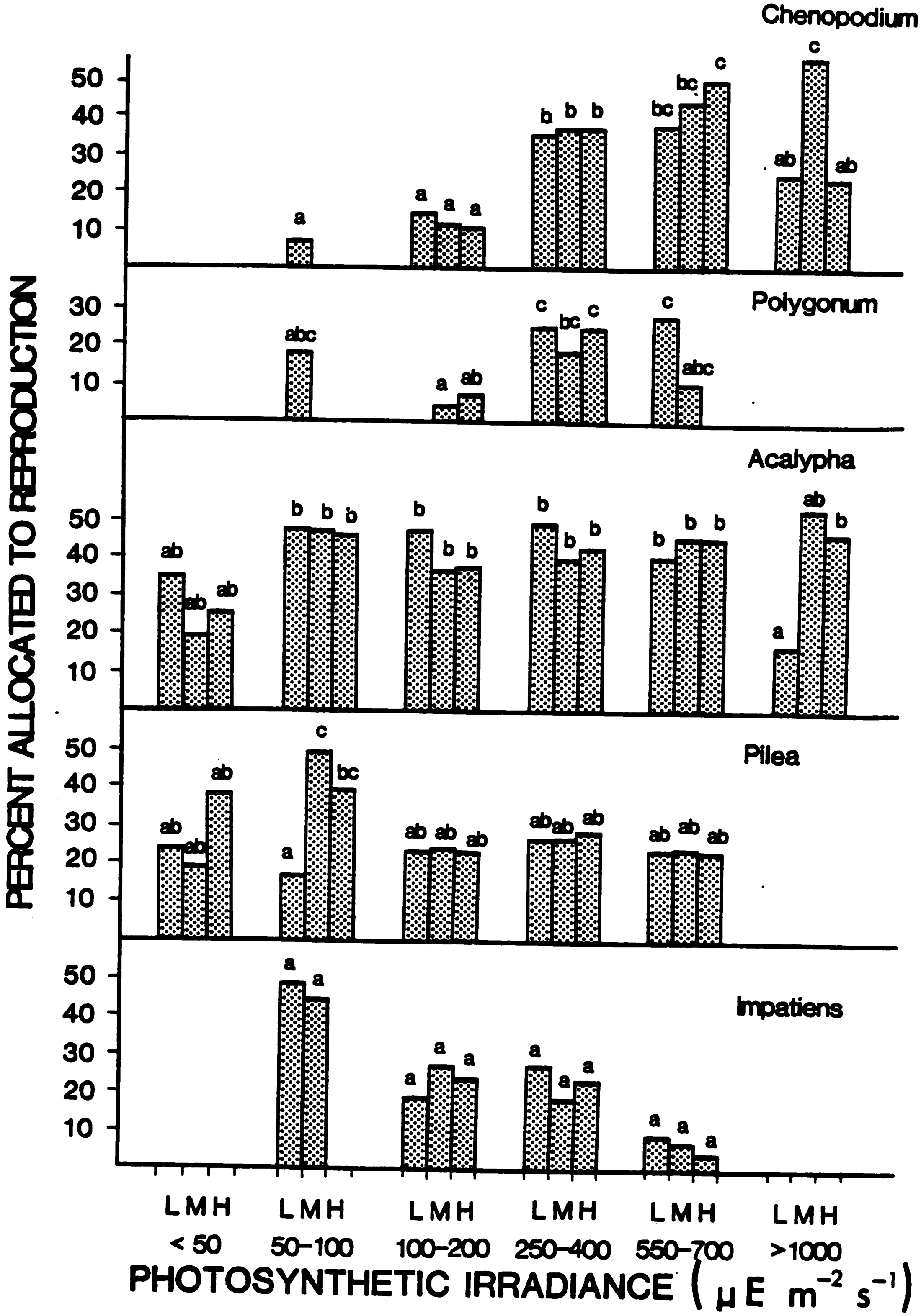
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
PERCENT ALLOCATED TO REPRODUCTION
10
20
30
40
50
LMH
< 50
50-100
100-200
250-400
550-700
>1000
PHOTOSYNTHETIC IRRADIANCE ($\mu E\ m^{-2}\ s^{-1}$)
a
b
c
ab
bc
abc

Figure 4-4

effort. *Acalypha* had the highest overall mean reproductive effort and *Polygonum* the lowest mean reproductive effort (Table 4-1).

Old field annuals allocated a smaller proportion of total biomass to reproduction at light levels <250 μE m^{-2} s^{-1} than at higher light levels. For woodland annuals there were few or no significant differences among light levels in the fraction of total biomass allocated to reproduction. *Acalypha* had lower reproductive effort in the unshaded treatment, in the sandiest soil than in most of the other treatment combinations. *Pilea* had the lowest and highest reproductive effort values at different soil moisture levels at the 50-100 μE m^{-2} s^{-1} light treatment. For *Impatiens*, reproductive effort did not differ significantly among treatments but it tended to decrease with increasing photosynthetic irradiance.

Reproductive effort was positively correlated with reproductive yield (absolute biomass) for the old field and for two of the three woodland annuals (*Acalypha*, *Pilea*). However, the relationship between reproductive effort and vegetative weight (dry weight of either aerial vegetative or root tissue) differed between groups of annuals. In old field annuals, reproductive effort was significantly positively correlated with aerial vegetative and/or root weight. In contrast, in woodland annuals, reproductive effort was significantly negatively correlated (or showed no significant correlation) with aerial vegetative weight and root weight (Table 4-3).

DISCUSSION

The two groups of species differed in how they regulated the distribution of biomass between reproductive and vegetative structures in a way that can provide a mechanism for explaining the usual absence of old field and woodland annuals from each other's habitats. With

Table 4-3. Correlation coefficients of percent of total dry weight allocated to reproduction with reproductive weight, aerial vegetative weight and root weight, for two old field and three woodland annuals grown over light and soil moisture gradients in the greenhouse. Data for all treatment combinations are lumped for each species. ** = $p<0.01$; * = $p<0.05$; n.s. = not significant.

	Species	Reproductive Weight	Aerial Vegetative Weight	Root Weight	
OLD FIELD	Chenopodium	+0.77**	+0.55**	+0.49**	(n=118)
	Polygonum	+0.71**	+0.16$^{n.s.}$	+0.29*	(n= 64)
WOODS	Acalypha	+0.33**	-0.02$^{n.s.}$	-0.04$^{n.s.}$	(n=190)
	Pilea	-0.05$^{n.s.}$	-0.24**	-0.21**	(n=178)
	Impatiens	+0.51**	-0.42**	-0.28*	(n= 90)

increasing irradiance, old field annuals showed an increase in overall plant size and reproductive effort. In contrast, for two of the three woodland annuals, Pilea and Impatiens, vegetative shoot and root weights increased and reproductive effort decreased, with increasing available light. For Acalypha and also for Impatiens reproductive effort increased as the mean weight of the reproductive structures increased. This pattern is consistent with the hypothesis that plants should allocate a greater proportion of their biomass to roots only under low soil moisture conditions so as to help maximize photosynthetic efficiency (Mooney and Gulmon, 1979), given that soil moisture availability decreased with increasing available light.

No other data are available for any group of annuals as to their mechanism of regulating reproductive effort. There is only one study that deals with this subject, for goldenrod species of old field and woods. Primack et at (1981) reported that five species increased reproductive effort by increasing reproductive yield, and in one species found at the forest edge, by also increasing weight of stems and leaves. The goldenrod species allocated the largest proportion of total biomass to vegetative shoot tissue and only allocated more biomass to roots at high light, where soil moisture availability was lower than at low light levels. The old field annuals regulate reproductive effort in a similar way to Solidago odora, the goldenrod species of forest edge habitats, which increased reproductive effort by increasing biomass allocation to setems, leaves and reproductive structures. However, of the woodland annuals, only Acalypha increased reproductive effort in the way that these goldenrod species of old field and woods do.

Old field annuals increased reproductive effort by increasing allocation to all plant components. At low light, old field annual plants were very small and thus their reproductive effort was very low. For the old field annual species in this experiment, photosynthetic rates at light levels <250 $\mu E\ m^{-2}\ s^{-1}$ were probably less than half their photosynthetic rates in full sunlight (Bazzaz and Carlson, 1982). Total plant weight for old field annuals was several times smaller than for woodland annuals at low light levels. The data suggest that old field annuals are not able to replace themselves at low light levels, typical of the light conditions in disturbed woodland, because they cannot increase relative biomass allocation to reproduction at the expense of biomass allocation to other plant components and because their shoot morphology (much non-photosynthetic stem tissue and narrow, linear leaves) is not conducive to high photosynthetic efficiency at low light.

The vegetative shoot morphology of woodland annuals was generally better suited for maximizing photosynthetic rate at low light. Woodland annuals have thin, broad, flat leaves which are expected to be more photosynthetically efficient in low light environments than the narrow, upright, lanceolate leaves of these old field annuals (Givnish, 1979). Two of the three woodland species (*Pilea*, *Impatiens*) were able to increase reproductive effort at low light levels by decreasing the proportion of total biomass allocated to roots and vegetative tissue.

Of the three woodland annuals, *Acalypha* and *Impatiens* could not replace themselves at the lowest light level, either due to low survivorship (*Impatiens*) or due to low seed reproduction (*Acalypha*). Although *Acalypha*'s shoot morphology is consistent with the type which favors high photosynthetic efficiency at low light, this species could not allocate enough biomass to reproduction at the lowest light level.

