

PUERARIA LOBATA WILLD. (OHWI), KUDZU:
LIMITATIONS TO SEXUAL REPRODUCTION


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Title of Thesis: Pueraria lobata Willd. (Ohwi) kudzu:
Limitations to Sexual Reproduction

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ABSTRACT

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The success of kudzu, Pueraria lobata Willd. (Ohwi), as a weedy invader in the southeastern United States is a result of its rapid growth rate, high leaf area index and ability to reproduce vegetatively. Populations at three sites near College Park, Maryland varied in their growth and reproduction, leaf area index, specific leaf weight, vine elongation rates, raceme density and seed production and dispersal. Soil characteristics, air temperature, humidity and photosynthetically active radiation (PAR) were measured at each site. The site which had the greatest vegetative productivity received significantly higher levels of PAR. Virtually no flowers or seeds were produced at the other two sites. At the site which produced a large number of flowers, successful sexual reproduction was limited by insufficient pollinator service during some periods of the season and low germination and seedling survivorship.

Measurements of specific leaf weight, leaf area index, biomass, raceme production and seed set suggest that kudzu

is a sun adapted plant. Even though it is capable of establishing itself in habitats of low or moderate irradiance, a greater ability for sexual reproduction was apparent in sun populations versus no sexual reproductive success in populations occurring in shaded habitats.

While its primary mode of reproduction is vegetative, successful sexual reproduction may occur despite several limiting factors.

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INTRODUCTION

Kudzu, Pueraria lobata (Willd.) Ohwi, was introduced into the United States from Japan in 1876 as a leguminous ornamental vine. Prior to 1950 it was planted extensively in the southern United States, both as forage and to increase soil stability and fertility, through nitrogen fixation and the addition of organic matter. Due to its rapid spread by the formation of crowns at the nodes of trailing stems, and its adverse affect on surrounding vegetation, it has since been considered a pest. Flowers are borne on axillary racemes which initiate anthesis in late July and continue until the first frost, generally mid-October in central Maryland. It partitions very little of its biomass into sexual reproduction (Wechsler, 1977) and has a very low seed production (Bailey, 1944; Dubadghao, 1949; O'Brien and Skelton, 1946; Tabor, 1942a).

Low seed set has been suggested as being due to insufficient pollinator service in some plants (Bierzychudek, 1981) and attributed to low raceme density in others (Platt, Hill, and Clark, 1974). Poor germination and seedling vigor has been positively correlated with low seed weight in many plants, including 9 tree species (Grime and Jeffrey, 1965), Lupinus texensis (Schaal, 1980) and soybean (Obendorf, Ashworth, and Rytko, 1980). Similar phenomenon with kudzu may explain why there have been no prior reports

of the establishment of new sites by natural seeding.

Numerous studies have examined the variability in the allocation of resources into reproductive and vegetative tissues and the implications of these strategies in plants (Grime, 1979; Harper and Ogden, 1970; Tripathi and Harper, 1973).

The focus of this study has been on the factors affecting the differing vegetative and reproductive output between populations and the low germination and seedling survivorship observed in the field. The following questions have been addressed: (1) How do the study sites differ in terms of the environmental variables which may be responsible for measurable differences in growth and reproduction? (2) What prevents the vast majority of ovules from being successfully fertilized? (3) When ovules are fertilized are there environmental constraints which decrease the viability and vigor of the seeds? (4) What are optimum conditions for seed germination and survival? How do they correspond with field conditions?

MATERIALS AND METHODS

Study Sites. Three field sites in College Park, Maryland were selected and observed for differences in several vegetative and reproductive growth characteristics over a two year period. The first and largest site, approximately 730 m², is on a north-facing slope along Md Highway 320. As the solar zenith decreases later in the season the site receives less and less direct beam solar radiation due to shading by large trees (Quercus spp. and Fagus grandifolia Ehrh.) located midway up the slope at the upper edge of the population. For the purposes of light measurements the site was divided into a "sun" and a "shade" area, each approximately one third of the site, while the remainder received intermediate levels of irradiance. The population is prevented from spreading at the bottom of the hill by the roadway.

The second site was planted about 15 years ago and occupies approximately 275 m² of a west-facing slope bordered on three sides by Md Highway 650 and a driveway. It receives direct solar radiation for the majority of the day throughout the season due to the absence of surrounding trees.

The third and smallest site, only 18 m², is on the edge of a wooded island which is encircled by a driveway and is separated from the west site by approximately 20m, with some

trees and the driveway between them .

Environmental variables. To elucidate microclimatic differences between sites which may contribute to observed differences in vegetative and reproductive growth, several environmental variables were measured. Daily temperatures were monitored at all three sites using a shaded Taylor Instruments maximum-minimum thermometer located within the canopy. Diurnal fluxes in photosynthetically active radiation (PAR, 400-700 nm), air temperature and humidity and soil temperature at a depth of 1 cm were measured at times during the 1982 season using a LI-COR Model LI-185 Quantum sensor, Psychro-Dyne PP100 ventilated psychrometer and a YSI 42SC Tele-Thermometer, respectively. The 4 sampling periods were: late May, mid July, late August and early October, which corresponded to early vegetative growth, peak vegetative growth, peak flowering and end of flowering-early senescence. Soil samples were collected from 5 randomly selected locations within each site and pooled. Two replicate samples per site were analyzed for pH, texture, magnesium, phosphorus, potassium, and percent organic matter by the Soil Testing Lab of the Maryland Cooperative Extension Service.

Vegetative growth measurements. Vine elongation rates (VER) were measured at all sites monthly during the 1982 season. Rates were calculated by measuring the distance from the youngest mature node to the shoot tip on two consecutive days.

Estimates of vegetative productivity were measured for each of the 3 sites by sampling twice during the 1981 season and 4 times during the 1982 season. In 1981 the sampling periods corresponded to the onset of peak vegetative growth and the end of peak flowering. The 1982 sampling periods were the same as those used for the environmental measurements. At each sampling date, five 0.5m^2 areas were randomly chosen within each site and all aboveground plant material was collected. Estimates of sexual reproductive effort (SRE) were made using all parts of the raceme including flowers, pods, seeds, and peduncles. Leaf area index (LAI), the ratio of leaf surface area to ground area, was determined by measuring the leaves with a LI-COR 3100 Area Meter. Leaves were dried to a constant weight at 60 C and weighed to determine specific leaf weight (SLW). All petioles and vines were also dried and weighed. Root material was not collected because of the disruption it would have caused to the sites. Estimates of leaf area ratio (LAR), the ratio of leaf area to total plant dry weight, and biomass determinations were therefore made using only aboveground tissue. There were 2 exceptions to the sampling scheme. At the first 1982 sampling period (May 5), additional leaf samples were collected at the north- and west-facing sites for SLW and LAI measurements because the sites were relatively bare as growth had just begun. The other exception was that no fresh material was collected at the east-facing site until the last sampling period

(October) in an effort to minimize disturbance to the small site. LAI was calculated at this site by using leaf imprints of the attached leaves on photoreactive Diazon paper which was later fixed in ammonia vapor. The imprints were then measured with the LI-COR Area Meter.

