1988

Aspects Of The Dispersal Ecology Of Solanum Dulcamara L (solanaceae) Near London, Ontario

Daniel Hugh Broderick

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NL-339 (r. 88/04)

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Aspects of the dispersal ecology of Solanum dulcamara L. (Solanaceae) near London, Ontario.

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
February, 1988

ISBN 0-315-40760-3

ABSTRACT

Field and laboratory studies of aspects of the dispersal ecology of Solanum dulcamara, a perennial species bearing fleshy fruits, were conducted near London, Ontario. Although there were annual and inter-habitat variations, 51.9% of the dispersant fruits were not ripe. Each fruit type contained some viable seeds, but germination and seedling emergence were more rapid from ripe fruits. Seeds from which the flesh had been removed produced seedlings at a faster rate than seeds sown within intact fruits. Seeds sown within intact fruits were more likely to produce seedlings in later years. In one such study the bulk of seedlings emerged in the second rather than first year. Annual differences in the number of fruits, the probability of dispersal, and the retention period of dispersant fruits at various stages of development were observed in the field habitats. More fruits were set per inflorescence early in the season, but later fruits had more flesh and higher flesh-to-seed dry weight ratios when ripe. There were no seasonal differences in the retention period of dispersant fruits. Seeds from early fruits germinated more slowly than those from later fruits. Differences in the attributes of ripe fruits were mostly the results of adjustments to the flesh rather than the seeds, and inter-habitat differences may have been the result of phenotypic plasticity. The highest percentage of unripe fruits dispersed in the seasonally flooded and heavily shaded swamp habitat. The number of buds per inflorescence, the number of inflorescences per stem, the probability of fruit-set, and the probability of dispersal were generally low at the swamp, however. Fuits ripened most rapidly at the more open riverbank, where the number of buds per inflorescence, the number of inflorescences per stem, the percentage fruit-set and the probability of dispersal were high. Comparable patterns at the seasonally flooded marsh habitat and field-edge environment of the field station habitat were intermediate. However values at the marsh tended to parallel those at the swamp, and the values at the field station approached those at the riverbank.

ACKNOWLEDGEMENTS

I would not have been able to complete this project with out the assisstance of many people. To all I am gratefull, but especially to the following:

Dr. P.B. Cavers for advice, consultation, encouragement, criticism and financial support throughout all stages of the project.

Dr. S.E. Weaver for kindly shouldering the consultative and administrative burdens of supervision during the final months of preparation.

Dr.R.C. Jancey for advice and criticism at all stages of the project.

Dr. L. Orloci for comments on an earlier draft.

Dr. J.B. Phipps and Dr. K.B.Cawker for advice at early stages of the project.

Dr. R. Bailey and Dr. R.Green for assistance with computer programing

Dr. J.M. Bowles for consultation and preparation of diagrams.

M. Bough for preparation of diagrams.

B. Frick, L. Hermanutz and T. Kasenburg for criticism of the final draft of the thesis.

D. Rowley for sewing, counting, weighing and many trifles.

P. Duenk for maintenance of the study areas at the field station.

A. Noon for photographs and the preparation of slides.

Dr. R. Gardiner for rectifying software problems.

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CHAPTER ONE

THESIS INTRODUCTION

1.1 Introduction

The dispersal of seeds to habitats suitable for germination and seedling survival is crucial to the temporal and spatial persistence of higher plant species (Howe and Smallwood 1982, van der Pijl 1982, Janzen 1971, Stebbins 1971). Not only does dispersal impart mobility to the species, and thereby provide escape from hostile environments (Howe and Smallwood 1982, Janzen 1971) and an opportunity to invade receptive habitats (Howe and Smallwood 1982, A. Smith 1975, Livingston 1972, Janzen 1971), it also facilitates evolutionary change. New genotypes arise from sexually produced seeds and new information can be added to disparate gene pools (Levin and Kerster 1974).

In a narrow sense, dispersal can be defined as those actions which result in the removal from the parent and lead to the final deposition of the propagule. However, the costs of dispersal cannot be fully evaluated unless dispersal is considered in a broader context. Attention must also be given to those factors that influence the production, make-up and presentation of the propagule and those factors that come into play after deposition. In an attempt to gain some understanding of the role of dispersal, in the broad sense, towards the reproduction of a plant species, the dispersal ecology of Solanum dulcamara L. (Solanaceae) was examined in a series of field and laboratory studies.

The remainder of this introductory chapter is divided into three sections. The first consists of a review of the existing knowledge and theory concerning the dispersal of species like S. dulcamara that produce fleshy propagules, that is, dispersal units having seed(s) at least partially covered in pulpy, often succulent tissues. The emphasis of this review will be upon temperate rather than tropical species. The second section will focus upon the biology of S. dulcamara, especially upon the body of information concerning the production, development and loss of its fleshy berries and the germination of its seeds. The third section will serve as an outline to the remaining body of the thesis.

1.2 The dispersal of fleshy propagules

1.2.1 Introduction

Fleshy propagules vary greatly in their attributes (van der Pijl 1982, Ridley 1930), and like all propagules each represents a multi-faceted compromise to a myriad contingencies. Amongst these are the evolutionary legacy of the species, the growth requirements of the plant, interactions with predators and pathogens, the physical and biotic nature of the regeneration environments and their accessibility in time and space (Hererra 1986 1985, Howe 1984, Howe and Smallwood 1982, Stephenson 1981, Grime 1979, Grubb 1977, Howe and Estabrooke 1977, Stearns 1976, MacArthur and Wilson 1967, Corner 1964, 1954). In most assessments, however, the hallmark of the fleshy propagule, and in some views (Regal 1977, van der Pijl 1982, 1966, Corner 1964, 1954) the driving force behind their evolution, is a linkage with animals that, while consuming all or a portion of the propagule, disperse the seeds. This linkage with animals represents the principal theme in the majority of attempts to model the dispersal ecology of fleshy propagules.

The greatest range in the make-up of individual fleshy proagules is found in the tropics where the diversity of plant and animal species is often great and where specialized plant/frugivore interactions have been described (Terborgh 1986, Janson 1983, Gauthier-Hion et al. 1985, Knight and Seigfried 1983, Howe and Smallwood 1982, McKey 1975, Morton 1973, Snow 1971). However, few specialized frugivores exist in temperate settings (van der Pijl 1982), and most animals feed opportunistically on fleshy propagules and show strong preferences for other foods, at least during part of the year (Stapanian 1986 1982b, Herrera 1984b, Stiles 1980, Thompson and Willson 1979, Morton 1973, Snow 1971). Although some plant species may be dispersed by mammals (Stiles 1980, Staniforth and Cavers 1977), most temperate trees and shrubs seem to produce and display fleshy propagules conducive to dispersal by birds (van der Pijl 1982, Thompson and Willson 1979).

1.2.2 The ecological roles of the flesh and seeds

It is common in most theoretical treatments to consider the fleshy propagule as comprised of two parts: the flesh and the seed(s). Together and seperately, and at different times, the flesh, which represents the package, and the seed(s), which represents the regenerative payload, play certain key roles. At some stages of development, their qualities may serve to protect the seeds from predation and premature dispersal. At other stages, seed dispersal at opportune times and by efficient pathways may be promoted. Even following deposition, the flesh may continue to play a role in seed survival, but ultimately it is the seed, its nutritive content and germination pattern, which charts the course of early development in a new habitat.

During the early phases of development the fleshy propagule is commonly small, coloured a cryptic green and capable of making a substantial contribution to its carbohydrate requirements (Stephenson 1981, Bazzaz et al. 1979). In addition, the immature flesh is often thin, and because of repulsive combinations of tannins, alkaloids, and sour acids, unpalatable (Hererra 1982b, Stiles 1980, Janzen 1977, Corner 1954). These qualities are felt to aid in the deflection of predators and decay organisms and/or to postpone animal-mediated dispersal until conditions are suitable. The seeds, too, play important roles during the early stages of development. Much of the pattern of growth, even the likelihood of abortion, is influenced by hormone emissions from the developing seeds (Stephenson 1981). Gorchov (1985) and others (Brewer and Dobson 1969, Brewer et al. 1969, Dempsey and Boynton 1964, Aalders and Hall 1961) have identified, at an intraspecific level, positive correlations of seed size and/or number with the final size of the propagule, the quantity of flesh produced, and the rate of ripening. Seeds may also play important protective roles at this time. Toxic or unpalatable compounds, for example, may deter predators or pathogens (Hererra 1982b , Janzen 1977 1971 1969, Kear, 1968).

The need to protect the propagule from predators and decay organisms persists through the process of ripening, which in most views precedes successful dispersal (Stapanian 1982b, Stiles 1980, Thompson and Willson 1979, Howe and Estabrooke 1977, Foster 1977, Sherbourne 1972). Although typically occurring in reduced quantities, toxic or noxious compounds may still be present in ripe flesh (Herrera 1986 1982b, Janzen 1977, 1971), or the growth of decay organisms may be limited by an unbalanced complement of nutrients in the flesh (Herrera 1982b). In most views, the flesh of ripe propagules takes on an additional ecological role: that of promoting seed dispersal by animals or particular sets of animals. Janzen (1977) considered this promotional role to be paramount. In his rather strong terms: " ... the entire adaptive function of the ripe fleshy fruit is to get the seeds moved to particular places (and, on occasion, directly or indirectly protect the seeds).".