Acalypha increased reproductive effort by increasing reproductive yield and not by decreasing biomass allocation to vegetative tissue, as observed for the other woodland annuals. Impatiens could not survive to the time of flowering at the lowest light level probably because its large seed reserves resulted in tall, highly etiolated seedlings which were more susceptible to lodging than those of the smaller-seeded woodland annuals. Impatiens is known to allocate most of its vegetative shoot biomass to stems rather than leaves (regardless of environmental conditions, Abrahamson and Hershey, 1977) and this may make this species less photosynthetically efficient at very low light levels.

Of the three woodland annuals, Pilea and Impatiens allocated as great as or a slightly greater proportion of their total biomass to vegetative shoot and to roots at high light levels than the fraction of total biomass allocated to vegetative tissue by old field annuals at high light, although at the expense of reproductive effort. However, neither species survived to reproduce at the highest light treatment and only Pilea was able to replace itself at the next to highest light level. The data suggest that the shoot morphology of Pilea and Impatiens is not as efficient at conserving water as that of old field annuals, and that perhaps their root systems, although as heavy as those of old field annuals, are not as efficient at reaching the ground water supply as are those of old field annuals. Pilea and Impatiens have thin, broad, flat leaves which can result in higher evaporation rates at high irradiance than for the thicker, linear, narrower leaves of old field annuals.

These results suggest that Pilea and Impatiens are not found in the old field because they are inefficient at conserving water and poorer competitors for soil moisture than old field annuals. Although these annuals increase the proportion of total biomass allocated to vegetative shoot tissue, the plant body is shorter and more compact than that of old field annuals at high light, and thus cannot shade the larger old field annuals and prevent the old field annuals from competing for their water supply. Moreover,in increasing biomass allocation to vegetative tissue, these two woodland annuals decrease reproductive effort and are not able to produce enough seeds to replace themselves in the presence of old field annuals. Only Acalypha, of the three woodland annuals occurs infrequently in the old field and that species regulates reproductive effort by increasing reproductive yield. It has no trade-off between reproductive effort and vegetative tissue. Acalypha can maintain a high reproductive effort at high light and allocate a greater proportion of total biomass to roots than at low light. However, Acalypha plants are also small, compact and highly branched at high light levels and its leaves are also broad and flat. Thus, Acalypha cannot pre-empt a site through large above ground plant size and its leaves are probably less efficient at conserving water than those of old field annuals. Thus, its high reproductive effort is not sufficient to insure its constant presence in the old field. In addition, Acalypha seeds are not as long lived as seeds of old field annuals and may not remain viable in the soil long enough to colonize a newly disturbed site as do the seeds of old field annuals.

The mean reproductive effort values obtained for old field and woodland species in this greenhouse experiment are consistent with values published for old field and woodland annuals (Struik, 1965; Abrahamson and Hershey, 1977; Newell and Tramer, 1978). Even so, the difference in reproductive effort between the two groups of annuals is not consistent with the theory that predicts that species in early successional habitats should have higher reproductive effort than species in late successional habitats (Gadgil and Solbrig, 1972). In fact, the old field annuals had lower overall mean reproductive effort, on average, than did woodland annuals. Instead, allocation patterns were consistent with the hypothesis that species which are plastic in their reproductive allocation pattern are responding to the availability of essential resources, regardless of successional maturity of the community (Soule and Werner, 1981).

But within each habitat, differences in resource allocation to vegetative shoot and roots vs. reproduction can also explain why species within each group occupy certain areas of each habitat. Species with higher overall reproductive effort (*Chenopodium*, *Acalypha*, *Pilea*) replaced themselves over a broader range of environmental conditions in the greenhouse than species with low reproductive effort (*Polygonum*, *Impatiens*) (Table 4-1). The species with low reproductive effort allocated more to vegetative shoot and root tissue than the other species in their group, and may be able to monopolize resources at a site, thus keeping out the other species.

Small-seeded species (*Chenopodium*, *Acalypha*, *Pilea*) had higher overall reproductive effort than large-seeded species (*Polygonum*, *Impatiens*), in both old field and woods. Small-seeded species were able to replace themselves over a broader range of light and soil moisture conditions than large-seeded species in each habitat. Species with high reproductive effort may be selected to be more tolerant of environmental change than species with low reproductive effort because the former produce many seeds that may reach more different types of microsites within a habitat. The large-seeded species with low reproductive effort will have to be better competitors and have greater survivorship on one type of microsite (allocating more of total resources available to vegetative shoot and to roots) to be able to coexist with the species which produce a large number of seeds in the same habitat. This pattern has been observed for a group of closely related annuals which co-occur in montane regions of the northwestern United States (Hickman, 1977), for which the species with higher reproductive effort have a broader distribution across moisture and vegetation density gradients than species with low overall reproductive effort.

The species within each of the two groups of annuals studied in this experiment resemble each other in ways which allow them to establish successfully in their particular habitats. However, it is those differences among the species in seed size, reproductive capacity, biomass allocation pattern, and physiological tolerance of light and moisture conditions, traits which were selected for in the habitat of their particular evolutionary origin, which allow for the coexistence of several annuals in each habitat. For both old field and woodland annuals, there is an inverse relationship between seed size and reproductive effort. As seed size increases, plants are more likely to allocate a greater proportion of total biomass to vegetative tissue. Plants with large seeds allocate more to vegetative tissue and specialize in monopolizing resources early in the season in the more favorable areas of each habitat. This pattern limits biomass allocation to reproduction in these species and prevents them from having as high a reproductive effort as the small-seeded annuals with which they co-occur.

In conclusion, differences between old field and woods in the relative availability of light and soil moisture are reflected in the resource allocation pattern of old field and woodland annuals. The resource allocation pattern of old field annuals is one most likely to provide greater efficiency in obtaining and in conserving water, as well as in above-ground site pre-emption. For woodland annuals, their resource allocation pattern is most likely to allow for higher photosynthetic efficiency at low light than that of old field annuals, often at the expense of biomass allocation to root tissue.

Differences in resource allocation patterns among annuals of old field and of woods, can in large part explain the distribution of annual species within each habitat. *Polygonum*, which allocates a greater proportion of its biomass to aerial vegetative tissue and to roots than other old field annuals, can outcompete other old field annuals by overtopping them, but only in areas of high resource availability (Pickett and Bazzaz, 1976, 1978a). *Chenopodium* performs better in sites with less available resource within the old field than do several other old field annuals (Wieland and Bazzaz, 1975; Pickett and Bazzaz, 1978a). For woodland annuals, *Impatiens* performs best in large woodland gaps, in areas with a consistenly high moisture supply, where it can increase shoot biomass, both vegetative and reproductive, at the expense of root tissue, and where it can suppress the growth of neighbor species (Winsor, 1983). *Pilea* is better suited for low light, high moisture regions of the woodland environment than other woodland annuals because under low light conditions, it can allocate more biomass to both reproduction and vegetative shoot at the expense of roots than do the other two woodland annuals in this study. *Acalypha* is more successful in the high light, drier areas of the woods, and is able to occur in the old field infrequently. Lack of a persistent seed bank, which is a typical life history feature of old field annuals, a relatively late time of seedling emergence (mid-May in southwestern Michigan), coupled with small above-ground plant size may be the reasons why Acalypha is not more common in the old field.

Differences in the mode of regulating biomass allocation to aerial vegetative tissue, roots and reproduction over light and soil moisture gradients can explain why old field annuals cannot reproduce at low light levels typical of disturbed woodland and explains in large part why woodland annuals are generally absent from the old field.

Chapter 5

CONCLUSIONS

The purpose of this research was to determine the various differences between old field and woodland in both physiological tolerances and life history characteristics which were responsible for the restricted distribution of these two groups of annuals, and how these characteristics could be applied to explaining the existence of several ecologically distinct groups of annuals.

Firstly, in natural field sites, I showed that one old field and one woodland annual could not colonize each other's habitat even in the absence of competition from other herbs. The woodland annual germinated in the old field both in bare ground and in vegetated plots but did not survive to maturity at either microsite. The old field annual germinated and survived to the time of flowering in the woods but did not flower, regardless of the degree of competition from herbs.

Under controlled greenhouse experiments, I examined two main physical factors which were likely to influence the distribution of these species, by growing five species of annuals across a wide range of light and soil moisture levels, representing the ranges of these two factors in the old field and woods. The results were consistent with the field experiment, and further allowed an evaluation of the importance of these two essential resources and of their interactions in determining the distribution of these two groups of annuals. Old field annuals set few or no seeds at low light levels. Only one of the two old field annuals survived to the time of flowering and set seed in the unshaded treatment, which suggests that the moisture and possibly the temperature conditions for that treatment were harsher than experienced by these species in the one-year-old field. Old field annuals could not replace themselves at the light levels found in open woodland whereas two of three woodland annuals could not replace themselves in full sunlight, a treatment which also was characterized by higher temperatures and lower soil moisture than any of the shaded treatments. One of the three woodland annuals could replace itself over the entire range of environmental conditions found in abandoned fields of any age and only rarely occurs in the old field. The other woodland annuals had high net reproductive rates in environmental conditions similar to those found in shaded areas of old abandoned fields, but are generally absent from such areas.

Finally, I proposed a mechanism based on biomass allocation patterns to explain why these species could not replace themselves at certain light and soil moisture levels. In general, both groups of annuals allocated the largest proportion of total biomass to aerial vegetative tissue, and the least to roots, but the two groups differed in the way in which they regulated the fraction of total biomass allocated to reproduction. In old field annuals, reproductive effort (i.e. percent of total plant dry weight allocated to reproduction) was positively correlated with root, aerial vegetative and reproductive weights (absolute dry weight). Old field annuals increased all parts of the plant (shoot + root) as reproductive effort increased whereas woodland annuals increased reproductive effort either by increasing biomass allocation to reproductive structures or by decreasing allocation to vegetative structures (shoot + root) or by doing both.