Pollination studies. Pollinator activity was observed at the west-facing site in 1982 during 3 periods: 1) when there was a high raceme density (19 - 21 August) and racemes were only found in an exposed hanging position; 2) mid-season (2 - 7 September) when racemes were found both in the hanging and the ground canopy; and 3) late in the season (23 - 24 September) when there was a low raceme density and most racemes were within the ground canopy. At each sampling period, 4 areas were chosen within the site containing at least 3 racemes within 1 m of each other. Within each area 3 racemes were observed and the number of pollinator visits counted over a 10 minute period 3 times before and 4 times after solar noon. These counts were repeated on 3 consecutive clear days. During the second sampling period (mid-season) measurements were made over 6 consecutive days, alternating between a day of observation of hanging racemes and a day of ground canopy racemes. Observations were made on only 2 days during the third period due to inclement weather. Mean air temperatures were recorded hourly during the observation period. Analyses were conducted to determine the effects of position and seasonality on the number of pollinator visits using the

following statistical models.

To compare pollinator visits between sampling periods the following model was used:

$$Y_{ijklm} = u + W_i + D_{j(i)} + A_{k(ij)} + R_{l(ijk)} + T_m + WT_{im} + E_{ijklm}$$

where:

W_i = sampling period effects, $i=1,2,3$.

$D_{j(i)}$ = random day effects nested within sampling period, $j=1,2,3$.

$A_{k(ij)}$ = random area effects nested within day, $k=1,2,3,4$.

$R_{l(ijk)}$ = random raceme effects nested within area, $l=1,2,3$.

T_m = time effects, $m=1,\dots,8$.

WT_{im} = interaction of sample period and time.

E_{ijklm} = random error effects assumed to be normally and independently distributed.

The following model was used to compare the effects of raceme position within the canopy on pollinator visitation during the second sampling period:

$$Y_{ijkl} = u + D_i + P_j + DP_{ij} + R_{k(ij)} + T_l + PT_{jl} + E_{ijkl}$$

where:

D_i = random day effects, $i=1,2,3$.

P_j = position effects, $j=1,2$.

DP_{ij} = random interaction of day and position.

$R_{k(ij)}$ = random raceme effects nested within position and day, $k=1,\dots,12$.

T_l = time effects, $l=1, \dots, 8$.

PT_{jl} = interaction of position and time.

E_{ijkl} = random error assumed to be normally and independently distributed.

To test for floral abortion, hand pollinations were performed on all flowers which opened on a group of 10 racemes over 7 days. Another 2 groups of 10 racemes had only 10 flowers per raceme pollinated. Pollinations were made with the attached anthers of flowers from other racemes selected just prior to being used for pollination. All racemes were covered with bridal veil to prevent insect pollination. In addition, one group of 10 racemes was covered and left unpollinated to serve as a control. The term "abortion" as used in this paper may include numerous events between pollination and seed set which may ultimately limit seed set.

Pollen viability was also examined. Pollen samples were collected from 10 flowers of 10 racemes at the west-facing site on 9 September 1982 and at the west and north-facing sites on 1 October 1982. Pollen was stained using a solution of cotton blue in lactophenol (Radford, Dickison, Massey, and Bell, 1974). Dark staining pollen after several minutes was used as an indication of viability. Viability counts were analyzed among sites and times.

As an additional indication of variations in seed

course of the 1982 season and allowed to be naturally pollinated by bees. Numbers and positions within the raceme of seeds and pods were recorded and analyzed at the end of the season to determine the effects of position and seasonality on seed set.

Germination. Mature seeds were divided into the following classes based on pod location at the time of collection: 1) pods which had fallen to the ground; 2) pods subjected to wetting and drying in the litter; and 3) pods collected from the vines. Each class was subdivided into A) large, round seeds and B) small, flat seeds. The weights of these classes were determined after drying at 35 C for 60 h.

Seeds from all classes were germinated in the Seed Testing Laboratory at the University of Maryland at 15, 20, 25 and 20/30 C and nearly 100% humidity, following AOSA (1970) recommendations. Normally and abnormally germinated seeds and the number lost to fungal infection were recorded weekly for eight weeks. Abnormally germinated seeds were those in which the hypocotyl emerged but did not elongate. At 20, 25 and 20/30 C 2 replicates of 25 seeds each were used for classes 1A and 1B, and 1 group of 25 seeds was used for the others. At 15 C, the temperature most closely approximating field soil temperatures throughout most of the season, 4 replicates were used for classes 1A and 1B, and 2 replicates were used for all other classes.

Field germination tests were begun on 20-24 June 1982,

using 450 large, round seeds from classes 1 and 3. The seeds were divided among 10 0.2m^2 quadrats located at the edge of the west-facing site, at the east-facing site and on the bank between the 2 sites. Germination and seedling survivorship were recorded for 8 weeks. Numbers of naturally occurring seedlings and their survivorship were also recorded throughout the season.

Pod and seed dispersal were estimated by spray painting all pods within a 4m^2 area, each m^2 a different color. The distance and direction travelled by each pod was recorded in 1m intervals.

All analysis were made using regression or analysis of variance (Statistical Analysis System, 1979). Significant differences were tested at the 95% level unless otherwise noted.

RESULTS

Environmental Measurements. For all of the environmental variables measured in 1982 there were significant differences between sites and dates and, for PAR, the interaction of site and date (Table 1). The mean maximum monthly air temperatures in 1982 were similar in both the west- and north-facing sites, and these were significantly greater than the east-facing site throughout most of the growing season (Table 2). There was little difference in the mean monthly minimum temperatures between the sites (Table 2). Soil temperatures were highest during the middle of the growing season and at the east-facing site (Table 3) and decreased as the season progressed as a result of increased canopy cover. Relative humidities were similar at the 3 sites at each sampling time except 30 May, 1982 (Fig. 1). On this date the east-facing site had higher relative humidities as a result of the low levels of irradiance which it received due to shading by large trees surrounding the site.

Figure 2 illustrates the representative radiation environment the sites received during the 1982 growing season. The west-facing site consistently received the highest PAR throughout the season, while the east-facing site consistently received the lowest levels. The "sunny" portion of the north-facing site is exposed to higher levels

early in the season but by August the levels almost decreased to those of the "shady" portion.

The soils at all 3 sites were very similar as determined by the Soil Testing Laboratory of the Maryland Cooperative Extension Service. All are loams with very high levels of potassium and very low phosphorus levels. Levels of magnesium were rated as either high or very high. The highest mean percent organic matter was found at the west-facing site (3.4%), which had the densest vegetative cover, while the site with the least cover, the east-facing, had the lowest percent organic matter (1.8%). The north-facing site had an intermediate level (2.8%). The soil pH for the north-, west- and east-facing sites, 5.7, 5.2 and 4.7, respectively, are all within the normal range found in central Maryland.

Vegetative growth measurements. Table 1 lists the F-values by site, date, and the interaction of site and date for the characteristics analysed in 1982, and by site only in 1981. Where comparisons could be made, similar results were found in growth characteristics between 1981 (Table 4) and 1982 (Table 5). For vine elongation rates (VER) there were significant differences by site ($P < .001$) and date ($P < .001$) and the interaction of site and date ($P < .001$) in 1982. During 1982 VER in the west and north-facing sites were similar until September 14 (Table 5). While VER continued to increase in the north-facing site, rates at the west-facing site halved during the period of peak flower

during all sampling intervals.

Total aboveground biomass differed significantly among sites ($P < .001$) and sampling dates ($P < .001$) in 1982. Estimated aboveground biomass was greatest in the west-facing site during all sampling periods (Table 5) and biomass increased as the season progressed at all sites.

Leaf area index (LAI) differed significantly among sites ($P < .001$) and sampling dates ($P < .001$) and the interaction of site and date ($P < .001$). LAI at the west-facing site was significantly greater than in the north site or the east-facing site throughout the growing season (Table 5). LAI at the west-facing site began 6-fold greater than at the north-facing site early in the season, but these differences diminished over time. By the end of the flowering period (5 October), LAI was similar in both sites.