Amongst the qualities of the propagule which are felt to promote their dispersal by animals are shifts to more conspicuous colouration (Willson and Hoppes 1986, Wheelwright and Janson 1985, Gauthier-Hion et al. 1985, Knight and Seigfried 1983, Willson and Melampy 1983, Moermond and Denslow 1983, Willson and Thompson 1982, Turcek 1963) and the development of strong odours (van der Pijl 1982, Stiles 1980, Corner 1954), both of which may serve to draw animals towards the propagule display. Once enticed to the display, changes in the texture and chemical compounds of the flesh may make the propagule more attractive as a foodstuff (Herrera 1986, Stephenson 1981, Stiles 1980). From the plant's perspective, it is an advantage if the foodstuff of interest is the flesh, since a focus on the seeds would reduce the probability of any surviving the encounter. In this context, the role of the flesh is to serve as a "bribe" payable to animals for the dispersal of the seed which should, preferably, represent unwanted "ballast" to the animal.

In a qualitative sense, the bribe offerred by the fleshy propagule may be chiefly caloric, since the flesh of most propagules, especially in temperate environments, appears not to be very nutritious nor to offer a balanced combination of nutrients (Herrera 1982b). Herrera (1982b) described the fleshy component as: "... typically high in carbohydrates and water, low to medium in lipids, and extremely low in protein.". There is, however, considerable variation in the qualities of the flesh offered by many temperate species (Piper 1986b, Stapanian 1986 1982b, Johnson et al. 1985, Herrera 1984b 1982c 1981a, Sorensen 1984 1981, Best 1981, Stiles 1980), although many of the differences seem to be in the caloric composition --- proportions and quantities of lipids, sugars, starches.

Quantitative aspects of the reward offered by the flesh of a propagule may serve as a better indication of food value (Piper 1986b) and may mask some of the qualitative differences. This seems especially so in terms of energy, a factor that in Stapanian's view represents a crucial dispersal currency. Using data from Johnson et al. (1985), Herrera (1982d), Stapanian (1982a); Sorensen (1981) and Best (1981), for which both dry flesh weights and caloric yields were available, I obtained a positive correlation coefficient of 0.813 ($p < .0001$) between the two variables for 110 species of temperate plants. If the four most deviant species --- Olea europaea and Laurus nobilis with very rich flesh (Herrera 1982d), and Prunus spinosa and Rosa canina with very poor flesh (Sorensen 1981) --- were removed from the analysis, the coefficient was raised to 0.939 ($p < .0001$). There is some evidence from feeding trials that quantitative aspects of the reward may be most important (Piper 1986b, Johnson et al. 1985, Best 1981). Johnson et al. (1985), for example, found that the dry weight of the flesh per propagule gave the best indication of the feeding preferences of captive birds. They found, further, that the mass of consumed flesh also served as a good index of subsequent energy retention.

It is important to consider the nature of the bribe offered by the fleshy component within the architectural context of the intact propagule. Herrera (1981a), in particular, demonstrated this. When the quantitative and qualitative rewards of the flesh were considered with respect to the bulk of the seed load, he showed that despite the relatively low quality of the flesh of many temperate species, the reward, given the relatively small bulk of the seed load, could often match that of certain tropical propagules with thin coatings of very rich flesh over large seeds.

The number, size and structure of the seeds confined within the propagule are also considered to have direct roles in dispersal, affecting food choice, handling and the likelihood of consumption and transport (Howe and Smallwood 1982, Herrera 1981a, Stiles 1980, Thompson and Willson 1979, Howe and Estabrooke 1977, McKey 1975). Jordano (1984) found that different species of birds consumed different portions of the seed size spectrum of *Rubus ulmifolius*, and Sorensen (1984) showed that blackbirds preferred fruits with seeds large enough to be regurgitated over fruits with small seeds that would pass through the digestive tract and represent undesired ballast. Seed size, hardness, and toxicity may also greatly influence the ability of seeds to withstand the rigors of consumption and passage through the gut (Thompson and Willson 1979, Salomonson 1978, Rick and Bowman 1961, Krefting and Rowe 1949, McAttee 1947, Swan 1944). In addition, seed size can affect the rates of passage through the gut (Levey 1986, Sorensen 1984).

Perhaps the most important roles played by the seeds, however, are fulfilled once the seed has reached a final resting place, and many seed attributes may be strongly linked with post-dispersal aspects of germination and seedling establishment. Certainly for many plant species, the importance of such seed attributes as shape and weight to germination and seedling survival are well known(Grime 1979, Harper 1977). Although the probability of a viable seed from a fleshy propagule reaching a site conducive to germination and establishment has received much theoretical attention (Herrera 1985; Howe et al. 1985; Howe 1984; Howe and Smallwood 1982; Stiles 1980; Thompson and Willson 1979; McKey 1975; Morton 1973; Smythe 1970), the bulk of information concerning post-dispersal seed fates is largely anecdotal or based on field observations (Becker and Wong 1985; Fleming 1981; Glyphis et al. 1981; Howe 1981, 1977; Howe and Vande Kerckhove 1979; Salomonson 1978; McDiarmid et al. 1977; Howe and Primack 1975; Smith 1975; Rick and Bowman 1961; Salisbury 1942; Ridley 1930). A few studies have focused on the direct impact of animal ingestion on seed germination under controlled conditions (Salomonson 1978; Staniforth and Cavers 1977; Lamprey 1967; Rick and Bowman 1961; Krefting and Rowe 1949; McAtee 1947; Swank 1944); other works have considered the germination of seeds from which the flesh has been mechanically removed (Howe et al. 1985, Howe 1981, Howe and Vande Kerckhove 1979, Livingston 1972, USDA 1948, Adams 1927). It has commonly been concluded that passage through the gut of many animals improves germination of those seeds that escape destruction, but rarely has evidence been given that untreated control seeds are not merely dormant and capable of eventually germinating under a different set of conditions (Holthuijzen and Sharik 1985). The number of detailed field studies of seed and seedling fates is growing (eg. Holthuijzen *et al.* 1987, Becker and Wong 1985, Howe *et al.* 1985, Ashmun and Pitelka 1985, Roberts and Boddrell 1983, Rust and Roth 1981 and Roberts and Lockett 1977), but the number of species studied still remains small. Particularly uncommon are studies of the impact of seed maturity, habitat or seasonality on the performance of the seeds from fleshy propagules. Holthuijzen and Sharik (1985) and Pegtel (1985) are, to my knowlege, the only ones to have formally contrasted germination patterns of seeds from fleshy propagules formed in different habitats. In both studies the habitat differences were slight. No one has examined germination trends for seeds taken from fleshy propagules produced over the course of a season.

Few considerations of the ecological roles played by the flesh extend beyond its influence on predators, pathogens and dispersers. This bias persists despite the common observation that large numbers of intact fleshy propagules may be incidentally detached by animals or dispersed by inanimate vectors such as wind or rainfall (Holthuijzen *et al.* 1987, Holthuijzen and Sharik 1985, Becker and Wong 1985; Howe *et al.* 1985, Borowicz and Stephenson 1985, Courtney and Manzur 1985, Stapanian 1982a, Rybczynski and Riker 1981, Howe and de Steven 1979, Smith 1975, Smythe 1970, USDA 1948). Though many of these propagules may be consumed at ground level by animals (Becker and Wong 1985; Borowicz and Stephenson 1985; Courtney and Mazur 1985, Rybczynski and Riker 1981), it is likely that some would escape, especially in areas where dispersal coincides with the seasonal defoliation of many species, snowfall or reductions in animal activity. The subsequent germination and seedling emergence patterns from these intact propagules could be directly influenced by the presence of the flesh itself and differ in important ways from the patterns arising from bare seeds alone.

Of the few studies that have examined the direct or indirect impact of the flesh on germination, a few (Lamont 1982a + b, McDiarmid et al. 1977, Johnsen 1962 USDA 1948) report that germination is inhibited or delayed when the seeds are in contact with the flesh. Howe and Vande Kerokhove (1979) found that the flesh of Virola surinamensis needed to be removed for germination to occur and McDiarmid et al. (1977) observed that no seedlings emerged in the field from seeds of Stemmadenia donnel-smithii that retained their fleshy aril. Johnsen (1962) found that cleaned seeds of Juniperus monospermum mixed in soil produced seedlings before those confined within the propagule. Moreover, few seedlings emerged from intact fruit, and even seeds removed from but still in contact with the flesh produced lower numbers of seedlings. For commercial and horticultural purposes the flesh need not be removed prior to sowing the seeds of some species (USDA 1948). Ashmun and Pitelka (1985) observed field survival of Clintonia borealis to be lower when the seeds were sown within intact fruits.

A persistent bias in most theoretical interpretations of the dispersal of fleshy propagules is a limitation of the discussion to the dispersal of ripe propagules, particularly those that are taken by animals. Losses of immature propagules have traditionally been given little attention (Thompson and Willson 1979) and in the early model of Howe and Estabrooke (1977) the losses of immature fruit were explicitly treated as unimportant to dispersal. Despite an observed preference of avian species for ripe propagules (Holthuijzen et al 1987, Moermond et al. 1986, Willson and Thompson 1985, Howe and Estabrooke 1977, Foster 1977, Sherbourne 1972), there is a growing body of knowledge suggesting that substantial portions of the propagule crop may be separated from the parent before ripening (Holthuijzen et al. 1987, Holthuijzen and Sharik 1985, Becker and Wong 1985, Howe et al. 1985, Borowicz and Stephenson 1985, Courtney and Manzur 1985, Stapanian 1982 a, Rybczynski and Riker 1981, Howe and de Steven 1979, Berg 1975, A.Smith 1975, Smythe 1970, USDA 1948). Some of these losses may even be attributable to animals (Moermond et al. 1986, Willson and Thompson 1982, Foster 1977, Sherbourne 1972). Unfortunately, viability of seeds taken from immature fleshy propagules has seldom been assessed and their possible contributions to future generations still remains generally unknown. The only detailed studies of the impact of fruit ripeness upon seed germination have been those of Foster (1977) for *Ardisia revoluta* in Costa Rica, and Lamont (1982a) for the Australian mistletoe, *Amyema preissii*. In the former case, seeds from unripe, ripening and ripe fruits were capable of reaching similar levels of germination, but the rate of germination increased with fruit maturity. In Lamont's study, seeds from immature fruits were not capable of germinating, but the number of seedlings arising from seeds of partially ripe and fully ripe fruit was not significantly different.