Thus, for both groups of annuals, differences in both physiological tolerances and life history features contribute to restricting species distributions to their particular habitats. However, the relative importance of each type of factor differs between the two groups of annuals. For old field annuals, physiological intolerance of the light levels most typical of disturbed woodland can explain why those species are not usually found in a woodland environment. At low light, old field annuals are not able to photosynthesize at high enough rates to allocate biomass to all plant parts, including reproductive tissue, and still allow for seed production. A mechanism which regulates reproductive effort by varying overall plant size can be highly adaptive in the old field because increasing shoot size can increase light availability. Low soil moisture availability is associated with high light levels. Such an environment would favor plants that could allocate more biomass to roots at high light levels without a decrease in allocation to other plant structures and functions.

For old field annuals, the low probability of obtaining the basic physiological requirements for essential resources such as light and soil moisture in the woods seems to have a more significant role in explaining their general absence from disturbed woodland than in explaining why woodland annuals do not generally occur in the old field. Two of the three woodland annuals (Pilea, Impatiens) did not survive at the highest light level in the greenhouse experiment probably because temperatures were too high and soil moisture too low in that treatment, since soils dry out quickly near the soil surface under high irradiance. In a one-year-old field, the same results were obtained for Pilea in the presence or in the absence of competition. However, all three woodland annuals could replace themselves at much higher light levels than are typical of their natural habitats, and which are characteristic of resource levels in some areas in the old field. Their replacement rates were often higher than those of the old field annuals at those light levels. Thus, woodland annuals may not be able to colonize old fields because they are relatively poor competitors for soil moisture because they can generally replace themselves well in the shade, in a moist environment.

If woodland annuals are to compete effectively for soil moisture in the old field, they must allocate more biomass to roots than in the woods, just as the old field annuals do in the greenhouse, and still allocate a substantial amount of biomass towards reproduction. However, the results under controlled conditions suggested a trade-off between biomass allocation to roots and reproductive effort for some woodland annuals. Woodland annuals have lower germination and lower survivorship in the old field than in the woods. Only high reproduction can make up for the other two to obtain a net reproductive rate ≥ 1. However, if reproductive effort is lower due to increased allocation to roots, then the woodland annuals cannot replace themselves. Indeed, the single woodland annual that could replace itself in the unshaded greenhouse treatment (*Acalypha*) did not exhibit a detectable trade-off between reproductive effort and root weight. However, *Acalypha* did not increase overall plant size as it increased reproductive effort in the way old field annuals did. These three woodland annuals do not have the shoot morphology conducive to conserving moisture or the long tap root systems of old field annuals. In the more shaded areas of the old field, there can be higher levels of moisture in the soil and more favorable temperatures for growth (Raynal and Bazzaz, 1975b) but the old field species may deplete the water supply near the soil surface too quickly to allow woodland annuals, with their relatively shallow root systems, to become established.

Thus, old field and woodland annuals are similar in several ways in their response to the complex environmental gradient extending from a field abandoned from cultivation to disturbed woodland. They differ primarily in their reproductive characteristics. The results show that the two groups of annuals differ in the amount of light needed to produce seeds, and in the mechanism for regulating reproductive effort over a light gradient.

There is much within-group variation for both old field and woodland annuals in physiological tolerance to the combined light and moisture gradients. Species within each of group of summer-flowering annuals that I have studied have several traits in common even though they have not coevolved in their particular habitats. However, summer-flowering old field annuals do have some similarities in their evolutionary history and the same may be true for summer-flowering woodland annuals. The center of species diversity for summer-flowering old field annuals is in temperate regions and the genera of summer-flowering woodland annuals are best represented in subtropical and tropical regions of the world. Thus, knowing the probable world region of origin of a summer-flowering annual species may be very helpful in predicting the type of habitat for which it will be preadapted. However, knowledge of the light and soil moisture conditions under which the species evolved may be more important in predicting the site within each habitat in which it will perform best.

The importance of evolutionary history in explaining the distribution of a group of annuals within one habitat type has been observed for three coexisting alpine annuals (Reynolds, 1984a).

The species with a narrow tolerance range over the light and soil moisture experimental gradients in the greenhouse (Polygonum, Impatiens) were those which in nature occupy areas within a habitat where resources are less likely to drop below tolerable levels (Wieland and Bazzaz, 1975; Raynal and Bazzaz, 1975b; Winsor, 1983) and plant productivity is highest. Within each group of annuals, species with narrow niches produce fewer and larger seeds than other species in their group of annuals. The large seeds allow for rapid seedling growth, which coupled with early emergence may make them better competitors (Abul-Fatih and Bazzaz, 1979a; Winsor, 1983). Generally, the more tolerant species produce many, small seeds relative to other annuals in their habitat. Old field and woodland annual species with wide physiological tolerance to the experimental gradients (Chenopodium, Acalypha and Pilea) are usually found in the more disturbed, sparsely vegetated areas within their particular habitats, where few other species occur in nature. Resource levels vary more in these areas, during the year and from year to year. Resources are more likely to reach levels unfavorable of growth in those sites (Struik, 1965; Menges and Waller,1983).

Thus, it seems that in both the old field and the woodland habitat, there is a positive correlation between intolerance of wide variations in essential resources, and life history features (large seeds, high seedling growth rates) which allow these species to pre-empt space faster than other species in sites where resource levels can permit high productivity. Species that can replace themselves under various light and soil moisture levels produce many small seeds relatively to other annuals in their particular habitat.

Annual plants differ considerably in their degree of fugitiveness. There are short-lived annuals which can complete their life cycle within the few weeks of very good environmental conditions which are typical of many habitats, even those which are highly stressed for most of the year (e.g. deserts). These annuals escape all periods unfavorable for growth. If an annual species is able to complete its life cycle during a period of continuously high light, moisture and nutrient conditions it can avoid extreme changes in these environmental conditions. Such species may or may not have a persistent seed bank depending on the predictability of the favorable period in their environment (desert annuals, Went, 1955; dune annuals, winter annuals of wet grasslands, Watkinson, 1981), but may be able to succeed in a wide range of habitats (Galium aparine, Grime, 1979; Rogers, 1981; Stellaria media, Turkington et al, 1980).

However, annuals with an above-ground life cycle which is as long as the maximum length of the growing season for a particular habitat cannot escape any unpredictable periods of low resource availability during the growing season. Many groups of co-occurring summer-flowering annuals, such as old field and woodland annuals, belong to this category. The results of the experiments reported here indicate that differences between old field and woodland annuals in light requirements for seed production and in the mechanism varying allocation to reproduction over resource gradients are most important in determining the distribution of these two groups of annuals.

Restrictions in the mode of seed dispersal, e.g. dispersing seeds mostly in time rather than in space or vice versa, can increase the probability of species being restricted to one particular habitat. However, if a species' physiological requirements and life history characteristics can enable it to establish successfully in a given habitat, poor seed dispersal alone will be unlikely to prevent its establishment in that habitat, but may make it a relatively rare occurrence in that habitat (e.g. Acalypha). The two groups of species do not differ in many life history and physiological characteristics but the differences in reproductive characteristics which do exist are of great importance in determining the type of disturbed habitat an annual species may colonize.

APPENDIX

APPENDIX 1

DESCRIPTION OF THE LIGHT, SOIL MOISTURE AND TEMPERATURE ENVIRONMENT IN THE GREENHOUSE AND IN NATURAL POPULATIONS OF OLD FIELD AND WOODLAND ANNUAL PLANTS

Figure A-1. Spectral energy distribution of photosynthetic irradiance (in $\mu E\ m^{-2}\ s^{-1}\ nm^{-1}$) on plants in the greenhouse for each of six light treatments (2% - 100% incoming sunlight), and atop the herbaceous layer, in the woods (woodland site of 1981 field experiment). Spectroradiometric measurements were done between 12:30 p.m. and 1:30 p.m., on 19 August 1982.