Site, sampling date and the interaction of site and date were significant in contributing to variability in specific leaf weight (SLW) ($P < .001$, $P < .001$ and $P < .01$, respectively) and total leaf weight ($P < .001$). The west-facing site had the highest SLW on all sampling dates except during the early stages of vegetative growth. Similar results were obtained using a subsample of ten mature leaves per site and time.

Leaf area ratio (LAR), the ratio of leaf area to total plant dry weight, measures the relative amount of resource allocation to light collecting surface relative to support tissue. LAR was significantly higher ($P < .001$) at the

east-facing site than at the other sites, which were not significantly different from each other. LAR was greatest during the period of peak vegetative growth.

Flowering was initiated on 15 July, 1982 at the west-facing site, on approximately 5 August at the north-facing site and mid-August at the east-facing site. The west-facing site produced an average of 15.2 racemes m^{-2} by 5 October 1982, while the north and east-facing sites produced only 0.4 per m^2 each. At the latter two sites, only 1 raceme was found among the 5 quadrats which were sampled, although the north-facing site produced many more racemes overall. Only 2 racemes were produced at the east-facing site throughout the growing season. Sexual reproductive effort (SRE), the percent of standing biomass invested in sexual reproductive tissue, was 2.126, 0.021 and 0.587% for the west-, north- and east-facing sites, respectively. SRE, in this study, is an overestimate of actual reproductive effort because it is based only upon aboveground biomass standing at the time of collection and therefore does not account for the leaves which had been shed or biomass invested in the extensive root system.

Pollination studies. There was a significant difference among sampling periods in the number of bee visits per raceme (Table 6). Within a sampling period, day, area of sampling within the site and raceme sampled within areas were not significantly different. In an analysis of the data for 2-9 September, when both hanging and ground racemes

were present, canopy position ($p < .05$) and time of day were significant ($P < .001$) in contributing to variability in the number of bee visits (Table 7) with the highest visitation rates occurring on the hanging racemes and at midday (Fig. 3). There were no significant differences in visits to ground canopy racemes over the course of the day (Fig. 3).

To determine if there were high levels of floral abortion, 2 groups of 10 racemes were compared. One group had a mean of 29.3 flowers per raceme hand pollinated, while the other had 10 flowers per raceme hand pollinated. The mean square root of the number of pods produced, 2.6 and 2.1 for the 2 groups respectively, were not significantly different. The control group, which was not hand pollinated, produced no pods. Square root transformations are used with small count values in order to make variances independent of the means (Sokal and Rohlf, 1981).

There were no significant differences in pollen viability among sites (mean percentage of viable pollen was 96.8 and 95.0 for the west- and north-facing sites, respectively). For the comparison of pollen collected from the west-facing site on 9 September and 10 October, 1982, no significant differences were found between dates (mean percentage of viable pollen was 99.0 and 96.8 for the two dates, respectively).

The percentage of ovules which produced seeds (S) was calculated as the product of the number of nodes per raceme (N) * the number of flowers per node (F) * the mean number

of ovules per flower(0) * 100, $S = N * F * O * 100$, where $F=3$ and $O=11$. The percentage of ovules which produced seeds increased to a maximum for hanging racemes in late August and for ground canopy racemes in early September (Fig. 4). Racemes which are produced earlier in the season tend to have more nodes than those produced later in the season and therefore flower for a longer period of time (Fig. 5).

569 marked pods were retrieved beyond 1 m of their point of origin. While 91.6% of all pods retrieved were found within 6 m of their point of origin, 1.7% were found 10-25 m away (Fig. 6).

Seed Germination. The mean seed weights of all seed classes were significantly different from each other (Table 8) except the large seeds of classes 1 and 3 (those which had fallen to the ground which were not subjected to wetting and drying and those collected from pods which were still on the vines). Seed class, temperature and time had a significant effect on germination. Highest germination percentages were among the larger seeds at higher temperatures (Fig 7). When all seed classes were pooled, there was no significant difference among temperature treatments 30/20 and 25 C, or 20 and 15 C but the two groups were significantly different from each other (Table 9). There was no significant difference in the percentage of abnormal germinations between seed classes or temperatures. Among large seeds, those which were subjected to wetting and drying while in the litter layer had the lowest germination rates and the

highest losses to fungal infection. There was no significant difference in the percentage of seeds lost as a function of temperature (Table 9). Most seeds lost to fungal infection were lost in the second week, there were no significant differences among the other weeks (Table 10).

Field germination and naturally occurring seedlings. Of the 450 seeds planted in 10 quadrats only 40, or 8.8%, germinated. In 1982 245 naturally occurring seedlings were found and observed during the growing season. Of these, 109 were located in gravel at the edge of the west-facing site, 7 at the east-facing site and 129 on the bank that separates the two sites. All of the seedlings in the gravel and most of the other seedlings died within a few weeks of germinating. Seedlings which did survive showed almost no perceptible growth. Only one seedling was found which survived into the following spring.

DISCUSSION

Kudzu is an aggressive competitor that is well suited for exploitation of above- and belowground resources by the rapid production of a dense canopy and large root surface area (Grime, 1979; Harper, 1977). Its dense canopy and viney growth habit allow it to capture a disproportionate amount of light resources (Wechsler, 1977) by growing up and over surrounding vegetation. Kudzu begins growth in May and may produce up to 12 m of new stem growth per season. Older vines often grow up into and hang from 25 m trees (Brender, 1960). Another successful exotic weedy vine is Lonicera japonica (honeysuckle). Like kudzu it spreads vegetatively by the formation of roots at the nodes of trailing stems. Although it begins growth 2 months earlier, honeysuckle does not spread as fast or as high as kudzu, elongating only 1.5 m per season under optimum conditions (Leatherman, 1955). While kudzu has an extensive rhizomatous root system, its demand for photosynthate is only a small portion of that which is produced by the leaves (Wechsler, 1977). The limited investment in tissue for sexual reproduction, approximately 1 to 2%, also allows more resources to be channelled into vegetative growth. Kudzu's reproductive investment is low when compared not only to weedy monocarps such as Senecio vulgaris (Harper and Ogden, 1970) or polycarpic grasses such as Agropyron (Tripathi and Harper,

1973) but even when compared with honeysuckle which is a prolific seed producer (Brender, 1960; Leatherman, 1955). Less than 10% of all kudzu flowers produce fruits, each of which contains an average of 2 seeds, while with honeysuckle 57% of all flowers produce fruits, each of which contains, on the average, 6 seeds (Leatherman, 1955). It is kudzu's ability to outcompete other vegetation for light and space, rather than a high capacity for successful sexual reproduction, that is the basis for its successful dominance of communities which it inhabits.

Photosynthetically active radiation (PAR) affects a number of plant characteristics, including the accumulation of aboveground biomass, leaf area ratio (LAR) (Loach, 1970) specific leaf weight (SLW) (Chabot and Chabot, 1977; Pearce and Lee, 1969) and sexual reproductive effort (SRE) (Grime, 1979). The west-facing site receives PAR levels which are 2 to 9-fold greater than the north- and east-facing sites, respectively. The effect on photosynthate production is reflected in large site differences in vegetative growth and productivity. The west-facing site has a rapid and sustained production of total aboveground biomass and leaf area, in addition to having a higher reproductive effort. Vegetative productivity at the west-facing site was approximately 6.5-fold greater early in the season (May 5) and continued to be significantly higher throughout the season. As indicated by the LAI, the canopies at the east and north-facing sites were less dense than at the

west-facing site, characteristic of sun adapted plants in areas which receive less irradiance. An additional assessment of canopy structure is leaf area ratio (LAR). As a result of high levels of assimilate being channelled into light collecting surfaces, plants from habitats with lower irradiances tend to have higher LARs, i.e., more leaf surface area relative to support tissue, than those at higher irradiances (Loach, 1970). In the present study the east-facing site which received the lowest irradiance had the highest LAR, while the site receiving the highest irradiance, the west-facing site, has the lowest LAR. Although the mean LAR for the east-facing site was calculated using the 5 October sample only, when the sites are compared on this date alone the relationship is the same.