1.2.3 Temporal trends in structure, production, and dispersal

Most temperate trees and shrubs ripen their fleshy propagules in late summer and into the fall (Stapanian 1985, Herrera 1984b, 1982a+c, Stiles 1980, Thompson and Willson 1979, Morton 1973, Snow 1971) at a time when the breeding territories of many bird species have broken down and local populations are swollen with the young of the year and the parapetetic flux of southbound migrants (Herrera 1982a, Willson and Melampy 1983 Stiles 1980, Thompson and Willson 1979, Morton 1973, Snow 1971). In some views, the feeding priority of birds at this time is upon the quick aquisition of energy reserves for migration and winter survival (Stapanian 1982b, Herrera 1982a 1981b, Stiles 1980, Thompson and Willson 1979, Morton 1973). Species that produce fleshy propagules early in the season may face a numerically smaller set of potential dispersers which prefer protein rich invertebrates to meet the demands of rapidly growing young (Herrera 1982a, Stapanian 1982b, Stiles 1980, Thompson and Willson 1979, Morton 1973).

There is at best equivocal evidence to suggest that the attributes of fleshy propagules in temperate environments shift in concert with seasonal differences in dispersal environments. In comparison to the flesh of propagules produced early in the growing season, Snow (1971) and Herrera (1984b 1982c) found the flesh of late ripening propagules in Europe to be more rewarding, being denser and more nutritious, and Herrera found it to be drier and richer in lipids. Stiles (1980) reported parallel trends in eastern North America, but identified two types amongst the later ripening propagules: 1) those propagules with particularly rich flesh that if not quickly dispersed would decay rapidly; 2) those propagules with a lower quality of flesh, less attractive to animals but also more resistant to decay. In contrast, Stapanian (1982b) claimed ~~that~~ early propagules had the more "expensive" flesh, richer in calories, especially relative to the seed load, than the flesh of those propagules ripening later in the season. Others have failed to identify strong seasonal trends in the attributes of fleshy propagules. Johnson *et al.* (1985), for example, found slight increases in the absolute quantities of potassium and proteins to be the only identifiable seasonal trends. Piper (1986b), too, found no consistent seasonal trends in the morphological and chemical attributes of the fleshy propagules borne in an area of Washington State.

Although detailed multi-year studies of fleshy propagule production and loss are uncommon, there is a growing body of evidence to suggest that annual variation can be pronounced in terms of both crop size (Wheelwright 1986, Gonzalez-Espinosa and Quintara-Ascencio 1986, Smythe 1986, Herrera 1984b, Stapanian 1982b, Mannasse and Howe 1983, Stephenson 1981, Solomonson and Balda 1977) and rates of ripening (Piper 1986b, Manasse and Howe 1983, Willson and Thompson 1982, Thompson and Willson 1979, Sherbourne 1972). A pertinent study is that of Sherbourne (1972) in which 10 stems of *Solanum dulcamara* produced 176 fruits of which 38% dispersed in one habitat in 1970, but in the same habitat in 1971, the crop size was 250 fruits and only 16% dispersed. In another habitat where 100% of the fruits dispersed in both years, dispersal rates differed considerably.

According to the interspecific observations of Stapanian (1982b), Stiles (1980) and Thompson and Willson (1979) for deciduous forests of eastern North America, species producing fleshy propagules early in the season have slower ripening rates than species maturing their propagules later in the season. The extended ripening period of the early fruits has been viewed as a possible adaptation to avoid over-saturation of the food requirements of the resident populations of potential dispersal animals and as a means of minimizing losses to decay organisms and predators. Asynchronous ripening patterns, which could promote visually attractive multi-coloured propagule displays, have also been viewed as additional adaptive features (Willson and Hoppes 1986, Willson and Thompson 1982, Stiles 1982). In contrast, fleshy propagules produced later in the season were seen as ripening over a more compressed interval. This pattern has been considered a means to maximize the attraction and availability of ripe propagules during the brief periods in which local bird populations are swollen by fall migrants. Stiles (1980) argued that "high quality" fall fruits should be dispersed more rapidly than the "low quality" type. The evidence for seasonal differences in dispersal rates is mixed. Thompson and Willson (1979) but not Sherbourne (1972) observed a tendency for a more rapid dispersal rate for later ripening propagules. Johnson et al. (1985) and Borowicz and Stephenson (1985) cite species with dispersal characteristics contrary to what would be predicted based on Stiles' (1980) model. In Spain, Herrera (1984b) found no correlation of propagule loss rates and the season of ripening.

Intra-specific variation in ripening rates has also been noted. The bulk of these studies, however, have concerned species which both produce their flowers and ripen their propagules over a rather narrow portion of the season (Gorchov 1985, McDonnell et al. 1984, Stapanian 1982a, Willson and Thompson 1982, Aalders and Hall 1961, Dempsey and Boynton 1964, Brewer et al. 1969). In most cases (Gorchov 1985, Brewer et al. 1969, Dempsey and Boynton 1964, Aalders and Hall 1961), the asynchrony of ripening was linked to differences in the numbers and sizes of seeds contained in a fruit rather than differences in the time of fruit initiation. However, both Gorchov (1985) and Willson and Thompson (1982) cite examples of fruits with invariate seed numbers that ripen fruits asynchronously, and Gorchov refers to unpublished reports of ripening being delayed by the pre-existence of fully ripe fruits.

1.2.4 Habitat differences

A commonly observed difference in the production of fleshy propagules attributable to habitat is that the individuals found in open and presumably more favourable environments produce larger crops than those which occupy poorer habitats. However, in the bulk of these studies, crop size, *per se*, has not been shown to strongly affect the proportion of fruits dispersed (Davidar and Morton 1986, Piper 1986a, Denslow et al. 1986, Herrera 1984b, McDonnell et al. 1984, Stapanian 1982a, Morden-Moore and Willson 1982, Manasse and Howe 1983, Howe and Vande Kerckhove 1981 1980, Sorensen 1981, Baird 1980, Howe and de Steven 1979). A few exceptions to this general pattern have been noted. Jordano (1982), for example, found that colonies of *Rubus ulmifolius* bearing small crops later in the season or growing where plant densities were low, tended to have a lower probability of dispersal. In Piper's (1986a) study, artificial infructescences with larger fruit displays had a higher proportion dispersed when placed at the edge of the forest. Courtney and Manzur (1985) noted a weak relationship, at best, between crop size and the proportion of fruits dispersed, and observed that more birds were attracted to large displays of fruits. In another work, Howe and Vande Kerckhove (1979) reported higher proportional dipsersal for individuals with intermediate sized crops.

Few studies have reported that dispersal rates in open habitats were greater than those in more closed habitats (Willson and Melampy 1983, Morden-Moore and Willson 1982, Thompson and Willson 1979). Thompson and Willson (1979) attributed this to differences in the likelihood of discovery, noting dispersal rates to be similar once a crop was encountered. In Morden-Moore and Willson's (1982) work, the difference in rates was only initially faster in the open, but they further noted that all fruits of Lindera benzoin were ultimately dispersed. This propensity for faster dispersal in the gaps may be partially related to the tendency for frugivorous birds to be more commonly encountered in gap environments in the fall (Blake and Hoppes 1986) and for birds showing a tendency to forage in gap environments before venturing to more closed areas (Baird 1980).

1.3 The biology of Solanum dulcamara L.

Solanum dulcamara L. is a member of the Solanaceae and is Eurasian in origin (Gleason 1963). The nature of its introduction to North America is not known but it is possible that several deliberate introductions have been made. The berries have a high alkaloid content (Mathé et al. 1975) and the plant is reported to have medicinal properties (Salmon 1710). It has been cultivated since at least 1561 (USDA 1948). It is naturalized in North America and, as in Eurasia, occupies a wide variety of habitats (Pegtel

1985, Osmond 1983, Clough *et al.* 1983 1979a+b, Gauhl 1979 1976, Horvath *et al.* 1977, Alex and Switzer 1976, Mathé *et al.* 1975, Muenscher 1966, Salisbury 1961 1952 1942), such as dry, exposed sand dunes and riverbanks, fencerows, woodlot borders, agricultural lands, and deeply shaded, seasonally flooded marsh and swamp lands. The species is long lived (up to 20 years: Salisbury 1942) and its growth form varies from habitat to habitat. In marshy areas open to the sun, it may form dense tangles of rather weak stems, whilst in other habitats (fencerows or riverbanks, for example), its structure may be shrublike or its stems may clamber vinelike through the surrounding vegetation or other objects.

Solanum dulcamara produces cymes bearing perfect, self fertile flowers that might open in early June (Heinrich 1976). Although each flower is only about a centimeter in diameter, their five pointed light blue to violet or, rarely, white corollas, in conjunction with the five bright yellow connate anthers, make a rather attractive display. The production of flowers is continuous until the first severe frosts of the fall.

Soon after pollination, which is primarily effected by insects (Liu *et al.* 1976, Macior 1971, Knuth 1909, Muller 1883), the berries begin to form. At first green and rather hard, the berries change to an orange colour and then become red and juicy upon ripening. Coincident with the colour and textural changes during ripening, Mathé *et al.* (1975) reported a reduction in water content and about a 1.8 fold decrease in alkaloid content. Some fruits wither and remain attached to the infructescence as hard, dark coloured dessicated fruit. Fruit at all stages of development can be found well into the fall and a few desiccated fruits may last over the winter.