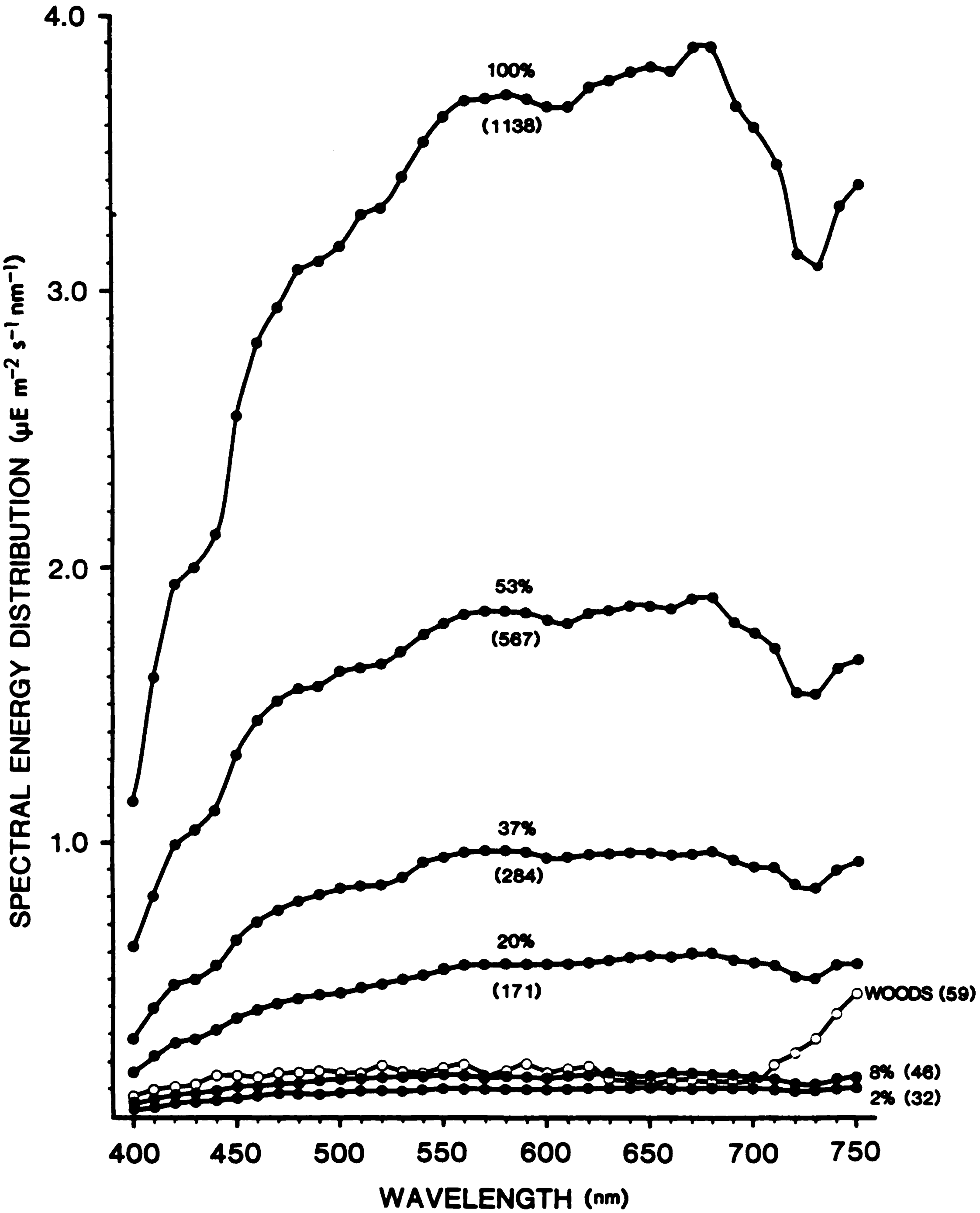
4.0
3.0
2.0
1.0
SPECTRAL ENERGY DISTRIBUTION (µE m^{-2} s^{-1} nm^{-1})
100%
(1138)
53%
(567)
37%
(284)
20%
(171)
WOODS (59)
8% (46)
2% (32)
400
450
500
550
600
650
700
750
WAVELENGTH (nm)

Figure A-1

Table A-1. Mean photosynthetic irradiance (PAR as $\mu E\ m^{-2} s^{-1}$) and mean percent full sunlight (± standard error) for six light treatments in the greenhouse (ranging from 2% to 100% incoming sunlight) measured at midday or in early afternoon at plant height, March-September 1982. (n=6 per light treatment for March-19 July; n=12 for 29 July; n=15-80 for September). Means not sharing a superscript (each date taken separately) differ significantly from each other with $p < .05$.

Date		2%	8%	20%	37%	53%	100%
27 March	PAR	$7^a \pm 3.5$	$49^a \pm 16.4$	$80^a \pm 12.0$	$212^b \pm 12.4$	$448^c \pm 47.8$	$805^d \pm 33.2$
P.M.	% Full Sunlight	0.3 ± 0.29	3.8 ± 1.27	7.0 ± 1.04	19.7 ± 1.16	44.8 ± 4.77	86.6 ± 3.57
14 April	PAR	$25^a \pm 7.9$	$43^a \pm 17.1$	$120^a \pm 25.1$	$410^b \pm 25.3$	$690^b \pm 31.9$	$1080^b \pm 230.7$
midday	% Full Sunlight	1.5 ± 0.47	2.6 ± 1.0	8.0 ± 1.49	24.2 ± 1.49	40.5 ± 1.88	63.2 ± 13.49
14 April	PAR	$5^a \pm 0.9$	$68^b \pm 25.8$	$75^b \pm 6.7$	$94^b \pm 12.2$	$310^c \pm 35.2$	$553^d \pm 48.6$
P.M.	% Full Sunlight	0.7 ± 0.14	10.6 ± 4.03	11.4 ± 1.02	14.9 ± 1.91	46.4 ± 5.27	81.6 ± 7.16
2 June	PAR	$25^a \pm 7.1$	$80^a \pm 17.5$	$350^{bc} \pm 81.9$	$440^b \pm 31.6$	$790^c \pm 20.0$	$1285^d \pm 144.2$
midday	% Full Sunlight	1.4 ± 0.39	4.4 ± 0.97	19.0 ± 4.44	22.7 ± 1.64	42.0 ± 1.08	71.4 ± 8.01
9 July	PAR	$15^a \pm 3.9$	$115^b \pm 9.2$	$189^{ab} \pm 33.7$	$430^c \pm 26.5$	$740^d \pm 34.4$	$1205^e \pm 112.2$
midday	% Full Sunlight	0.9 ± 0.22	6.7 ± 0.54	10.9 ± 1.95	24.8 ± 1.52	42.7 ± 1.98	69.7 ± 6.47
29 July	PAR	$18^a \pm 5.3$	$78^b \pm 6.9$	$210^c \pm 18.6$	$340^d \pm 25.6$	$665^e \pm 23.5$	$1256^f \pm 18.4$
P.M.	% Full Sunlight	1.2 ± 0.36	5.2 ± 0.46	14.2 ± 1.26	23.2 ± 1.75	45.9 ± 1.62	85.5 ± 1.22
29 September	PAR	$4^a \pm 0.2$	$19^b \pm 0.5$	$85^c \pm 7.0$	$264^d \pm 10.8$	$458^e \pm 15.3$	$880^f \pm 27.6$
midday	% Full Sunlight	0.3 ± 0.01	1.4 ± 0.04	6.3 ± 0.52	19.6 ± 0.80	33.9 ± 1.13	65.2 ± 2.04

Table A-2. Results of laboratory analyses of the potting soil used (in sand and soil mixtures) to establish the soil moisture gradient, over which two old field and three woodland annuals were grown in the greenhouse.

			Mineral Fraction Distribution (% soil dry weight)[a]						% total	Nutrient Content (ppm)				
Soil Type	Soil pH	Percent Organic Matter	Sand					Silt & Clay	N (per g soil dry wt.)	NO_3^-	$PO_4^{\equiv}$	K	Ca	Mg
			(>1mm)	(1-.5mm)	(.5-.25mm)	(.25-.7mm)	(.1-.05mm)	(≤.05mm)						
Sandy Organic	6.9	59.62	10.2	25.9	21.2	22.7	10.2	9.6	2.14	458.5	16.0	28.0	4894.0	746.5

a = Werner, unpublished

Table A-3. Results of laboratory analyses of soil taken from sites occupied by natural populations of each of two old field and three woodland annuals. Means of three samples (each a composite of 3 cores taken to a 10 cm depth) are reported for each site.

	Species	Soil	Soil	% Organic	Percent Total N	Nutrient Content (ppm)				
	Present	Type	pH	Matter	(per g soil dry wt.)	NO_3	PO_4	K	Ca	Mg
OLD FIELD	*Chenopodium*	Sandy Loam	5.9	1.5	0.09	3.5	15.5	128.8	725.8	85.0
	Polygonum	Sandy Loam	7.5	6.0	0.16	15.1	198.2	346.8	1588.2	145.5
WOODS	*Acalypha*	Loamy Sand	7.4	7.0	0.12	9.0	47.5	48.5	1564.3	190.3
	Pilea	Sandy Loam	6.8	7.7	0.33	7.2	76.3	140.7	1983.0	243.7
	Impatiens	Loamy Sand	7.5	9.4	0.35	18.5	59.0	291.2	2228.5	250.3

Table A-4. Mean % soil moisture (± standard error) for soil samples taken from each of six light treatments (ranging from <50 to >1000 $\mu E\ m^{-2}s^{-1}$) between April and October, 1982. Flats (n=2 per soil type, April-June) or pots (n=2 per soil type, August-September; n=4-6 for October) to be sampled were filled with one of three types of sand:soil mixtures of low (L), medium (M) and high (H) water-hold capacity, and randomly scattered under each light treatment. The number of days without watering is shown in parentheses under each sampling date.