Specific leaf weight (SLW) is also affected by irradiance, with sun leaves having higher SLWs (Chabot and Chabot, 1977; Lichtenthaler, Bushman, Doll, Fietz, Bach, Kozel, Meier and Rahmsdorf, 1981). In kudzu the highest SLW occurred at the west-facing site which received the highest irradiance, and the lowest was at the east-facing site which received the lowest irradiance.

Not only does the west-facing site invest relatively less for light collecting surfaces, i.e. LAR, and more on supportive tissue, it also expends more for sexual reproductive effort (SRE), i.e. the percent of biomass invested in reproductive tissue. More profuse flowering and

seed production in habitats receiving higher irradiances has also been reported in honeysuckle (Leatherman, 1955). The more shaded north- and east-facing sites have sparse flower production and virtually no seed production. The east-facing site produced only 2 racemes during the entire season. No pods or seed were found at the north-facing site. One explanation for the differences observed may be that within the more shaded populations sexual reproduction is resource limited because only PAR, of the measured environmental variables, differed significantly between sites. While the cause of the sharp decrease in VER during the period of peak flowering at the west-facing site may be hypothesized to be a resource drain resulting from flower and seed production, it could also be due to water stress as indicated by the vertical orientation of the leaves during the day. These two hypotheses could be resolved by an examination of water relations and leaf temperatures between populations.

Raceme density and seed production varied greatly between sites. One reason may be that low seed set is often correlated with limited pollinator activity (Bierzychudek, 1981). Higher seed production at higher floral density has been attributed to preferential visitation by pollinators to areas with higher raceme densities. (Platt, Hill and Clark, 1974). The north-facing site had a very low raceme density and no observed seed set. Virtually no bees were observed at this site at any time of day during the season. The

west-facing site had a relatively high raceme density and seed production and a high level of pollinator activity during some periods of the season. The east-facing site was probably pollinated because of its proximity to the west-facing site. Bees were often seen moving between the two sites. Pollinators include Xylocopa virginica, Bombus impatiens and Apis mellifera. Pollinator limitation may also be inferred if seed set among hand pollinated racemes is higher than among open pollinated racemes (Bierzychudek, 1981; Schall, 1980). This was found in the present study with seed set for the hand pollinated racemes being approximately 14% while that for the open pollinated racemes ranged between 0%-3.3%. Schaal (1980) hypothesized that in Lupinus texensis the effects of pollinator limitation are minimized by producing a large number of flowers during a period which extends over many weeks, thus the chances of pollination are greater. Therefore, while only 1.5% of all L. texensis ovules develop into seeds the absolute number of seeds is increased as a result of the long flowering period. This hypothesis fits the flowering events observed in kudzu equally as well.

Based on observations at the west-facing site, the period of greatest seed set correlated with the highest pollinator visitation rates. These in turn correlated with the occurrence of high raceme densities. The second observation period (the peak of flowering) had the highest number of visits per raceme. During this period there was

also the highest recorded percentage of ovules producing seed. Conversely, the lowest seed set was found during the time corresponding with the lowest bee visitation (late season). This trend in visitation rates and seed set was also seen during the peak flowering period, when hanging and ground racemes were compared the hanging racemes had significantly more bee visits. During this period the percentage seed set in the hanging racemes was nearly twice that of the ground racemes. It may be implied that at high pollination levels abortion may limit high seed set based on the results of 2 experiments. First, in the hand pollination experiment, there was no significant difference in the number of pods produced by racemes which had a 3-fold difference in the number of flowers pollinated. Second, between hanging and ground canopy racemes there was a greater magnitude of difference in pollinator visits than in seed set. There are several reasons why pollinators preferentially visit and thereby facilitate higher seed set in hanging racemes. These racemes are in a position where they are exposed for the entire day unlike the racemes within the ground canopy which are generally exposed only in the afternoon. In kudzu, a pulvinus vertically orients the leaves around midday at sites where they are exposed to high irradiances and are water stressed. In addition, ground canopy racemes are generally evenly distributed, with relatively low raceme density, while those on hanging and climbing vines have a higher density and are more clumped.

High density on the hanging and climbing vines has been observed in kudzu by numerous investigators (Dabadghao, 1949; McKee and Stephens, 1943; Tabor, 1942a) and has led to the erroneous conclusion by some that kudzu produces flowers and seeds on these vines exclusively.

Numerous factors, both endogenous and exogenous, provide obstacles between fertilization and successful seedling establishment. As previously mentioned, insufficient pollinator visitation and abortion may significantly limit the number of pods and seeds which are produced. In addition, the vast majority of pods are dispersed within the canopy. Seeds from these pods are not likely to germinate and become successfully established for several reasons. Pods tend to become trapped in the extremely thick litter layer, which often attains depths of 0.3 m or more, so that the seeds may not reach the soil surface. Seeds within these pods are also subjected to periods of wetting and drying which decrease viability and increase fungal infection as suggested in the laboratory germination tests. Should seeds reach the soil surface beneath the canopy and germinate, the seedlings are likely to have a high mortality rate. Vaartaja (1952) found damping-off to be very high in Pinus sylvestris seedlings under dense canopies where the light intensity is very low. Similarly, Wardle (1959) reported that even when Fraxinus seeds germinated freely under a dense canopy the light intensities encountered were far below their compensation point.

Angevine and Chabot (1979) discuss these difficulties encountered by seedlings in a dense population of mature plants and suggest that in such communities seeds which are produced are most likely to germinate successfully in disturbed areas where they do not have to compete for light and space with the mature plants.

For those seeds in pods which are dispersed away from the thick litter layer, establishment is still not guaranteed. Edges of the population are often more exposed, decreasing the probability of damping-off and problems encountered with low irradiances. Soil temperatures may be higher and thus also more conducive to germination than those directly beneath the canopy. However, these areas are often inhospitable for long term growth. This is because of the nature of the habitat where kudzu typically occurs such as bare hillsides and road edges which are subject to erosion and much greater fluctuations in soil moisture. Leatherman (1955) reports that honeysuckle seedlings, which germinate in March and become rapidly established and partially woody by the end of the season, suffer 30% mortality due to drought. Even higher mortality was observed in hand planted seeds and naturally occurring kudzu seedlings.

Many weeds, both annuals and perennials, have relatively high germination rates. Leatherman (1955) reports a potential of 85% germination for honeysuckle, although actual germination under field conditions is 53-63%.

Numerous annuals, such as Lupinus texensis and Torilis japonica, have germination of at least 90% (Schaal, 1980) and 63% (Baskin and Baskin, 1975), respectively. In contrast, kudzu has very low germination under both field and laboratory conditions. A large portion of kudzu seeds produced are of relatively low seed weight and even under optimum conditions have less than 10% germination. Seeds of low weight have been shown to have low levels of germination and survivorship as a result of less endosperm (Grime and Jeffrey, 1965; Obendorf, et al., 1980; Schaal, 1980). Seeds planted in the field experiment, were taken from seed classes with the highest germination in the laboratory, yet had considerably lower germination than the same seeds under laboratory conditions. Even the 8.8% germination found in the field experiment may be an overestimate of naturally occurring germination since seeds in this experiment were chosen from the most vigorous classes and were carefully planted at an appropriate depth. Thus, as was observed in the naturally occurring seedlings, mortality in the field is extremely high. It appears, however, that some seedlings do survive. For instance, there are 2 pieces of evidence suggesting that the east-facing site was established from seeds produced at the west-facing site. First, while the west-facing site was intentionally planted approximately 15 years ago, the east-facing site was not. Nor could it have been established vegetatively because of a driveway separating the two sites. Second, numerous pods and

seedlings were found at the east-facing site and in the area between the two sites.