The small, rather soft seeds (ca. 1.5 mm in diameter) of *S. dulcamara* are light coloured irregular discs reminiscent of tomato seeds (*Lycopersicon esculentum* L.). Each seed weighs about 1 mg (Grime 1979, Salisbury 1942), and in England, there is an average of 38 and a range of 9-63 seeds within a fruit (Salisbury 1942). Based on a sampling of eight adult (sic) plants, Salisbury (1942) estimated annual seed production to range between 40 000 and 70 000 seeds per plant. Near London, Ontario, these seed yields might be approached in some habitats, but it is not uncommon for fecundity to be much less, and the number of seeds per fruit can range from one to 49[illegible]th an average of less than 30 seeds (pers. obs.)

No detailed investigations of the patterns of production, development and loss of the fruits of *S. dulcamara* have been conducted, but in general terms berries may be lost from the cymes throughout the growing season. Although quite firmly attached to the cyme, some fruits can be removed by wind or precipitation. In mid-August 1984, for example, a very severe but localized thunder/hail storm knocked to the ground upwards of 90% of all the fruits that I was individually monitoring at a common garden and in the field habitats. Other fruits are removed by wildlife. Many species of birds are known to consume the berries (Smith 1975, Martin *et al.* 1951, Salisbury 1942, Ridely 1930) as is an army of mammals (Staniforth and Cavers 1977, Martin *et al.* 1951). Birds are touted by some (Salisbury 1942, Ridely 1930) as the major dispersers of viable seeds to new habitats, and the fruiting display matches the general criteria of dipsersal tuned towards avian vectors (Thompson and Willson 1979, van der Pijl 1982). I have observed the following bird species consuming the *S. dulcamara* fruits in and around London Ontario: cardinals, robins, white-throated sparrows, field sparrows and goldfinches. I have never seen immature fruits taken, and to my knowledge, no reports of animals taking immature or desiccated fruits have been made. Cardinals often took only bites from the fruit and portions were sometimes left behind, but robins tended to pluck and swallow entire fruits. Viable seeds have been collected from the faeces of chickens (Bedford pers. comm.) and from rabbits (Staniforth and Cavers 1977). In August of 1985, I collected bird faeces from along the fencelines of the Labatt Field Station, a few kilometers north of the U.W.O. campus, and from the boulder strewn banks of a creek passing through the campus. Of the 35 faeces collected, 20 yielded *S. dulcamara* seedlings after being placed on the soil surface of flower pots placed on a green house bench. Both of the sites of collection were close to sources of the fruit, however, so the frequency of seedling occurrence cannot be considered to reflect the feeding practises of birds in general. There is also some evidence that fruits and seeds may be consumed on the ground, as rodents chewed through protective fiberglass mesh to obtain intact fruits used as a treatment in a field seedling emergence study, and slugs and other invertebrates were also observed to consume the flesh. The mature fruits can float for some days in still water, and even after several months of submergence most seeds are still viable (pers. obs.)

Most investigations of *S. dulcamara* have been conducted in Hungary by researchers primarily interested in the species as a source of steroid raw materials for the pharmaceutical industry. Soo (1968 as in: Horvath *et al.* 1977), recognized 17 taxa on a morphological basis, whilst Mathé and

Mathé (1923), distinguished four taxa on the the basis of different alkaloid contents. Horvath et al. (1977) found that some morphological variations among "ecotypes", grown under common conditions, were consistent with those found in the field, but less pronounced. Mathé et al. (1975) concluded that the chemical make-up of the plant was independent of ecological effects, and they observed variation in absolute and relative terms within a single taxon when cuttings from the same individual were grown under different conditions.

Gauhl (1979 1976), in Germany, examined the photosynthetic response of S. dulcamara to varying levels of light intensity and moisture stress and found sun and shade "ecotypes" which differed in response. Ferrar and Osmond (1986)and Osmond (1983), however, could not find evidence of an ecotypic separation amongst Gauhl's clones in terms of potential for photosynthetic acclimation. Clough et al. (1983 1980 1979 a+b), in North America, disputed Gauhl's findings and argued that responses attributable to phenotypic plasticity dominated. Clough et al. (1979a) attempted to investigate the frequency of the "ecotype" characteristics within different habitats; only one of fifteen individuals in a shady environment exhibited a response similar to the shady type of Gauhl. Gauhl (1976) claimed to have examined 30 morphologically and physiologically distinct "ecotypes", but in his detailed report he examined only five. Mathé et al. (1977) examined cuttings taken from a single individual and Horvath et al. (1977) used cuttings from only four field specimens. None of these reports have focused on the patterns of fruit production or dispersal.

Most reports on the germination of S. dulcamara seeds have been based on controlled laboratory or glasshouse studies of seeds washed free of all pulp (Pegtel 1985, Roberts and Boddrell 1983, Roberts and Lockett 1977, Kosikova 1960, Salisbury 1942, Adams 1927, Mitchel 1926,). The reports of Pegtel (1985), Roberts and Boddrell (1983), and Roberts and Lockett (1977) have been the most extensive, and, in general, their results agree. Seeds collected from ripe fruits in the fall and washed free of the pulp germinated best under regimes of alternating temperatures, with germination approaching 90 - 100% after 30 days exposure to regimes of 10/25° C, 10/30° C, 20/30° C (Roberts and Lockett 1977), or 35/25° C (Pegtel 1985), even when in complete darkness (Pegtel 1985). Cold stratification resulted in more rapid and complete germination over a wider, particularly, cooler, range of alternating or constant temperatures (Pegtel 1985; Roberts and Lockett 1977). Grime et al. (1981), however, reported that the germination of freshly collected S. dulcamara seeds was low (ca. 2%) until a chilling requirement had been met. Pegtel (1985) also noticed some increase in germination levels and rates following a cool, moist stratification.

In the studies of Roberts and Boddrell (1983) and Roberts and Lockett (1977), emergence and germination patterns of S. dulcamara were examined under experimental field conditions. In both studies an average of 49 - 68% of the seeds gave rise to seedlings in the first year; almost all of the seedlings emerged in April, some in May and very few afterwards, regardless of cultivation. Although most of the seedlings observed by Adams (1927) emerged in the spring, a few emerged in the fall. In mesic environments near London, Ontario, most S. dulcamara seedlings are observed in the spring, but in seasonally flooded habitats, emergence has not been observed until the flood waters subside (pers obs.).

Solanum dulcamara is a good species for examination of several aspects concerning the ecological implications of dispersal. Its flowers and fruits are continuously produced over a large portion of the growing season, providing an opportunity to investigate seasonal trends in propagule make-up, production and loss, plus germination and seedling emergence. The broad suite of environments in which it grows provides a good opportunity to examine the effects of habitat on dispersal. The ease with which stem cuttings can be rooted and established within a common garden facilitates examination of possible trade-offs between phenotypic plasticicty and genetic differences in propagule production.

1.4 Thesis organization

After this introductory chapter there are five others. The first of these, Chapter 2, provides a description of the four natural habitats in which field studies were conducted, and of the common garden in which stem cuttings from specimens in the natural settings were transplanted and allowed to grow. Also provided in this chapter is a brief description of the fruit developmental stages referred to throughout the thesis. Chapter 3 is the first chapter in which results will be ~~presented,~~ and there the focus is upon the morphology of individual propagules harvested at various stages of development at two points in the growing season of 1985 from the natural habitats and the common garden. Chapter 4 is an examination of the patterns of production, rates of ripening, and the retention periods of dispersant fruits in the natural habitats. These field studies were initiated at an early and late point in the growing seasons of 1982 and 1985. In Chapter 5, some aspects of germination and seedling emergence of seed taken from fruits at various stages of development and at different points in the growing season are described. These studies were variously conducted under field, growth cabinet and greenhouse conditions. The impact of the flesh upon seedling emergence is another important focus of the studies in this chapter. The aim of Chapter 6 is to provide an overall review of the various studies and to summarize these in terms of theoretical frameworks concerning the ecological implications of the dispersal, in the broad sense, of fleshy propagules.

CHAPTER TWO

HABITAT DESCRIPTIONS AND FRUIT CLASSIFICATION

Preliminary field surveys conducted near London, Ontario (43° 02' N. lat.; 81° 16' W. Long.), identified a broad suite of habitats in which populations of *Solanum dulcamara* could be found. From amongst these, four quite different habitats on and near the main campus of The Univesity of Western Ontario were selected for detailed study.

Two of these habitats were adjacent and both were seasonally flooded and had organically rich soils. In the "marsh" habitat, a dense tangle of rather weak stems of *S. dulcamara* was found (Plate 2.1). Adventitious roots were common and the recognition of discrete individuals was impossible. This habitat was exposed to direct sunlight for most of the day and, though bounded by trees and shrubs, there were very few good perching sites near the fruiting displays. The "swamp" habitat bordered the marsh and shared a similar physiography, but it was subject to very heavy shade once the leaf canopy of *Salix nigra* Marsh. trees had expanded in the spring. As at the marsh, the stems of *S. dulcamara* were weak and tended to intertwine and produce adventitious roots; but the overall density of stems was lower (Plate 2.2). Again, the stems likely represented poor perching sites, but the presence of the trees and the abundance of fallen branches may have offered better access to the fruits here than at the marsh. Standing water was present at both habitats over most of the fall, winter and spring. In 1982, 1983, 1984 and 1985, the years in which

Plate 2.1. The marsh habitat.

Plate 2.2. The swamp habitat.

observations were made, the water table fell below the soil suface on the third week of June, the third week of June, the third week of July and the second week of June, respectively. Occasionally through the summer months, rainfall would raise the water table to a height above the soil surface and both habitats would be flooded for a few days.