Sampling Date	Soil Mixture	Mean % Soil Moisture (± S.E.) At Each Light Level					
		<50	50-100	100-200	250-400	550-700	>1000
20 April	L	25.1 ± 0.00	22.2 ± 0.56	20.4 ± 0.13	23.1 ± 0.74	29.6 ± 12.07	14.9 ± 5.86
(2)	M	51.9 ± 0.31	40.1 ± 2.33	71.0 ± 1.11	49.2 ± 1.46	44.4 ± 4.81	25.5 ± 0.27
	H	72.0 ± 0.91	64.4 ± 3.62	62.9 ± 11.30	71.4 ± 0.91	68.9 ± 0.94	51.8 ± 2.07
29 April	L	22.5 ± 0.45	15.5 ± 0.25	17.1 ± 0.08	18.1 ± 0.71	12.7 ± 0.07	6.8 ± 0.27
(2)	M	45.3 ± 0.41	34.2 ± 1.78	49.0 ± 0.46	44.9 ± 0.44	34.1 ± 0.82	19.1 ± 0.03
	H	74.7 ± 2.34	46.8 ± 0.60	68.2 ± 3.23	70.6 ± 0.80	49.4 ± 3.24	52.4 ± 1.39
21 May	L	14.1 ± 3.15	9.5 ± 0.16	12.2 ± 0.95	14.3 ± 0.01	15.3 ± 1.11	10.0 ± 1.43
(3)	M	31.4 ± 1.86	17.0 ± 2.96	24.5 ± 0.31	28.0 ± 4.55	24.0 ± 2.38	6.8 ± 1.96
	H	51.8 ± 2.41	39.8 ± 1.62	51.6 ± 10.57	36.1 ± 2.03	20.2 ± 7.73	20.9 ± 2.60
2 June	L	13.6 ± 1.27	8.3 ± 0.06	12.8 ± 0.41	10.6 ± 0.15	6.0 ± 0.09	2.8 ± 0.02
(4)	M	39.8 ± 1.87	21.3 ± 2.24	38.0 ± 2.13	34.0 ± 3.37	17.4 ± 0.72	3.4 ± 0.34
	H	56.5 ± 3.10	29.9 ± 0.66	46.5 ± 0.93	36.5 ± 3.05	25.5 ± 5.25	11.7 ± 0.13
8 June	L	11.1 ± 0.10	7.0 ± 0.09	10.3 ± 0.55	9.0 ± 0.40	5.4 ± 0.05	3.1 ± 0.75
(5)	M	39.4 ± 3.04	13.7 ± 2.90	31.6 ± 3.79	24.5 ± 2.27	18.5 ± 1.20	1.3 ± 0.18
	H	48.3 ± 1.53	30.1 ± 0.13	39.3 ± 0.13	42.8 ± 1.00	18.4 ± 1.42	7.0 ± 0.84
13 June	L	9.5 ± 0.06	5.5 ± 0.36	9.0 ± 0.22	9.0 ± 0.03	4.8 ± 0.01	1.3 ± 0.24
(4)	M	38.5 ± 0.41	14.6 ± 1.44	41.0 ± 1.74	36.1 ± 1.44	17.9 ± 1.30	0.8 ± 0.04
	H	54.0 ± 1.56	25.9 ± 0.75	43.9 ± 1.37	41.5 ± 1.96	18.1 ± 1.93	6.6 ± 1.46
19 August	L	7.5 ± 0.70	10.0 ± 1.25	6.6 ± 1.70	3.4 ± 2.00	0.5 ± 0.13	0.4 ± 0.03
(10)	M	42.9 ± 4.75	43.6 ± 7.23	23.8 ± 7.64	8.3 ± 2.57	2.6 ± 0.35	2.4 ± 0.50
	H	67.3 ± 3.17	57.9 ± 14.14	41.5 ± 0.51	13.0 ± 3.00	3.1 ± 0.26	2.7 ± 0.35
23 August	L	11.1 ± 3.25	10.7 ± 0.85	10.8 ± 0.11	13.1 ± 1.26	7.5 ± 1.72	3.0 ± 0.99
(3)	M	35.7 ± 2.58	37.4 ± 1.84	38.1 ± 2.16	39.7 ± 0.40	37.1 ± 4.94	21.3 ± 1.78
	H	68.9 ± 0.54	70.6 ± 1.47	69.2 ± 1.32	69.9 ± 4.19	63.7 ± 3.27	41.5 ± 2.32
14 September	L	6.7 ± 2.13	11.5 ± 2.23	7.2 ± 1.66	10.8 ± 0.30	6.4 ± 2.01	3.2 ± 0.18
(6)	M	34.7 ± 4.63	47.8 ± 4.65	51.3 ± 5.17	51.1 ± 11.56	55.9 ± 2.24	23.3 ± 0.30
	H	74.5 ± 1.72	72.5 ± 0.27	62.3 ± 3.47	93.2 ± 1.66	73.8 ± 11.74	37.9 ± 5.09
29 September	L	14.9 ± 1.04	17.5 ± 1.35	16.2 ± 0.88	18.8 ± 0.49	18.6 ± 0.88	6.4 ± 1.62
(3)	M	48.1 ± 2.97	51.8 ± 2.85	53.1 ± 0.13	51.7 ± 2.22	57.8 ± 2.30	23.7 ± 0.18
	H	82.1 ± 0.00	87.9 ± 2.33	84.6 ± 6.38	94.5 ± 2.10	84.9 ± 0.99	51.5 ± 1.07
7 October	L	6.7 ± 1.05	6.9 ± 0.53	4.5 ± 1.66	2.7 ± 1.14	1.1 ± 0.21	1.6 ± 1.00
(8)	M	41.2 ± 2.35	40.4 ± 3.12	31.8 ± 4.85	20.1 ± 9.65	5.8 ± 0.73	5.2 ± 1.01
	H	60.1 ± 4.41	57.1 ± 6.32	32.4 ± 8.72	19.6 ± 2.02	7.0 ± 0.40	12.9 ± 2.12

Table A-5. Watering schedule for plants grown in the greenhouse for April-October 1982.

Month	Mean # days without watering (±S.E.)	Range	
April	1.8 ± 0.19	1-3 days	n=16
May	3.2 ± 0.36	2-5 days	n=9
June	2.9 ± 0.53	1-6 days	n=11
July	3.2 ± 0.80	1-9 days	n=9
August	3.6 ± 0.94	1-10 days	n=9
September	2.8 ± 0.88	1-10 days	n=10
October[a]	3.7 ± 2.19	1-8 days	n=3

a = plants were harvested the 2nd week in October

Table A-6. Mean maximum and minimum air temperature per month (°C ± standard error) in the greenhouse and in the field (the latter from weather station data) for April-October, 1982.

Month		Greenhouse	Field
April	max.	22.5 ± 0.53	12.1 ± 1.27
	min.	10.2 ± 0.22	-0.6 ± 1.16
May	max.	27.8 ± 1.06	24.6 ± 0.74
	min.	14.6 ± 0.47	11.9 ± 0.64
June	max.	27.9 ± 0.70	23.8 ± 0.44
	min.	14.1 ± 0.39	11.9 ± 0.61
July	max.	32.6 ± 0.50	28.3 ± 0.37
	min.	17.2 ± 0.49	16.8 ± 0.61
August	max.	31.0 ± 0.89	26.8 ± 0.53
	min.	16.0 ± 0.74	14.4 ± 0.77
September	max.	27.3 ± 1.16	22.9 ± 0.89
	min.	13.9 ± 0.64	11.7 ± 0.77
October	max.	27.1 ± 1.22	18.7 ± 1.04
	min.	12.8 ± 0.48	5.9 ± 1.04

Figure A-2. Mean photosynthetic irradiance (E m^{-2} s^{-1} ± range) measured at midday atop the herbaceous layer and at ground level, in a one-year-old field, two-year-old field and woodland sites, from May to September, 1982 (n=21 plots per 900 m^2 site).

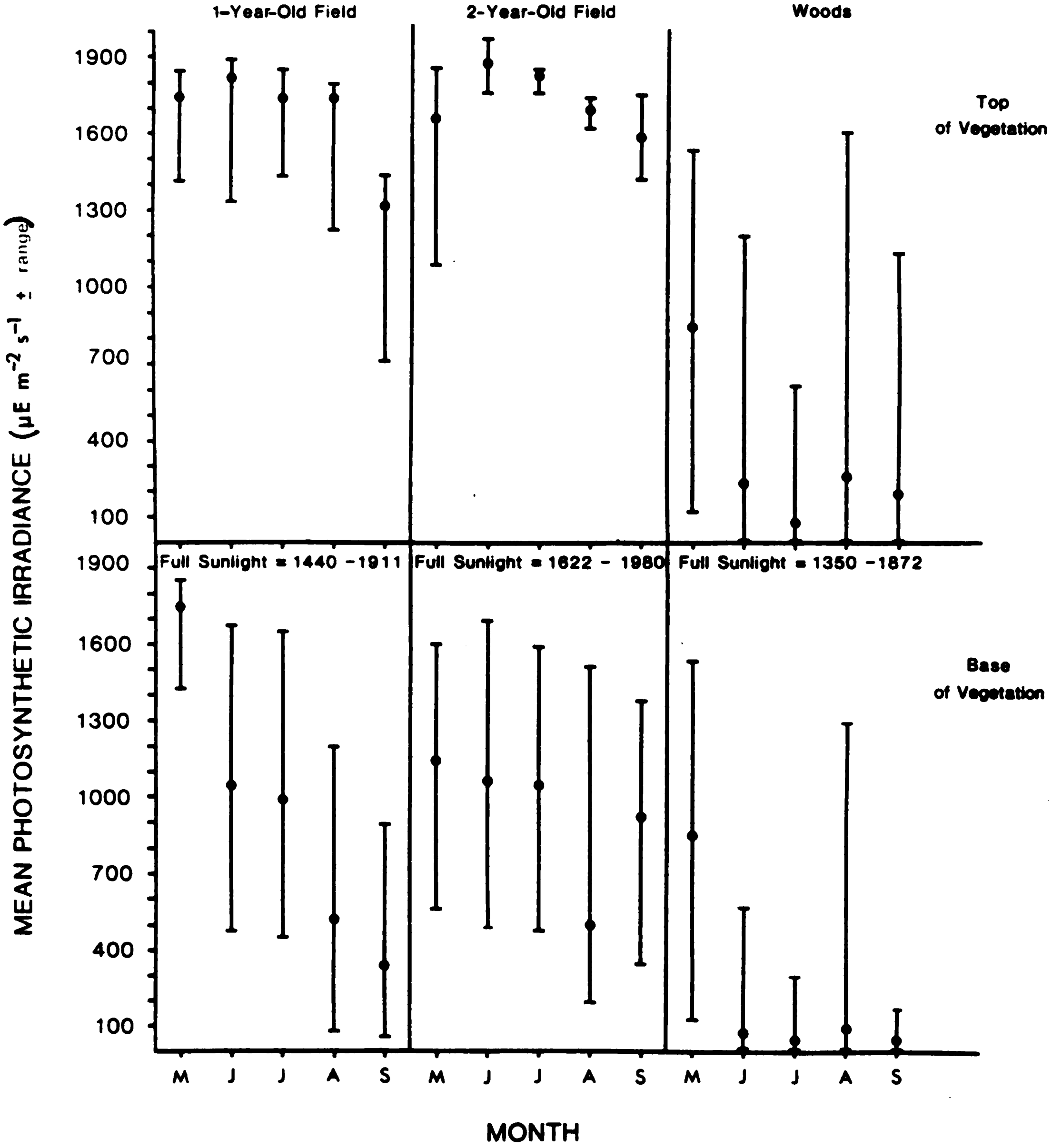
1-Year-Old Field
2-Year-Old Field
Woods
Top
of Vegetation
Base
of Vegetation
Full Sunlight = 1440 -1911
Full Sunlight = 1622 - 1980
Full Sunlight = 1350 -1872
MEAN PHOTOSYNTHETIC IRRADIANCE (μE m-2 s-1 ± range)
1900
1600
1300
1000
700
400
100
M
J
J
A
S
MONTH