Based on the results of numerous estimates of vegetative and reproductive effort made in this study two general conclusions may be drawn. First, it appears that kudzu has the vegetative plasticity to exploit a wide range of irradiances, however, it maintains higher vegetative productivity and sexual reproductive effort in habitats with higher irradiances. Second, there are numerous potential barriers to successful sexual reproduction in kudzu: low irradiance, insufficient pollinator service and high abortion during various parts of the season, short distance seed dispersal and, low germination and seedling survivorship. However, kudzu maximizes genetically low seed set by extending the flowering period so that at some sites despite periods of pollinator limitation the absolute number of seeds produced is increased so that the genetic material is provided for the establishment of new sites.

APPENDIX

KUDZU, BACKGROUND INFORMATION

Kudzu, Pueraria lobata Willd. (Ohwi), is a perennial leguminous vine which is best known for its rapid growth and invasive nature. It is characterized by long, twining pubescent vines, a typical leguminous trifoliate leaf, and reddish-purple flowers which hang in racemes below the leaf (Gleason and Cronquist, 1963).

Kudzu was introduced into the United States by Japan at the 1876 Centennial Exhibition in Philadelphia as an ornamental vine for its lush foliage, fragrant flowers and the cool shade it provided (Stevens, 1976). It remained strictly an ornamental until early in the 20th century when it was promoted as a forage crop by C.E. Pleas, a Florida farmer, and David Fairchild, a United States Department of Agriculture plant explorer.

The Federal Government and the Agriculture Experiment Stations in the southern states took over the task of developing, testing, promoting and distributing kudzu for use as a forage, for erosion control, and for soil improvement. Methods of propagation and establishment were tested and published (Bennett, 1940; Johnston, 1945; McKee and Stephens, 1943; Nixon, 1948; Pieters, 1932; Sturkie and Grimes, 1939). The most successful method of establishment required planting crowns. Seedlings and cuttings generally

produced poor results. The Soil Conservation Corps produced over 73 million seedlings by 1940 and distributed 85 million crowns between 1935 and 1942 (Dickens, 1974). Some of the actual planting was carried out by the Civilian Conservation Corps (Stevens, 1976).

The effectiveness of kudzu in erosion control is due to its root system, its rapid growth rate, its dense foliage and its copious litter production. It has a massive central taproot, up to 2 m long (Brender, 1960), an extensive fibrous root system, and it forms adventitious roots at the nodes of trailing stems. Leaf and stem litter also act to protect the soil. Increases in soil organic matter and water holding capacity due to litter production (O'Brien and Skelton, 1946) combined with the extensive nitrogen fixing root system also improved the structure of depleted and abused soils in the south. Numerous reports were published on the increased yields of crops on fields which were previously planted with kudzu (Cope and Scarsbrook, 1964; Pieters, 1932; Miles and Gross, 1939).

Although several insects and diseases have been reported on kudzu, none have had a major deleterious effect. Minor damage by the velvetbean caterpillar Anticarsia gemmatilis Hubner (Lyle, 1944), for which kudzu acts as an alternate host (Buschman, Whitcomb, Neal and Mays, 1977), nematodes (McKee and Stephens, 1943) and the spotted skipper Epargyreus claurus (personal observation) have been noted, but none are considered serious. Likewise, reports of

angular leaf spot caused by Cerospora pureraricola Yamamoto (Weimer and Luttrell, 1948) and Halo spot caused by Bacterium medicaginis var. phaseolicola Byrk (Higgins, 1930) and rust indicate that these, too, are relatively unimportant.

A shift in agricultural practices has assisted kudzu's spread in the United States and Japan. Dickens (1974) asserted that as more land was taken out of row crops and committed to forests and pastures the kudzu which had been planted to stabilize gullies in the fields was free to invade the forests, since it was no longer mowed, plowed, or grazed. These methods, as well as herbicides such as 2,4-D, 2,4,5-T and Picloran were frequently recommended for the control and eradication of kudzu (Bailey, 1939; McKee and Stephens, 1943). Similarly, in Japan, kudzu's weedy effects have increased since it is no longer collected as cattle feed or used as compost due to the wider use of cultivating machines (Manabe, 1976).

Kudzu's competitive success apparently does not result from a high photosynthetic capacity. Two independent investigators, Wechsler (1977) and Wolf (1969), measured photosynthetic rates of kudzu and concluded that it does not have an unusually high rate of photosynthesis for a plant with the C_3 pathway. Wechsler (1977) calculated a maximum rate of $16 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ at $200 \text{ uE cm}^{-2} \text{ s}^{-1}$ between 20 and 30 C. It is kudzu's ability to outcompete other vegetation for light and space that is the basis for it's

dominance of the communities which it inhabits.

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Table 1. F-values for environmental and growth parameters by site, date, and site by date interactions.

Characteristic	Site	Date	Site * Date
<u>Environmental parameters-1982</u>			
Max. temp.	19.01*** a	18.23***	1.23 ^{ns} d
Min. temp.	3.32* c	30.18***	1.00 ^{ns}
PAR	91.87***	37.33***	9.42***
<u>Growth parameters-1982</u>			
VER ^e	30.00***	12.46***	12.87***
Total above ground biomass	58.59***	39.45***	0.92 ^{ns}
Total leaf weight	113.17***	142.70***	12.41***
LAI	86.11***	98.58***	13.36***
SLW	53.48***	33.44***	7.41** b
LAR	11.56***	15.79***	0.71 ^{ns}
SRE	3.56*	6.11**	5.87**
<u>Growth parameters-1981</u>			
Total above ground biomass	3.01 ^{nsd†}		
Total leaf weight	12.99***a†		
LAI	13.01***		
SLW	7.08***		
LAR	0.44 ^{ns†}		

a***Significantly different at the 99.9% level.

b** Significantly different at the 99% level.

c* Significantly different at the 95% level.

d^{ns} Not significantly different at the 95% level.

e VER F-value for date analyzed as a quadratic function.

† Includes data for north and west-facing sites only.

Table 2. Mean daily air temperatures (°C) at three Maryland kudzu sites in 1982.

Site	May		June		July		Aug		Sept		Oct	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
West	29.5 ^{a*}	13.5 ^{ab}	29.5 ^a	15.6 ^a	31.2 ^a	17.6 ^a	29.2 ^a	15.4 ^a	25.8 ^a	12.6 ^a	21.5 ^a	8.2 ^a
North	29.7 ^b	11.7 ^b	27.4 ^a	16.7 ^a	30.2 ^a	18.3 ^a	26.8 ^a	15.9 ^a	23.1 ^a	12.5 ^a	19.3 ^a	8.7 ^a
East	23.9 ^b	14.4 ^a	23.9 ^b	16.3 ^a	27.3 ^b	18.9 ^a	26.2 ^a	17.8 ^a	--	--	--	--

* Means within each column with identical superscripts are not significantly different at the 95% level (Duncan's Multiple Range Test).