The third habitat, the "riverbank", consisted of two sections, each about 100 m in length, along the banks of Medway Creek where it passed through the campus (Plate 2.3). This habitat was exposed to direct sunlight for most of the day and its surface was strewn with large boulders and its soil texture was sandy. During high water, the creek might rise by two or three meters, and portions of the banks would be scoured by the current. Vegetation was sparse; herbs, shrubs and a few saplings emerged from gaps between the boulders. Both sections of this habitat were backed by tended lawns but woody areas were nearby. The growth form of Solanum dulcamara was weakly shrublike and discrete clusters of stems were dotted amongst the boulders, some in areas prone to flooding. Many of the stems were more sturdy than those of the swamp and marsh habitats, and they could have represented suitable perching sites. Access to the fruits for birds and/or mammals might also have been promoted by the tendency for the fruits to be displayed in positions close to the boulders.

The fourth habitat was at the University's ~~Labatt~~ Field Station where the soil is a clay loam (Hawthorn 1973). Scattered clusters of stems of S. dulcamara occurred along the fencelines that bordered the cultivated fields and pastures of this "field station" habitat (Plate 2.4). For the most part, the stems emerged from a turf of forbs and grasses and grew

Plate 2.3. The riverbank habitat.

7

Plate 2.4. The field station habitat.

intertwined with the fencing material. Most of the stems were subject to partial shading by other trees and shrubs distributed along the fence lines. The fruits were usually formed at a distance of only a few centimeters from the good perching sites offerred by the fencing materials, even squirrels and smaller mammals could conceivably have had good access to the fruits.

The fifth field study area was a common garden constructed during June of 1982 on soil that had been plowed and cultivated at the field station. The common garden was arranged in a rectangular grid comprised of three rows, each 38 m in length and spaced three metres apart. At each two metre interval along a row, a transplant site was prepared. At each transplant site, a column of steel wire fencing material (mesh size approximately 15 x 25 cm) was attached to a 1.3 m long wooden stake driven about one quarter of the way into the ground. The columns of fencing material, each about 1.3 m high and 0.45 m in diameter, were to provide support for the growth produced from stem cuttings transplanted at each site.

On June first and second, 1982, sections of stems were cut from S. dulcamara plants growing in the four natural habitats. At the field station and riverbank, all the clusters of stems were enumerated and 15 were selected at random. A 45 cm long section was cut from the top of a stem randomly selected from those in a cluster. At the marsh and swamp habitats, where discrete clusters of stems could not be identified, a section of stem was cut at three locations spaced three metres apart along each of five transects spaced at five metre intervals across the habitat.

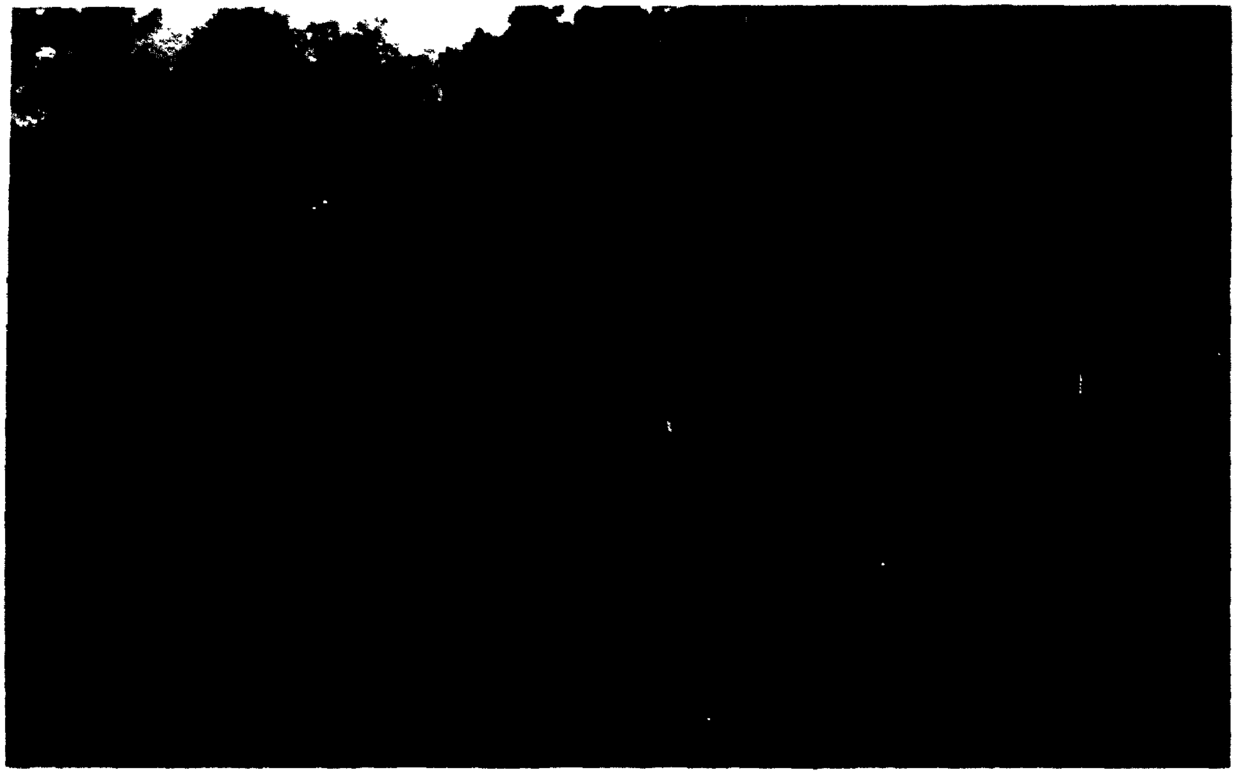
In the laboratory, each stem section was cut into three pieces and these were inserted into the potting soil contained in a six centimeter plastic flower pot. All 60 sets of cuttings were treated similarly, and the pots were placed on a greenhouse bench under intermittent mist irrigation.

On July 5, the rooted cuttings from each of the collected stems were transplanted at the common garden. The cuttings derived from a single stem were planted at one transplant site. Five sets of cuttings from each of the natural habitats were randomly assigned to the twenty transplant sites along each of the rows.

After transplantation, the soil around the stems was saturated with water and the soil was maintained at a moist condition until August 4, when all but the most vigorous shoot at each transplant site were removed. Throughout the growing season, the garden was hoed at roughly two week intervals to check the growth of weeds and any shoots of _S. dulcamara_ that encroached upon an adjacent plant were redirected to their own collar of wire mesh. The garden was tended in a similar fashion during my absence in 1983. In addition to the periodic hoeing, studies concerned with fruit production were initiated in 1984. Unfortunately, a severe hail storm in mid-August caused great damage to the plants and the information collected was of little use. The studies were repeated in 1985 (see subsequent chapters).Plate 2.5 depicts the common garden in early August of 1985.

Throughout the thesis four types of fruit will be referred to, and it is convenient to define them at this point. The first type included those at an early state of development. These were known as "unripe" fruits,

Plate 2.5. The common garden at the Labatt Field Station.



and this class included all fruits that were green and had a hard flesh. An arbitrary lower size limit of 5 mm in diameter was set to distinguish these fruits from flowers which had lost their petals but might have been inadequately fertilized or had failed to set fruit for other reasons. Preliminary examinations suggested that ovaries that had expanded to 5 mm or more did contain developing seeds and usually they continued to grow. Any bud, flower, etc., failing to reach the size limit was considered to be an abortion. The second developmental stage was distinguished by a change in colour from green to orange. These fruits were classified as "ripening", and often they were observed in this state at only one or two of the weekly observations. A further shift in colour and a marked change in the texture of the pulp were the hallmarks of "ripe" fruits. The colour change was from orange to red and the flesh became soft and juicy. The fourth stage of development that was recognized consisted of desiccated fruits. Commonly these were comprised of ripe fruits that had for some reason dried and withered on the infructescence, but in some other cases unripe or ripening fruits could suffer a similar fate. Plates 2.6 and 2.7 show fruits at each of these developmental stages.

Plate 26. Unripe (1), ripening (2) and ripe (3) fruits.