Figure A-2

Figure A-3. Mean photosynthetic irradiance ($\mu E\ m^{-2}\ s^{-1} \pm$ range) measured at midday at plant height in natural populations of two old field and three woodland annuals, from May to September, 1982. Light readings were taken at 0.25 m^2 plots established on 1-3 parallel transects over the area covered by each population. The total number of plots established at each site were: 21 plots for *Chenopodium* (900 m^2 area), 6 plots for *Polygonum* (30 m^2 area), 6 plots for *Acalypha* (10 m^2), 20 plots for *Pilea* (30 m^2 area) and 11 plots for *Impatiens* (150 m^2 area).

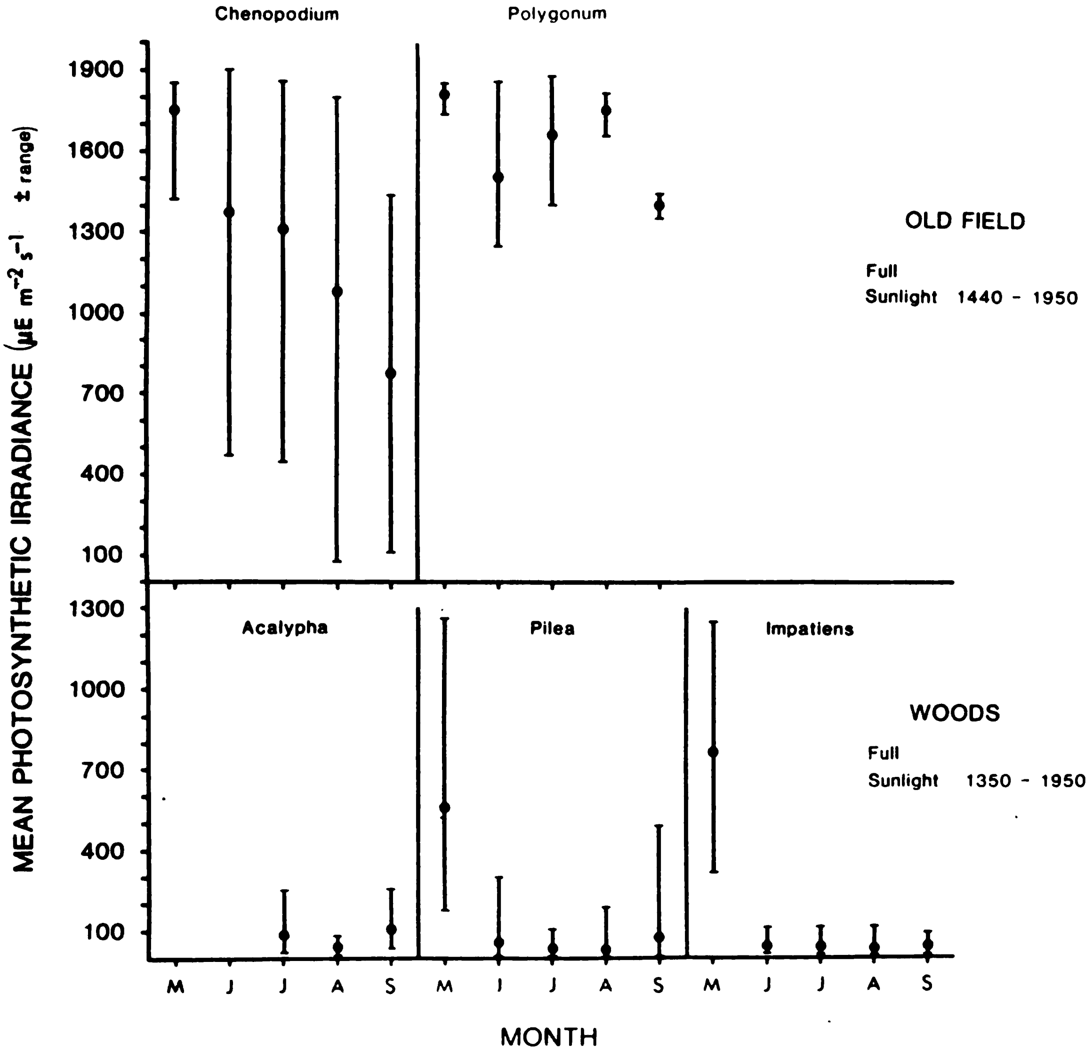
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
OLD FIELD
Full
Sunlight 1440 - 1950
WOODS
Full
Sunlight 1350 - 1950
MEAN PHOTOSYNTHETIC IRRADIANCE (μE m-2 s-1 ± range)
1900
1600
1300
1000
700
400
100
1300
1000
700
400
100
M
J
J
A
S
M
J
J
A
S
M
J
J
A
S
MONTH

Figure A-3

Figure A-4. Mean percent soil moisture (g H_2O/g dry soil ± range) for 0.25 m^2 plots established in a one-year-old field, two-year-old field and woodland sites, and for natural populations of two old field and three woodland annuals. One soil sample was taken from each plot, four days after a rainstorm, June-September, 1982. The total number of plots sampled at each site were: 21 plots for *Chenopodium* in the one-year-old field (900 m^2 area), 6 plots for *Acalypha* (10 m^2 area), 5 plots for *Pilea* (30 m^2 area), 11 plots for *Impatiens* (150 m^2 area) and 21 plots for the woodland site (900 m^2 area).

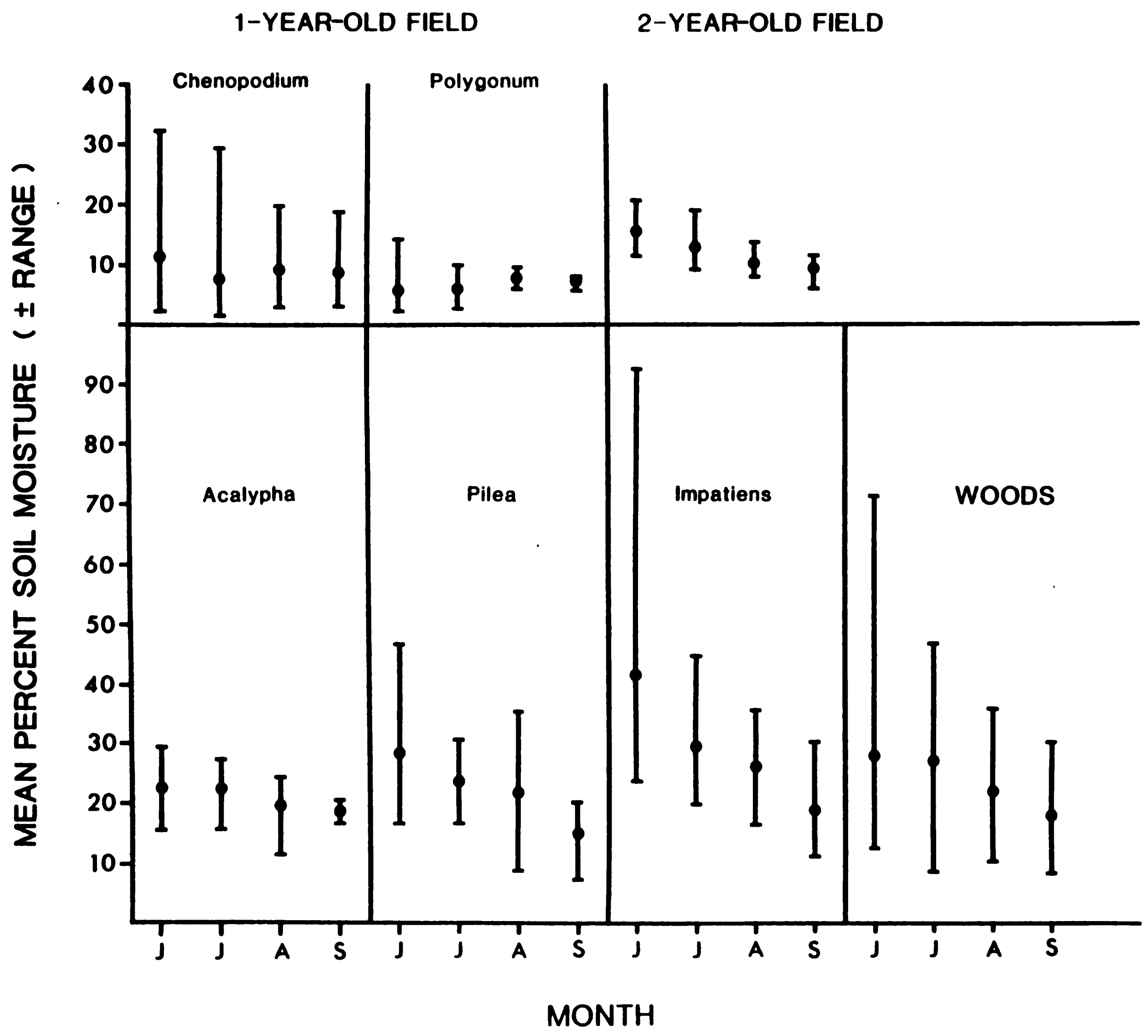
1-YEAR-OLD FIELD
2-YEAR-OLD FIELD
Chenopodium
Polygonum
Acalypha
Pilea
Impatiens
WOODS
MEAN PERCENT SOIL MOISTURE (± RANGE)
40
30
20
10
90
80
70
60
50
40
30
20
10
J
J
A
S
J
J
A
S
J
J
A
S
J
J
A
S
MONTH