Table 3. Mean (\pm S.E.) soil temperatures ($^{\circ}$ C) at three Maryland kudzu sites in 1982.

Site	n	8 June	22 July	29 Aug	23 Oct
West	12	18.4 \pm 0.1	20.6 \pm 0.3	17.5 \pm 0.2	9.7 \pm 0.1
North	12	19.1 \pm 1.8	20.8 \pm 0.3	16.0 \pm 0.1	8.2 \pm 0.4
East	12	18.5 \pm 0.3	23.8 \pm 0.4	18.6 \pm 0.2	10.3 \pm 0.2

Table 4. Growth characteristics at three kudzu sites in 1981.

Characteristic	Site	n	June
Biomass	West	9	163.08 ^{a†}
	North	5	93.01 ^b
LAI	West	10	2.14 ^a
	North	10	1.44 ^b
	East	5	0.36 ^c
SLW (g·m ⁻²) x 10 ²	West	10	0.2995 ^a
	North	6	0.2777 ^a
	East	4	0.2321 ^b
LAR	West	9	153.07 ^a
	North	5	144.31 ^a

† Means with identical superscripts are not significantly different at the 95% level (Duncan's Multiple Range Test).

Table 5. Seasonal growth characteristics at three kudzu sites
in 1982.

Characteristic	n	Site	Date					Oct
			May*	June	July	Aug	Sept	
VER ⁺ (mm·d ⁻¹)	20	West	73.96 ^a	79.70 ^a	94.64 ^{ab}	78.80 ^a	35.05 ^b	-
	20	North	74.10 ^a	95.91 ^a	108.07 ^a	87.70 ^a	119.14 ^a	-
	12	East	46.75 ^b	45.80 ^b	77.20 ^b	43.17 ^b	-	-
Biomass ⁺⁺ (g·m ⁻²)	5	West	164.34 ^c	-	308.80 ^{ab}	-	-	369.96 ^a
	5	North	25.62 ^d	-	147.17 ^c	-	-	277.16 ^b
	5	East	-	-	-	-	-	42.83 ^d
LAI ⁺⁺ (m ² ·m ⁻²)	5	West	0.68 ^d	-	3.30 ^a	3.11 ^a	-	2.09 ^b
	5	North	0.11 ^e	-	1.82 ^c	2.40 ^b	-	2.16 ^b
	5	East	0.07 ^e	-	0.51 ^c	-	-	0.53 ^d
SLW ⁺⁺ (g·m ⁻²)X10 ²	5	West	0.3309 ^b	-	0.2791 ^{cd}	-	-	0.3732 ^a
	5	North	0.3048 ^{bc}	-	0.2245 ^e	-	-	0.2866 ^{cd}
	5	East	-	-	-	-	-	0.2614 ^d
LAR ⁺⁺ (m ² ·g ⁻¹)	5	West	51.43 ^c	-	106.60 ^{ab}	-	-	58.58 ^c
	5	North	49.19 ^c	-	127.81 ^a	-	-	83.04 ^{bc}
	5	East	-	-	-	-	-	139.28 ^a

+ = Means within each date with identical superscripts are not significantly different (Duncan's Multiple Range Test, P < .05)

++ = Means across site and date with identical superscripts are not significantly different (Duncan's Multiple Range Test, P < .05)

* = N = 10 in May for LAI.

Table 6. F-values from an ANOVA comparing pollinator visitation at the west-facing site among three sampling periods.

Characteristic	F-value
Sample Period	6.19 ^{*a}
Day within sample period	1.08 ^{ns b}
Area	1.29 ^{ns b}
Raceme within area	0.61 ^{ns b}

^aSignificant at the 95% level.

^bNot significant at the 95% level.

Table 7. F-values from an ANOVA comparing pollinator visitation rates at the west site between hanging and ground racemes.[†]

Characteristic	F-value
Canopy Position	18.76 ^{*a}
Raceme (Day * Position)	1.07 ^{*a}
Time of Day	6.50 ^{***b}
Position * Time	11.79 ^{***b}

[†]Based on data collected during 2-7 Sept when racemes within both the hanging and ground canopy were observed.

^aSignificant at the 95% level.

^bSignificant at the 99.9% level.

Table 8. Weights and germination of six kudzu seed classes.

Seed Class	Weight (g)		n	Germination [†] (%)		
	n	mean		total	abnormal	infected
1A	25	93.76 ^{a*}	83	10.40 ^a	1.36 ^a	1.44 ^b
3A	25	82.56 ^b	16	7.04 ^{ab}	0.48 ^a	3.52 ^b
2A	25	66.00 ^c	17	4.72 ^{bc}	1.44 ^a	5.68 ^b
1B	25	43.60 ^d	80	1.28 ^c	0.48 ^a	22.72 ^a
3B	25	38.44 ^d	16	0.00 ^c	0.00 ^a	25.04 ^a
2B	25	26.88 ^e	16	1.28 ^c	1.04 ^a	21.04 ^a

[†] Percent germination after eight weeks at 15, 20, 25 or, 30/20 °C. Results at all temperatures combined.

* Means within each column with identical superscripts are not significantly different at the 95% level (Duncan's Multiple Range Test).

Table 9. Germination of kudzu seeds
at four temperatures.

Temp ($^{\circ}$ C)	n	Germination [†] (%)		
		total	abnormal	infected
30/20	32	9.28 ^{a*}	1.52 ^a	11.20 ^a
25	32	7.52 ^a	0.48 ^a	11.20 ^a
20	34	3.76 ^b	0.48 ^a	12.00 ^a
15	130	3.92 ^b	0.96 ^a	13.04 ^a

[†] Percent germination of six seed classes after eight weeks. Results of all seed classes combined.

* Means within each column with identical superscripts are not significantly different at the 95% level (Duncan's Multiple Range Test).

Table 10. Fungal infection of kudzu seeds germinated for eight weeks.

	Week							
	1	2	3	4	5	6	7	8
Mean (%) [†]	0.89 ^{b*}	10.07 ^a	1.46 ^b	0.11 ^b	0.04 ^b	0.04 ^b	0.00 ^b	0.00 ^b

[†] n= 2

* Means within each column with identical superscripts are not significantly different at the 95% level (Duncan's Multiple Range Test).