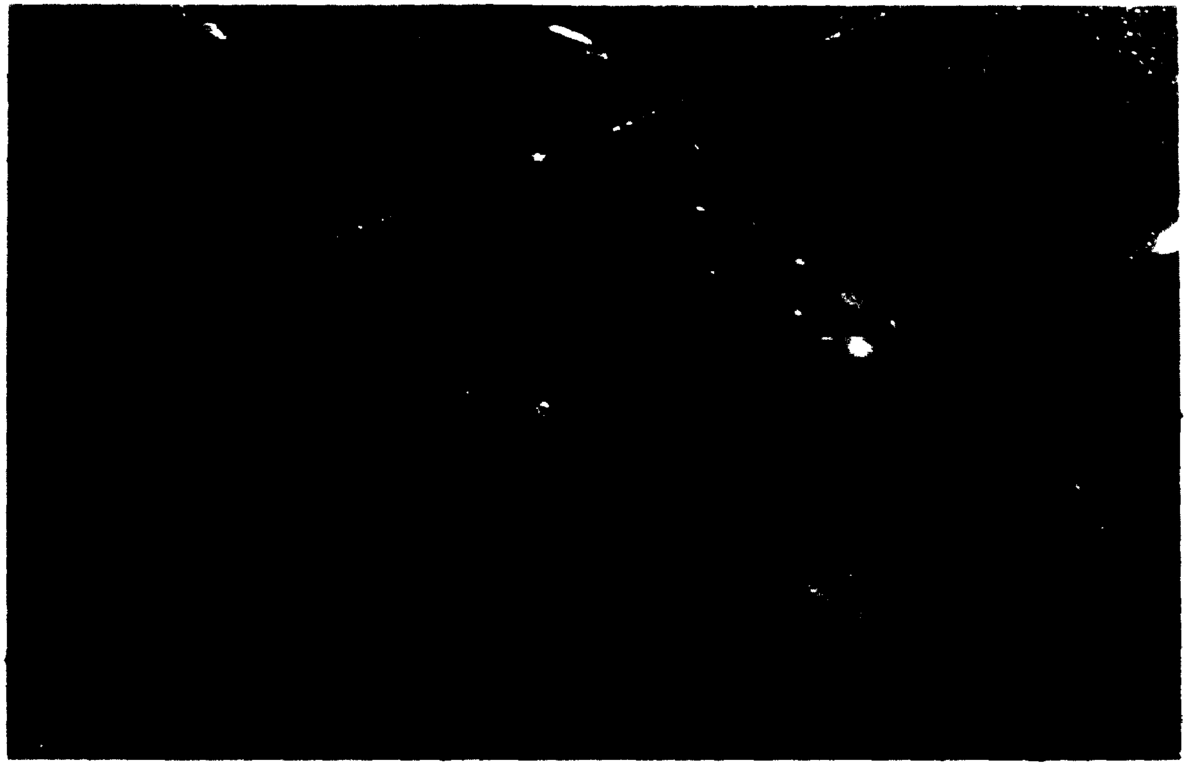
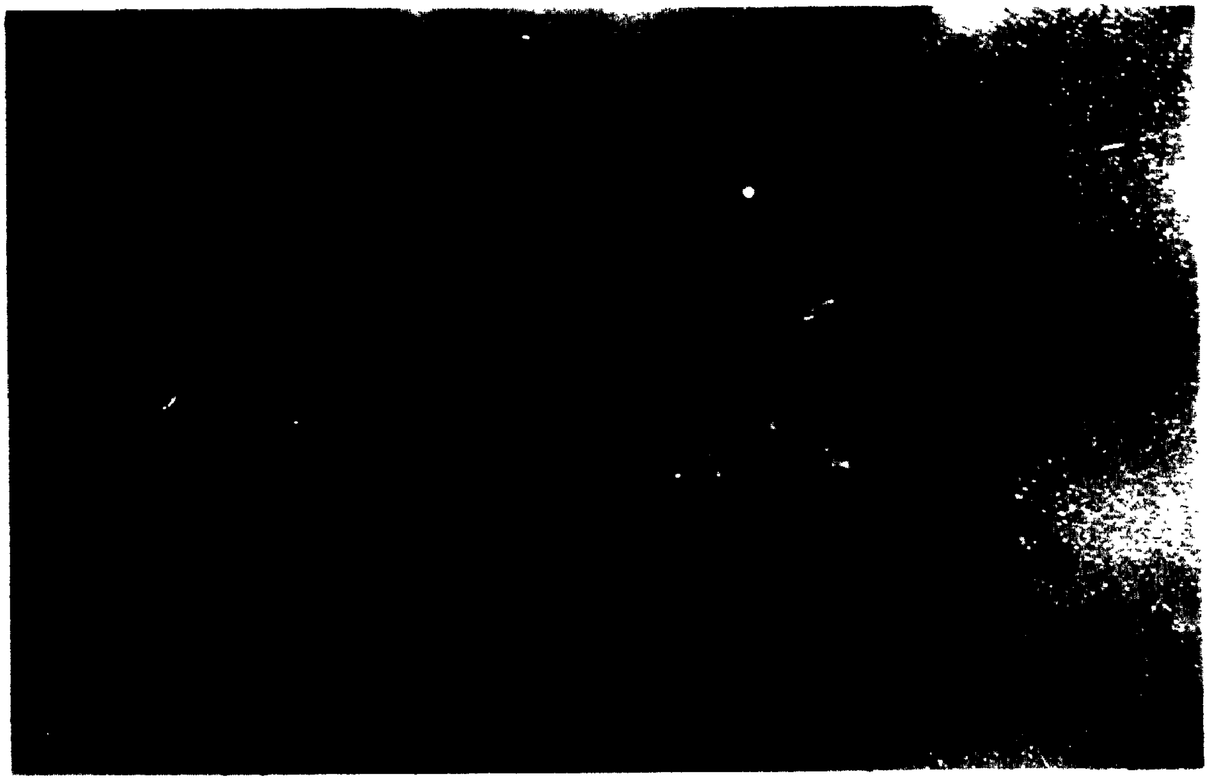


Plate 2.7. A desiccated fruit.



CHAPTER 3

THE ATTRIBUTES OF INDIVIDUAL FRUITS

3.1 Introduction

Variation in the attributes of fleshy propagules has been considered to have important implications for seed dispersal, particularly dispersal mediated by animals which consume the flesh and discard the seeds. In this chapter, studies are described that examined the attributes of the fleshy propagules produced by Solanum dulcamara in the four natural habitats and the common garden at an early and at a late point in the growing season of 1985. In order to place these patterns within the theoretical frameworks outlined in the introductory chapter, it is necessary to answer a number of interrelated questions:

> (1) Are there seasonal differences in the attributes of the propagules, particularly in terms of adjustments in the flesh versus seed component?
>
> (2) Are there habitat differences in propagule attributes?
>
> (3) Are seasonal and/or habitat differences expressed more strongly in the seed or fleshy component of the propagule?
>
> (4) Do differences in fruit attributes reflect plastic or genetic responses?
>
> (5) Are there differences in the morphologies of fruits at various stages of development that might influence potential dispersabilities?

3.2 Methods

On July 23, 1985, ripe, ripening and unripe fruits with their pedicels still attached were collected in the early morning from each of the field habitats described in Chapter 2. This process was repeated the following day for their common garden counterparts. At the field station and riverbank habitats, individual clusters of stems were selected at random from the entire array and, subsequently, an individual stem was selected randomly from within each cluster. In the marsh and swamp habitats, the stem nearest a point placed randomly within the tangles of stems was selected for fruit collection. From each selected stem, a maximum of three ripe, two ripening and two unripe fruits were collected, with no more than two fruits of a given ripeness coming from a single infructescence. This process was repeated until 30 ripe, 25 ripening and 25 unripe fruits had been harvested from each habitat. At the same time, 75 infructescenses bearing young fruit, but no flowers or buds, were selected throughout each site and tagged with a short length of yellow knitting yarn. Similarly, 75 inflorescenses bearing buds and, at most, a few flowers were tagged with blue yarn. During the second harvest, the yellow strands would identify infructescenses which had initiated fruit early in the season, and it was hoped that some would have retained sufficient fruit for harvest; the blue strands would identify infructescences with fruits initiated after the first harvest.. A similar program of fruit collection and tagging was conducted in the common garden. Ten of the fifteen plants established from cuttings taken from each natural habitat were selected at random and a single stem was randomly chosen from each of these. If insufficient numbers of fruits could be taken from the ten, additional plants were selected.

The second harvest from both the common garden and field populations was made on September 7 of the same year, following the same general procedures as in the first harvest. During this later harvest, the berries were collected from tagged infructescenses and an additional ripeness category was harvested, that of fruits formed and tagged early in the season (yellow yarn) which had not yet been removed from the plant. These were termed "persistent ripe fruit".

In the laboratory, during the same day of harvest, the fruits of each ripeness class were pooled by habitat and 20 ripe, 10 ripening and 10 unripe fruit were randomly selected for further analysis. To minimize loss of fluid, the pedicel was removed from each fruit just prior to measuring the maximum length and width with fine scale metal calipers. Each fruit was weighed and added to an individually labelled glass vial and placed in a drying oven at 80° C for 48 hours (as per Allen 1974), a point at which weights were stable. Upon removal from the oven, each vial was capped firmly and allowed to cool to room temperature and the fruit was then removed, weighed and returned to the vial. Sufficient distilled water to cover the fruit was added to the vial and the fruit was left to soak for three or four hours to allow the flesh to soften so that it could be removed from the seeds and discarded. Following their removal from the flesh, which comprised all non-seed material, the seeds were thoroughly rinsed to remove any remaining flesh, and the firmly filled "good" seeds were counted and separated from the soft, often discoloured and unfilled "bad" seeds which were also enumerated. Each lot of good seeds and each lot of bad seeds was wrapped individually in aluminum foil, placed in the vial and returned to the oven. After drying for 48 hours, the vials were cooled in a desiccator and the total weights of the good and bad seeds were then taken, as were the individual weights of all or up to a maximum of four randomly selected good seeds. From these data it was possible to calculate values for the following fruit attributes: 1). size (length plus width), 2). percent moisture content of the entire fruit, 3). flesh dry weight, 4). number of good seeds, 5). number of bad seeds, 6). mean weight of a good seed, 7). total weight of all seeds (seedload), 8). flesh-to-seed dry weight ratio. Subsequent analyses would involve these variables.

All data manipulations and analyses were conducted within the SAS (SAS 1985) statistical analysis framework. Factorial analyses of variance, using the habitat of collection and harvest date as factors, were conducted for the ripe fruits for each of the eight variables. In each case, the rejection probability was set at 0.05. Before examination of the main factors, the interactions, if significant, were examined for marked deviations. To meet the assumption of independence between the mean and variance, all percentage data were arcsine square root transformed prior to analysis and the counts of good and bad seeds were transformed by taking the square root of the count value plus one half (Steel and Torrie 1980). All subsequent comparisons were made with the Scheffé multiple contrast procedure. Separate analyses were performed on the data for ripe fruit from the common garden. To augment the univariate procedures, principal component analyses of the correlation matrices of the eight variables were performed on the mean values for the habitats and harvests.