Figure A-4

LITERATURE CITED

LITERATURE CITED

Abrahamson, W. G. 1979. Patterns of resource allocation in wildflower populations of fields and woods. American Journal of Botany 66: 71-79.

Abrahamson, W. G. and M. Gadgil. 1973. Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). American Naturalist 107: 651-661.

Abrahamson, W. G. and B. J. Hershey. 1977. Resource allocation and growth of *Impatiens capensis* (Balsaminaceae) in two habitats. Bulletin of the Torrey Botanical Club 104: 160-164.

Abul-Fatih, H. A. and F. A. Bazzaz. 1979. The biology of *Ambrosia trifida* L. II. Germination, emergence, growth and survival. New Phytologist 83: 817-827.

Austin, M. P. and B. O. Austin. 1980. Behavior of experimental plant communities along a nutrient gradient. Journal of Ecology 68: 891-918.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology 53: 997-1010.

Baskin, J. M. and C. C. Baskin. 1977. Role of temperature in the germination ecology of three summer annual weeds. Oecologia 30: 377-382.

Bassett, I. J. and C. W. Crompton. 1978. The biology of Canadian weeds. 32. *Chenopodium album* L. Canadian Journal of Plant Science 58: 1061-1072.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10: 351-371.

Bazzaz, F. A. and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54: 313-316.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: A review. New Phytologist 90: 757-776.

Black, J. N. and G. N. Wilkinson. 1963. The role of time of emergence in determining the growth of individual plants in swards of subterranean clover. Australian Journal of Agricultural Research 14:

628-638.

Bonner, F. T. 1974. Seed testing. pp. 136-152. In: Schopmeyer, C. S. (ed.), Seeds of woody plants in the United States. Agriculture Handbook Number 450. Forest Service. U.S. Department of Agriculture, Washington, D. C.

Cappel, E. D. 1969. A study of variation within the genus Pilea (Urticaceae) of temperate North America. Ph.D. dissertation. University of Massachusetts, Amherst, Mass. 168 pp.

Cavers, P. B. and J. L. Harper. 1967. Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. Journal of Ecology 55: 59-71.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment.Journal of Theoretical Biology 12: 119-129.

Cook, R. E. 1980. The biology of seeds in the soil. pp. 107-129. In: Solbrig, O. T. (ed.), Demography and evolution in plant populations. University of California Press, Berkeley. 222 pp.

Coombe, D. E. 1956. Impatiens parviflora DC. Journal of Ecology 44: 701-713.

Cumming, B. G. 1963. The dependence of germination on photoperiod, light quality, and temperature, in Chenopodium spp. Canadian Journal of Botany 41: 1211-1233.

Davis, R. H. and J. E. Cantlon. 1969. Effect of size area open to colonization on species composition in early old field succession. Bulletin of the Torrey Botanical Club 96: 660-673.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22: 283-314.

Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. Berichte der Deutschen Botanische Gesellschaft 65: 351-362.

Evans, G. C. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley. 734 pp.

Gadgil, M. and O. T. Solbrig. 1972. The concept of r and K selection: Evidence from wild flowers and some theoretical considerations. American Naturalist 106: 14-31.

Gartner, B. L., F. S. Chapin, III and G. R. Shaver. 1983. Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. Journal of Applied Ecology 20: 965-980.

Gill, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. Volume I. Iowa State University Press, Ames, Iowa.

409 pp.

Givnish, T. 1979. On the adaptive significance of leaf form. pp. 375-407. In: Solbrig, O. T., S. Jain, G. B. Johnson and P. H. Raven (eds.), Topics of plant population biology. Columbia University Press, New York. 589 pp.

Gleason, H. A. and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand, Princeton. 810 pp.

Grime, J. P. 1965. Comparative experiments as a key to the ecology of flowering plants. Ecology 46: 513-515.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, New York. 222 pp.

Grime, J. P. and D. W. Jeffrey. 1965. Seedling establishment in vertical gradients of sunlight. Journal of Ecology 53: 621-642.

Grime, J. P. and B. C. Jarvis. 1975. Shade avoidance and shade tolerance in flowering plants II. Effects of light on the germination of species of contrasted ecology. pp. 525-532. In: Evans, G. C., R. Bainbridge and O. Rackham (eds.), Light as an ecological factor: II. Blackwell Scientific Publications, Oxford. 616 pp.

Gross, K. L. 1980. Colonization by Verbascum thapsus (mullein) of an old field in Michigan: Experiments on the effects of vegetation. Journal of Ecology 68: 919-927.

Gross, K. L. and P. A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: Implications for their distributions in a successional sere. Ecology 63: 921-931.

Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennials. Journal of Ecology 72: 369-388.

Gross, R. S. and P. A. Werner. 1983. Probabilitie of survival and reproduction relative to rosette size in the common burdock (Arctium minus: Compositae). American Midland Naturalist 109: 184-193.

Grubb, P. J. 1976. A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk ecosystem. Biological Conservation 10: 53-76.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Review 52: 107-145.

Harper, J. L. 1977. Plant population biology. Academic Press, New York. 892 pp.

Henson, I. E. 1970. The effects of light, potassium nitrate and temperature on the germination of Chenopodium album L. Weed Research 10: 27-39.

Hickman, J. C. 1977. Energy allocation and niche differentiation of four co-existing annual species of Polygonum in western North America. Journal of Ecology 65: 317-326.

Hickman, J. C. 1979. The basic biology of plant numbers. pp. 232-263. In: Solbrig, O. T., S. Jain, G. B. Johnson, and P. H. Raven (eds.), Topics in plant population biology. Columbia University Press, New York. 589 pp.

Holmes, M. G. and H. Smith. 1975. The function of phytochrome in plants growing in the natural environment. Nature 254: 512-574.

Holzner, W., I. Hayashi and J. Glainzer. 1982. Reproductive strategy of annual agrestals. pp. 111-121. In: Holzner, W. and N. Numata (eds.), Biology and Ecology of Weeds. Dr W. Junk Publishers, The Hague. 461 pp.

Howell, N. 1981. The effect of seed size and relative emergence time on fitness in a natural population of Impatiens capensis Meerb. (Balsaminaceae). American Midland Naturalist 105: 312-320.

Huston, M. A. 1983. The effect of fertilization on size distributions of annual plants in a plowed old field. Bulletin of the Ecological Society of America 64: 171.

Jordan, J. L. 1982. Some effects of overwinter burial on Polygonum pensylvanicum L. achenes. Annals of Botany 49: 417-419.

Keddy, P. A. 1982. Population ecology of an environmental gradient: Cakile edentula on a sand dune. Oecologia 52: 348-355.

Kirkpatrick, B. L. and F. A. Bazzaz. 1979. Influence of certain fungi on seed germination and seedling survival of four colonizing annuals. Journal of Applied Ecology 16: 515-527.

Klemow, K. M. and D. J. Raynal. 1983. Population biology of an annual plant in a temporally variable habitat. Journal of Ecology 71: 691-703.

Kramer, P. J. 1969. Plant and soil water relationships: A modern synthesis. McGraw-Hill Book Co., New York. 482 pp.

Larcher, W. 1975. Physiological plant ecology. Springer-Verlag, New York. 252 pp.

Lawrence, G. H. M. 1958. Taxonomy of vascular plants. Macmillan Co., New York. 823 pp.

Leck, M. A. 1979. Germination behavior of Impatiens capensis Meerb. (Balsaminaceae). Bartonia 46: 1-11.

Leonard, E. R. 1962. Inter-relations of vegetative and reproductive growth, with special reference to indeterminate plants. Botanical Reviews 28: 354-410.

Marks, P. L. 1983. On the origin of the field plants of the northeastern United States. American Naturalist 122: 210-228.

Menges, D. C. and D. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. American Naturalist 122: 454-473.