FIGURE 1

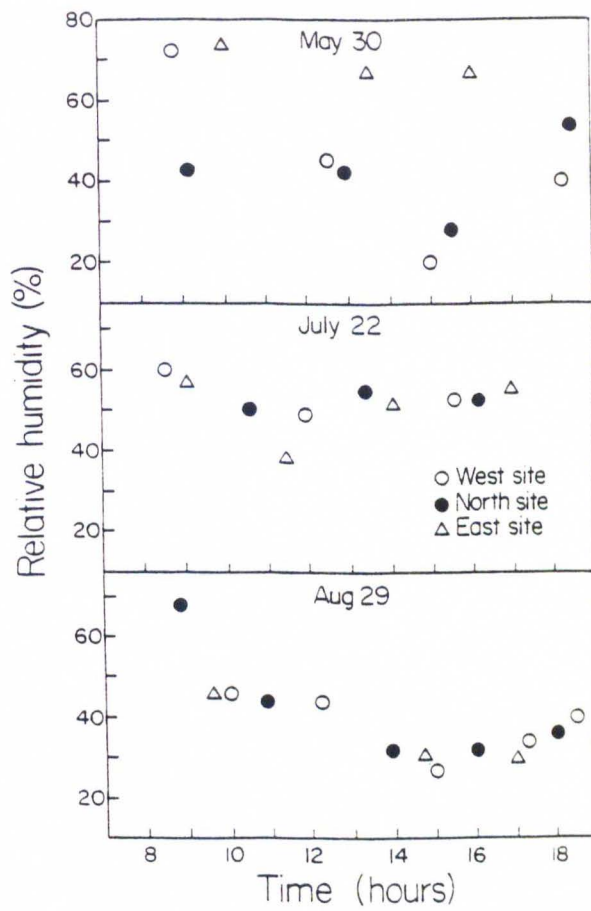


FIGURE 2

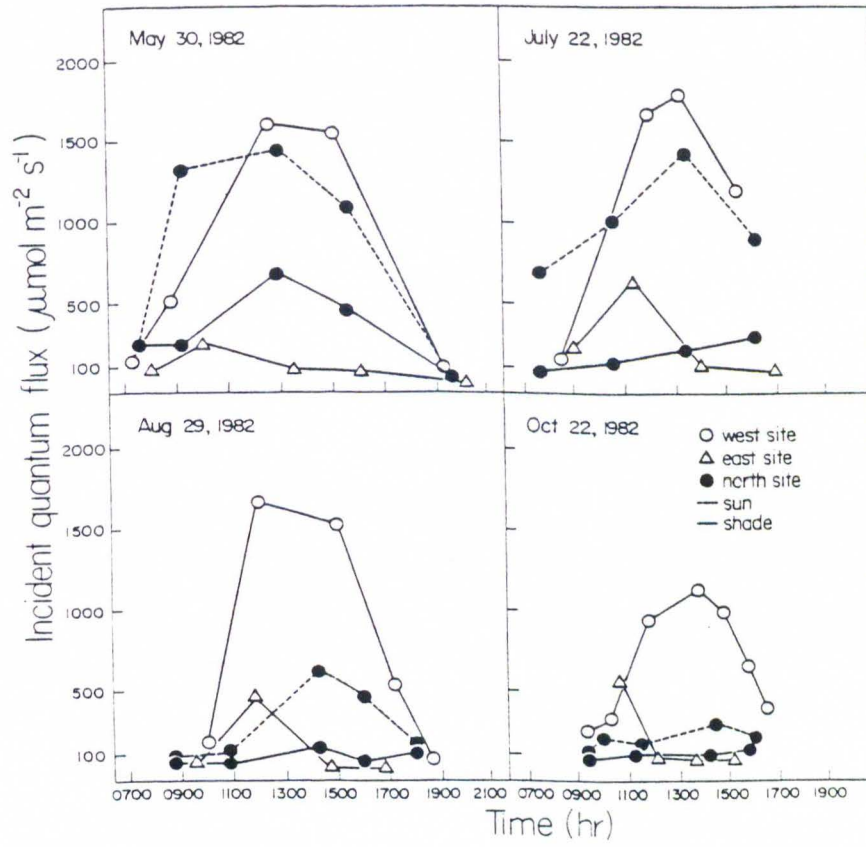


FIGURE 3

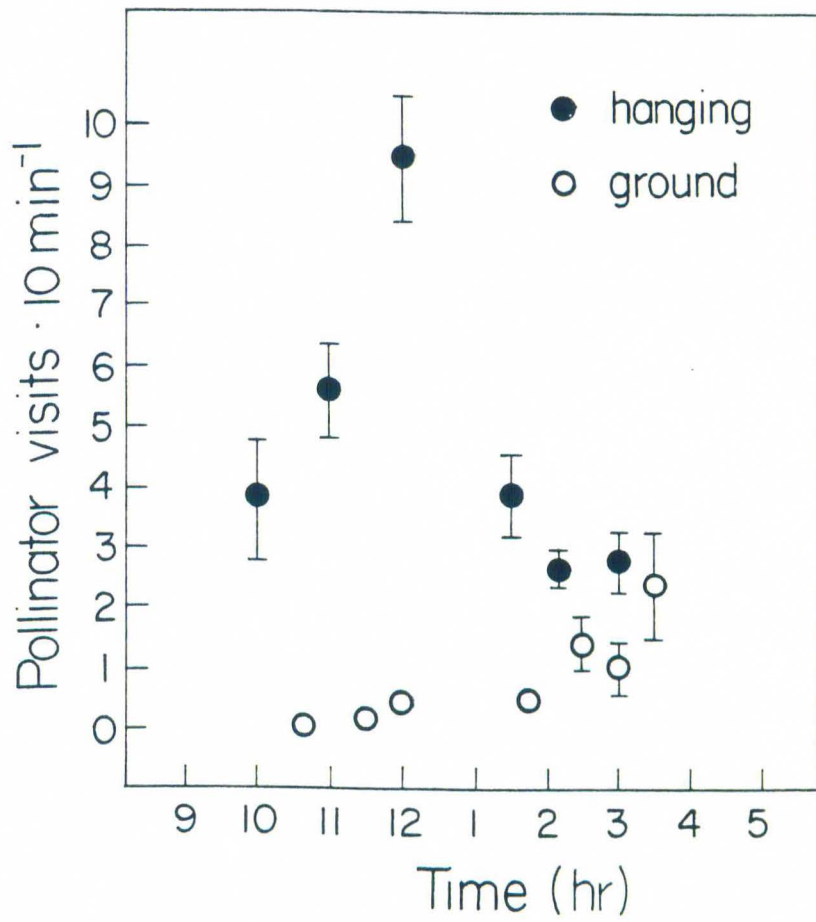
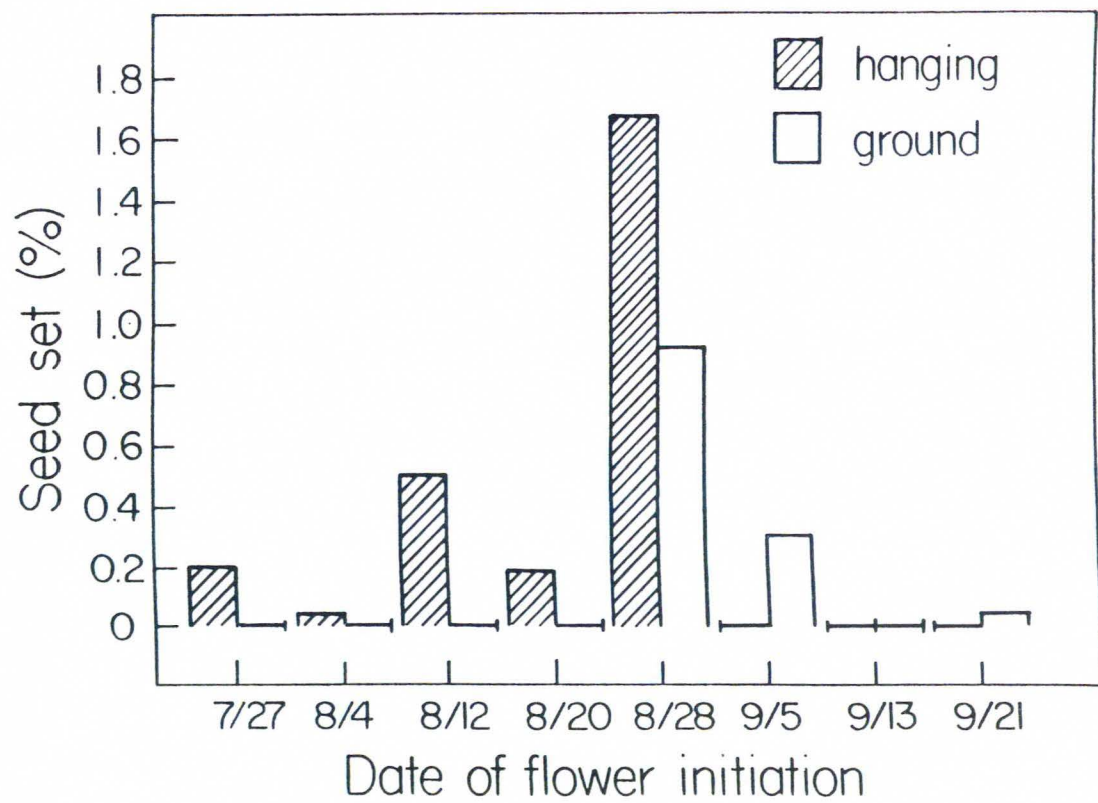