Although unripe, ripening, and ripe fruits were collected at each harvest, it is likely that true developmental sequences were not represented, as ripe fruits of the early harvest, say, would have been unripe some weeks before and the unripe fruits of the same harvest would not have ripened until some later time. Thus, detailed comparisons of the impact of fruit development upon fruit attributes could be unwarranted. However, to provide some general indication of the differences due to ripeness, analyses of variance of the data pooled only in terms of ripeness were conducted for each of the natural and common garden data sets.

Sufficient numbers of persistent ripe fruit to warrant analysis could be collected only in the marsh, swamp and field station habitats during the second harvest. To gain insight into differences between these and the ripe fruits of the first and second harvests, analyses were performed on this smaller habitat subset.

3.3 Results

3.3.1 Ripe fruit

3.3.1.1. Field habitats

The major contribution to the differences in the attributes of the ripe fruit over the four natural populations seemed to arise primarily from the flesh rather than from the seed component of the fruit (Figure 3.1). There were significant habitat differences for fruit size, moisture content and flesh dry weight. In contrast, there were no significant habitat effects

Figure 3.1a. The attributes of ripe fruits from the natural habitats· seasonal and habitat patterns. A. Mean values (± one standard deviation) of size, moisture content, good and bad seed number.

* $p(F)<.05$ ** $p(F)<.01$ *** $p(F)<.001$

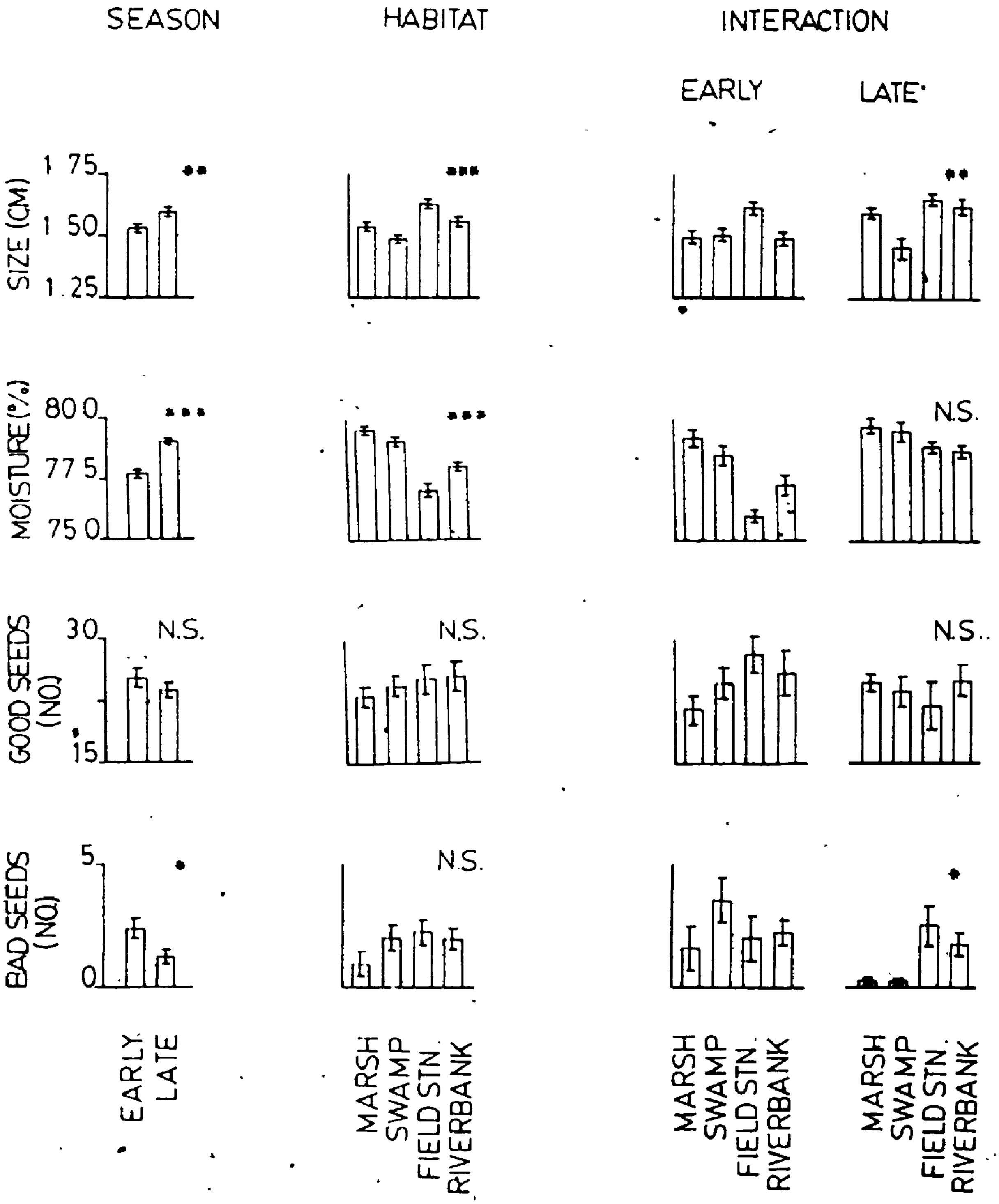
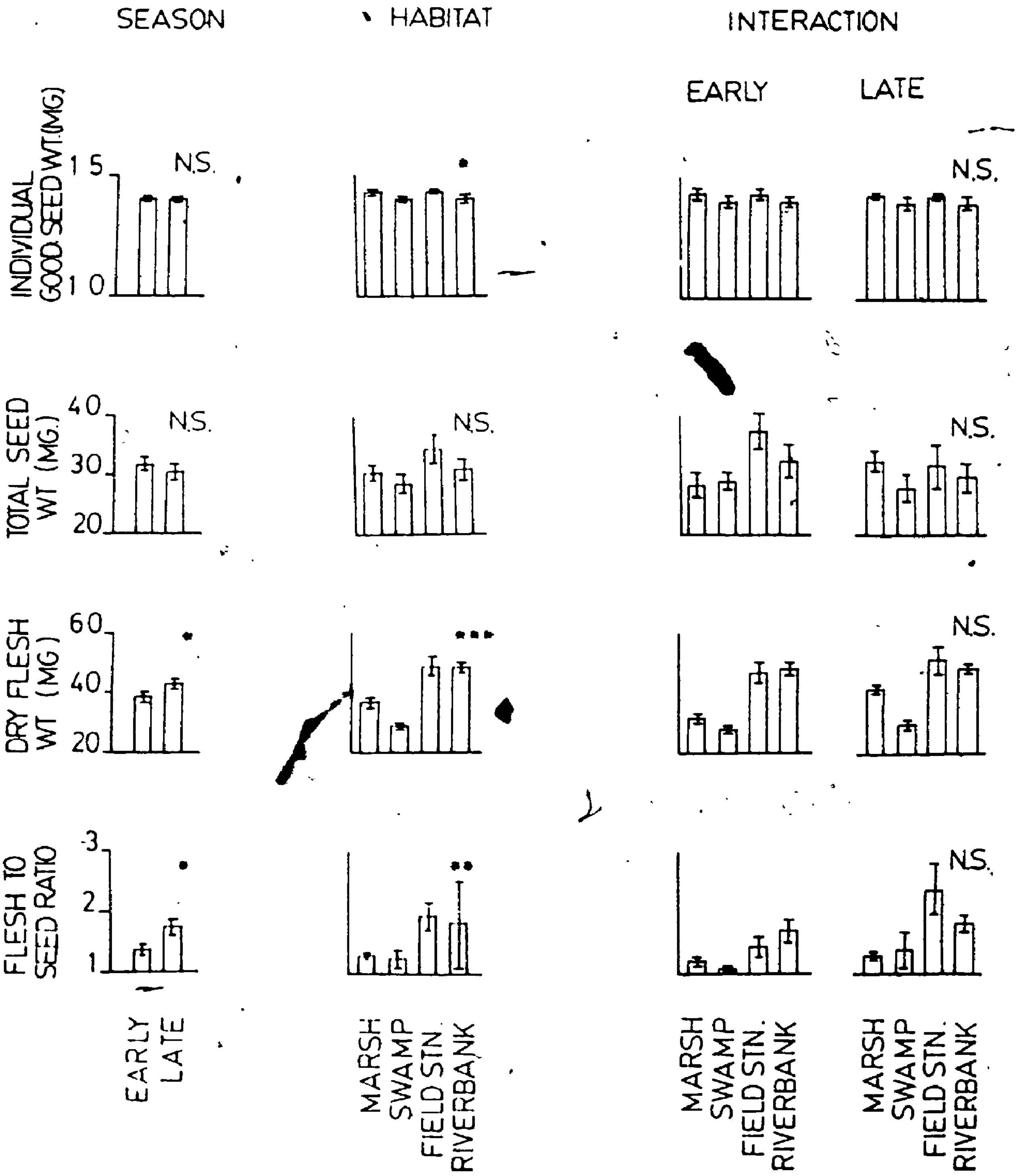

SEASON
HABITAT
INTERACTION
EARLY
LATE
SIZE (CM)
1.75
1.50
1.25
**
***
**
MOISTURE (%)
80.0
77.5
75.0
***
***
N.S.
GOOD SEEDS (NO)
30
15
N.S.
N.S.
N.S.
BAD SEEDS (NO)
5
0
*
N.S.
*
EARLY
LATE
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK

Figure 3.1b The attributes of ripe fruits from the natural habitats seasonal and habitat patterns. B. Mean values (± one standard deviation) of individual good seed weight, total seed weight, dry flesh weight, flesh to seed dry weight ratio.