Mooney, H. A. and S. L. Gulmon. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. pp. 316-337. In: Solbrig, O. T., S. Jain, G. B. Johnson, P. H. Raven (eds.), Topics in plant population biology. Columbia University Press, New York. 589 pp.

Morgan, D. C. and H. Smith. 1976. Linear relationship between phytochrome photoequilibrium and growth in plants under simulated natural radiation. Nature 262: 210-212.

Morgan, D. C. and H. Smith. 1978. Simulated sunflecks have large rapid effects on plant stem extension. Nature 273: 534-536.

Newell, S. J. and E. J. Tramer. 1978. Reproductive strategies in herbaceous plant communities during succession. Ecology 59: 228-234.

Ødum, S. 1965. Germination of ancient seeds: floristical observations and experiments with archaelogically dated soil samples. Dansk Botanisk Arkiv 24: 1-70.

Parrish, J. A. D. and F. A. Bazzaz. 1976. Underground niche separation in successional plants. Ecology 57: 1281-1288.

Pemadasa, M. A. and P. H. Lovell. 1974. Factors affecting the distribution of some annuals in the dune system at Aberffraw, Anglesey. Journal of Ecology 62: 403-416.

Pianka, E. R. 1974. Evolutionary ecology. Harper and Row, New York. 415 pp.

Pickett, S. T. A. and F. A. Bazzaz. 1976. Divergence of two co-occurring successional annuals on a soil moisture gradient. Ecology 57: 169-176.

Pickett, S. T. A. and F. A. Bazzaz. 1978a. Organization of an assemblage of early successional species on a soil moisture gradient. Ecology 59: 1248-1255.

Pickett, S. T. A. and F. A. Bazzaz. 1978b. Germination of co-occurring annual species on a soil moisture gradient. Bulletin of the Torrey Botanical Club 105: 312-316.

Pijl, van der L. 1972. Principles of dispersal in higher plants. Springer-Verlag, New York. 162 pp.

Potvin, M. A. and P. A. Werner. 1984. Seasonal patterns in water relations of two species of goldenrods (Solidago) grown on an experimental soil mixture gradient. Bulletin of the Torrey Botanical Club 111: 171-178.

Primack, R. B., A. R. Rittenhouse and P. V. August. 1981. Components of reproductive effort and yield in goldenrods. American Journal of Botany 68: 855-858.

Rabinowitz, D. 1978. Early growth of mangrove seedlings in Panama and an hypothesis concerning the relationship of dispersal and zonation. Journal of Biogeography 5: 113-133.

Rackham, O. 1966. Radiation, transpiration and growth in a woodland annual. pp. 167-185. In: Brainbridge, R., G. C. Evans and O. Rackham (eds.), Light as an ecological factor. Blackwell Scientific Publications, Oxford. 452 pp.

Ramakrishnan, P. S. and P. Kapoor. 1974. Photoperiodic requirements of seasonal populations of Chenopodium album L. Journal of Ecology 62: 67-73.

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

Raynal, D. J. and F. A. Bazzaz. 1975a. Interference of winter annuals with Ambrosia artemisiifolia in early successional fields. Ecology 56: 35-49.

Raynal, D. J. and F. A. Bazzaz. 1975b. The contrasting life-cycle strategies of three summer annuals found in abandoned fields in Illinois. Journal of Ecology 68: 587-596.

Reynolds, D. N. 1984. Alpine annual plants: phenology, germination, photosynthesis, and growth of three Rocky Mountain species. Ecology 65: 759-766.

Rice, E. L. 1974. Allelopathy. Academic Press. New York. 353 pp.

Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve, Ashford, Kent. 744 pp.

Roberts, H. A. 1964. Emergence and longevity in cultivated soil of seeds of some annual weeds. Weed Research 4: 296-307.

Roberts, H. A. and P. M. Feast. 1972. Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. Weed Research 12: 316-324.

Roberts, H. A. and P. M. Feast. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. Journal of Applied Ecology 10: 133-143.

Rogers, R. S. 1982. Early spring herb communities in mesophytic forests of the Great Lakes region. Ecology 63: 1050-1063.

Ross, M. A. and J. L. Harper. 1972. Occupation of biological space during seedling establishment. Journal of Ecology 60: 77-88.

Salisbury, E. 1961. Weeds and aliens. Collins Press, London. 384 pp.

Schaffer, W. M. and M. D. Gadgil. 1975. Selection for optimal life histories in plants. pp. 142-157. In: Cody, M. L. and J. M. Diamond (eds.), Ecology and evolution of communities. Belknap Press, Cambridge, Mass. 545 pp.

Schemske, D. W. 1978. Evolution of reproductive characteristics in Impatiens (Balsaminaceae): The significance of cleistogamy and chasmogamy. Ecology 59: 596-613.

Schemske, D. W. 1984. Population structure and local selection in Impatiens pallida (Balsaminaceae), a selfing annual. Evolution (in press).

Shelford, V. E. 1954. Some Mississippi valley flood plain biotic communities; their age and elevation. Ecology 35: 126-142.

Smith, B. H. 1983a. Demography of Floerkea proserpinacoides, a forest-floor annual. I. Density-dependent growth and mortality. Journal of Ecology 71: 391-404.

Smith, B. H. 1983b. Demography of Floerkea proserpinacoides, a forest-floor annual. III. Dynamics of seed and seedling populations. Journal of Ecology 71: 413-425.

Soule, J. D. and P. A. Werner. 1981. Pattern of resource allocation in plants, with special reference to Potentilla recta L.. Bulletin of the Torrey Botanical Club 108: 311-319.

Staniforth, R. J. and P. B. Cavers. 1976. An experimental study of water dispersal in Polygonum spp. Canadian Journal of Botany 54: 2587-2596.

Staniforth, R. J. and P. B. Cavers. 1977. The importance of cottontail rabbits in the dispersal of Polygonum spp. Journal of Applied Ecology 14: 261-267.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51: 3-47.

Stevens, O. A. 1932. The number and weight of seeds produced by weeds. American Journal of Botany 19: 784-794.

Stoller, E. W. and L. M. Wax. 1973. Temperature variations in the surface layers of an agricultural soil. Weed Research 13: 273-282.

Struik, G. J. 1965. Growth patterns of some native annual and perennial herbs in southern Wisconsin. Ecology 46: 401-420.

Taylorson, R. B. and H. A. Borthwick. 1969. Light filtration by foliar canopies: Significance for light-controlled weed seed germination. Weed Science 17: 48-51.

Toole, E. H. and E. Brown. 1946. Final results of the Duvel buried seed experiment. Journal of Agricultural Research 72: 201-210.

Turkington, R., N. C. Kenkel and G. D. Franko. 1980. The biology of Canadian weeds. 42. Stellaria media (L.) Vill. Canadian Journal of Plant Science 60: 981-992.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Review 19: 513-605.

Waller, D. M. 1979. The relative costs of self- and cross-fertilized seeds in Impatiens capensis (Balsaminaceae). American Journal of Botany 66: 313-320.

Waller, D. M. 1980. Environmental determinants of outcrossing in Impatiens capensis (Balsaminaceae). Evolution 34: 747-761.

Waller, D. M. 1982. Factors influencing seed weight in Impatiens capensis (Balsaminaceae). American Journal of Botany 69: 1470-1475.

Warner, J. H. 1963. Some ecological relationships of Impatiens pallida Nuttall in a mesic hardwood forest. M. Sc. thesis, University of Wisconsin, Madison, Wisconsins. 58 pp.

Watkinson, A. R. 1981. The population ecology of winter annuals. pp. 253-264. In: Synge, H. (ed.), The biological aspects of rare plant conservation. John Wiley & Sons, New York.

Weiss, P. W. 1981. Spatial distribution and dynamics of the populations of the introduced annual Emex australis in south-eastern Australia. Journal of Applied Ecology 18: 849-864.

Went, F. W. 1955. The ecology of desert plants. Scientific American 192: 68-75.

Werner, P. A. 1975. Predictions of fate from rosette size in teasel (Dipsacus fullonum L.). Oecologia 20: 197-201.

Werner, P. A. 1976. Ecology of plant populations in successional environments. Systematic Botany 1: 246-268.

Werner, P. A. 1979. Competition and coexistence of similar species. pp. 287-310. In: Solbrig, O. T., S. Jain, G. B. Johnson, and P. H. Raven (eds.), Topics in plant population biology. Columbia University

Press, New York. 589 pp.

Whittaker, R. H. and D. Goodman. 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. American Naturalist 113: 185-200.

Wieland, N. K. and F. A. Bazzaz. 1975. Physiological ecology of three codominant successional annuals. Ecology 56: 681-688.

Williams, J. T. 1963. Biological flora of the British Isles. Chenopodium album. Journal of Ecology 51: 711-725.

Williams, J. T. and J. L. Harper. 1965. Seed polymorphism and germination. I. The influence of nitrates and low temperatures on the germination of Chenopodium album. Weed Research 5: 141-150.

Winer, B. J. 1971. Statistical principles in experimental design. McGraw-Hill Kogakusha, Tokyo, 2nd edition. 907 pp.

Winsor, J. 1983. Persistence by habitat dominance in the annual Impatiens capensis (Balsaminaceae). Journal of Ecology 71: 451-466.

Young, D. R. and W. K. Smith. 1979. Influence of sunflecks on the temperature and water relations of two subalpine understory congeners. Oecologia 43: 192-205.

Young, D. R. and W. K. Smith. 1980. Influence of sunlight on photosynthesis, water relations, and leaf structure in the understory species Arnica cordifolia. Ecology 61: 1380-1390.