FIGURE 4



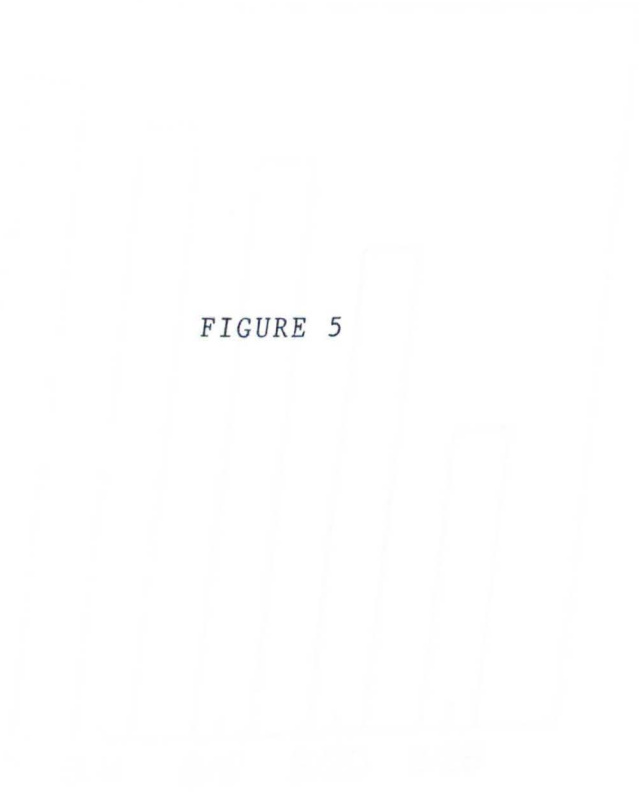


FIGURE 5

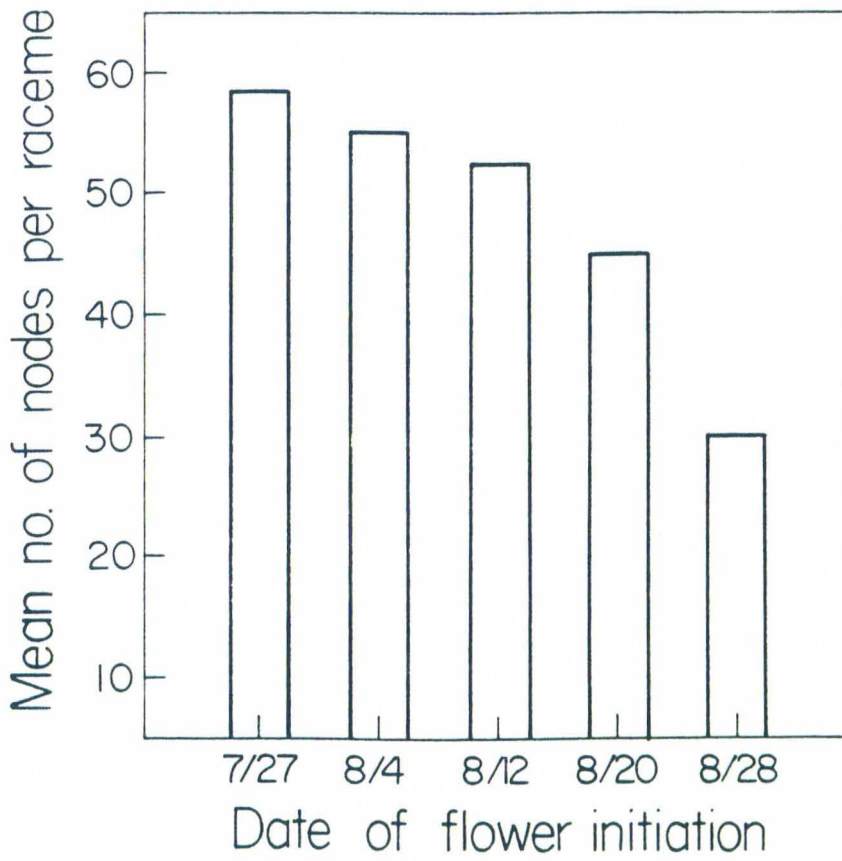


FIGURE 6

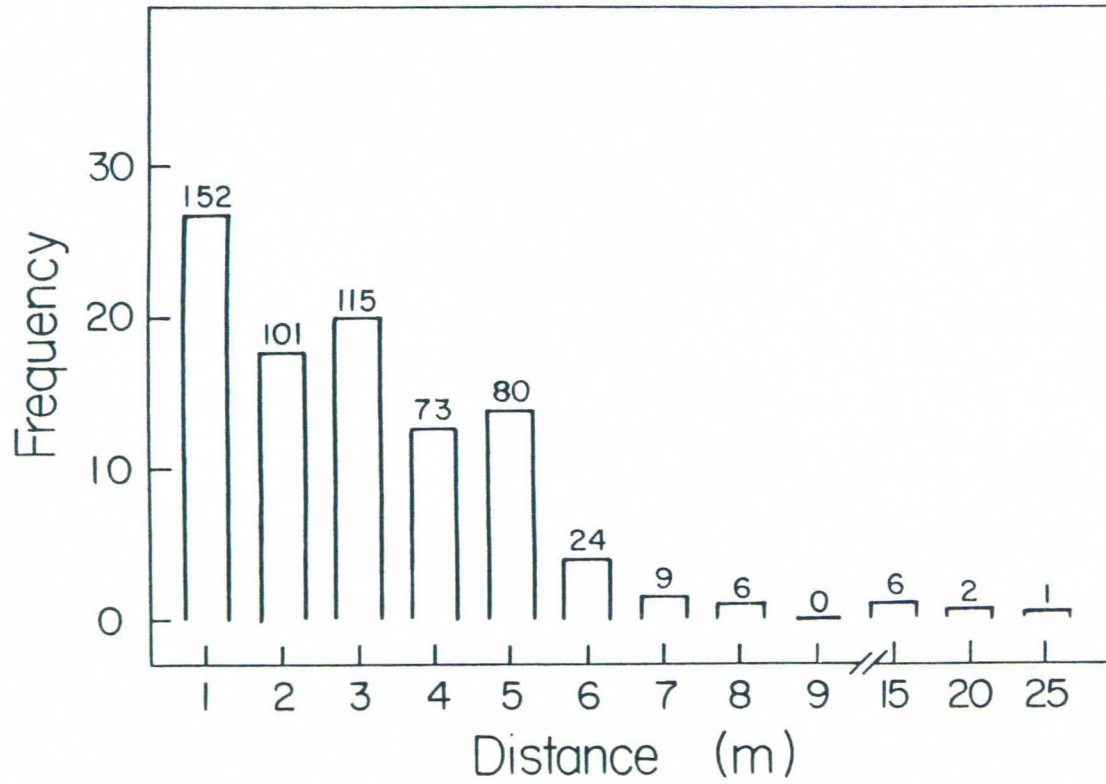


FIGURE 7