* $p(F) < .05$ ** $p(F) < .01$ *** $p(F) < .001$


SEASON
HABITAT
INTERACTION
EARLY
LATE
INDIVIDUAL GOOD SEED WT.(MG)
1.5
1.0
N.S.
*
N.S.
TOTAL SEED WT (MG.)
40
30
20
N.S.
N.S.
N.S.
DRY FLESH WT (MG)
60
40
20
*
***
N.S.
FLESH TO SEED RATIO
3
2
1
*
**
N.S.
EARLY
LATE
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK

in the number of bad or good seeds or in total seed weight. Although there was a significant habitat effect for average good seed weight, there were no significant pairwise contrasts. Flesh-to-seed dry weight ratios were also significantly different across the habitats.

Most of the differences between the habitats were small. For example, the fruits from the field station habitat were larger ($\bar{X}$= 1.63 cm) than those from the two seasonally flooded habitats (marsh $\bar{X}$= 1.54cm ; swamp $\bar{X}$= 1.49 cm); fruits from the riverbank were intermediate in size ($\bar{X}$= 1.56 cm) and not significantly different from the values at any other habitat. Similarly, fruits from the marsh and swamp habitats contained slightly more moisture (marsh $\bar{X}$= 79.6%; swamp $\bar{X}$= 79.2%) than either the field station ($\bar{X}$= 77.0%) or riverbank ($\bar{X}$= 78.0%) habitats. Habitat effects were more pronounced, however, for dry flesh weights and the flesh-to-seed dry weight ratios. Both the field station and riverbank plants produced fruits with heavier flesh (field station $\bar{X}$= 49.1 mg; riverbank $\bar{X}$= 48.5 mg) than those of either the marsh ($\bar{X}$= 36.6 mg) or the swamp ($\bar{X}$= 28.9mg) habitats, and the flesh of the marsh habitat was heavier than its swamp counterpart. Flesh-to-seed dry weight ratios also varied considerably, with the mean being greater at the field station habitat ($\bar{X}$= 1.92) than at either of the seasonally flooded habitats (marsh $\bar{X}$= 1.27; swamp $\bar{X}$= 1.23); the mean of 1.82 for the riverbank habitat was not significantly different from that of any habitat.

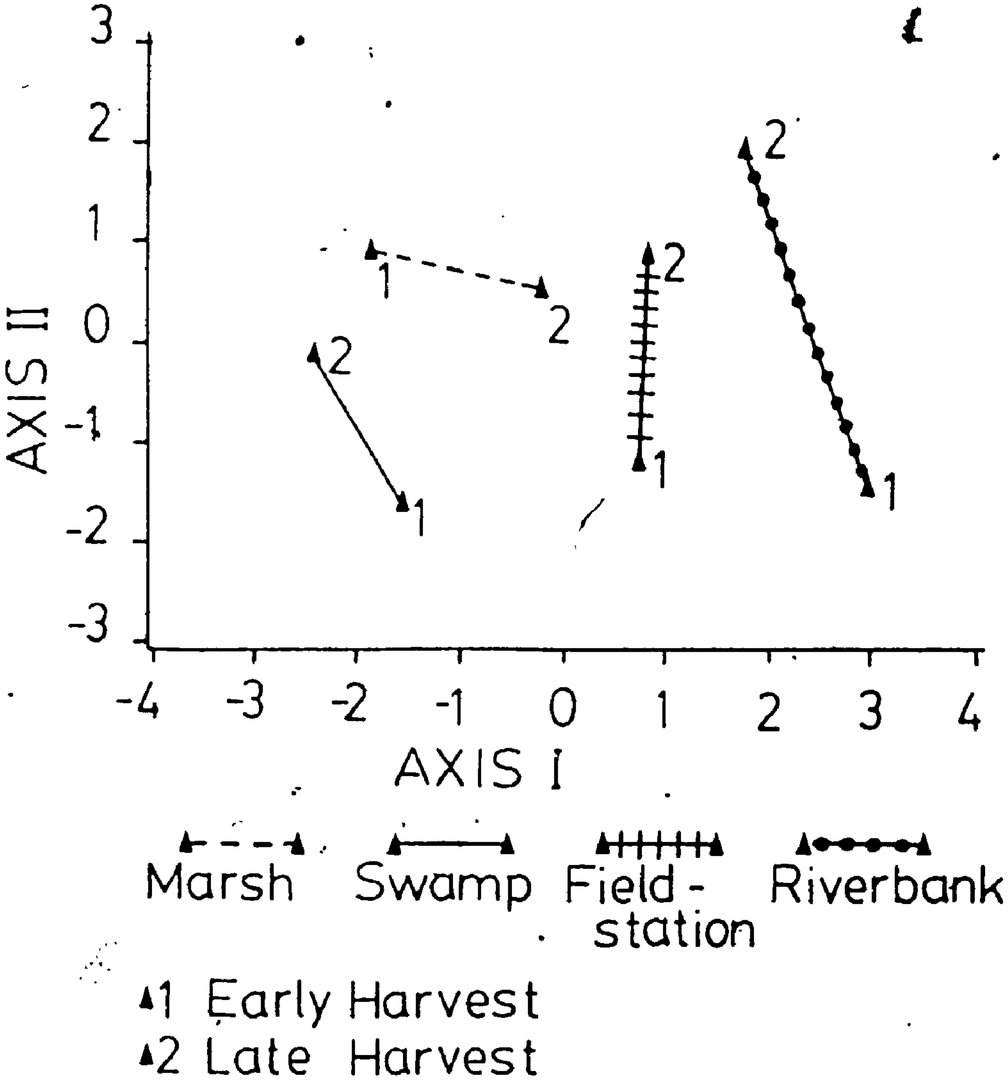
Harvest effects also seemed to be mostly attributable to the fleshy component of the ripe fruit (Figure 3.1). Fruits from the second harvest tended to be slightly but significantly larger (harvest 2 $\bar{X}$= 1.59 cm; harvest 1 $\bar{X}$= 1.53 cm), contain more water (harvest 2, $\bar{X}$= 79.1%; harvest 1, $\bar{X}$= 77.8%)

and have heavier dry flesh (harvest 2, $\bar{X}$= 42.9 mg; harvest 1, $\bar{X}$= 38.5 mg) than fruits from the first harvest. There were no significant harvest effects for the number of good seeds, average weight of a good seed or total seed weight; however, the fruits of the second harvest did have significantly fewer bad seeds than those of the first harvest ($\bar{X}$= 1.2 versus $\bar{X}$= 2.4). As with the habitat comparisons the flesh-to-seed dry weight ratios were quite different between harvests. That of the second harvest ($\bar{X}$= 1.75) was 1.28 times greater than that of the first ($\bar{X}$= 1.37), and again this might be primarily attributable to the flesh component.

There was a significant interaction between harvest date and habitat for only two of the variables that showed a significant main effect, these being propagule size and bad seed number. The values in three habitats showed small increases in propagule size in the second harvest, while the value at the swamp showed a slight decline. The habitat rankings at each harvest were, however, all consistent with the direction of the habitat effect. There was a small increase in the number of bad seeds confined in ripe fruits taken from the field station habitat from the first to second harvest, whereas the number of bad seeds in fruits from the other habitats showed consistent declines, with the effect perhaps being most pronounced for the swamp fruits.

The multivariate analysis of ripe fruit attributes supported the results of the univariate analyses. Figure 3.2, shows the projection of the habitats for each harvest upon the first two axes of a principal component analysis. The greatest habitat separation occurred on the first axis which accounted for 45% of the total variance. With increasing values along the first axis,

Figure 3.2 Principal component analysis of ripe fruit attributes. Projection of natural habitat and harvest on Axis I and Axis II. Component loadings: Axis I (45% of variation) -- size (.41), moisture (-.42), number of good seeds (.27), number of bad seeds (.13), individual good seed weight (.18), Flesh weight (.46), total seed weight (.45) and flesh-to-seed dry weight ratio (.31); Axis II (22% of variation) -- size (.30), moisture (.34), number of good seeds (-.56), number of bad seeds (-.24), individual good seed weight (.35), Flesh weight (.22), total seed weight (-.22) and flesh-to-seed dry weight ratio (.43)


AXIS II
3
2
1
0
-1
-2
-3
AXIS I
-4
-3
-2
-1
0
1
2
3
4
1
2
2
1
2
1
2
1
Marsh
Swamp
Field-station
Riverbank
▲1 Early Harvest
▲2 Late Harvest

the fruit tended to be fleshier, to have greater total seed weight, and to be drier, larger and to have higher flesh-to-seed weight ratios. The field station habitat scored highest on this axis, followed by the riverbank, the marsh and finally the swamp habitat. Aside from the case of the marsh habitat, most of the harvest effects were expressed on the second axis, which accounted for 22% of the variation. From the first to the second harvest, there was a trend towards increments in the flesh-to-seed dry weight ratio, average good seed weight, dryness and fruit size and decreasing numbers of good seeds.

3.3.1.2 Common Garden

Fewer significant habitat differences were identified amongst the ripe fruits taken from the common garden (Figure 3.3). There were no significant differences in the number of good or bad seed, fruit size, weight of a good seed, total seed weight or flesh-to-seed dry weight ratio. Slight differences in moisture content were identified, with the fruits from the riverside having more moisture than those from the marsh or swamp. The only other significant habitat effect was for flesh dry weight, when the fruits from the swamp plants had more flesh than those produced by the riverbank plants.

There was a significant effect of harvest date on ripe fruit attributes in the common garden (Figure 3.3). As with the fruit produced in the natural populations, those produced later in the season at the common garden contained slightly more water than those of the earlier harvest ($\bar{X}$= 78.8% versus $\bar{X}$= 77.7%). The size of the fruits differed slightly as well, with the

Figure 3.3a. The attributes of ripe fruits from the common garden: seasonal and habitat patterns. A. Mean values (± one standard deviation) of size, moisture content, good and bad seed number.

* p(F)<.05 ** p(F)<.01 *** p(F)<.001

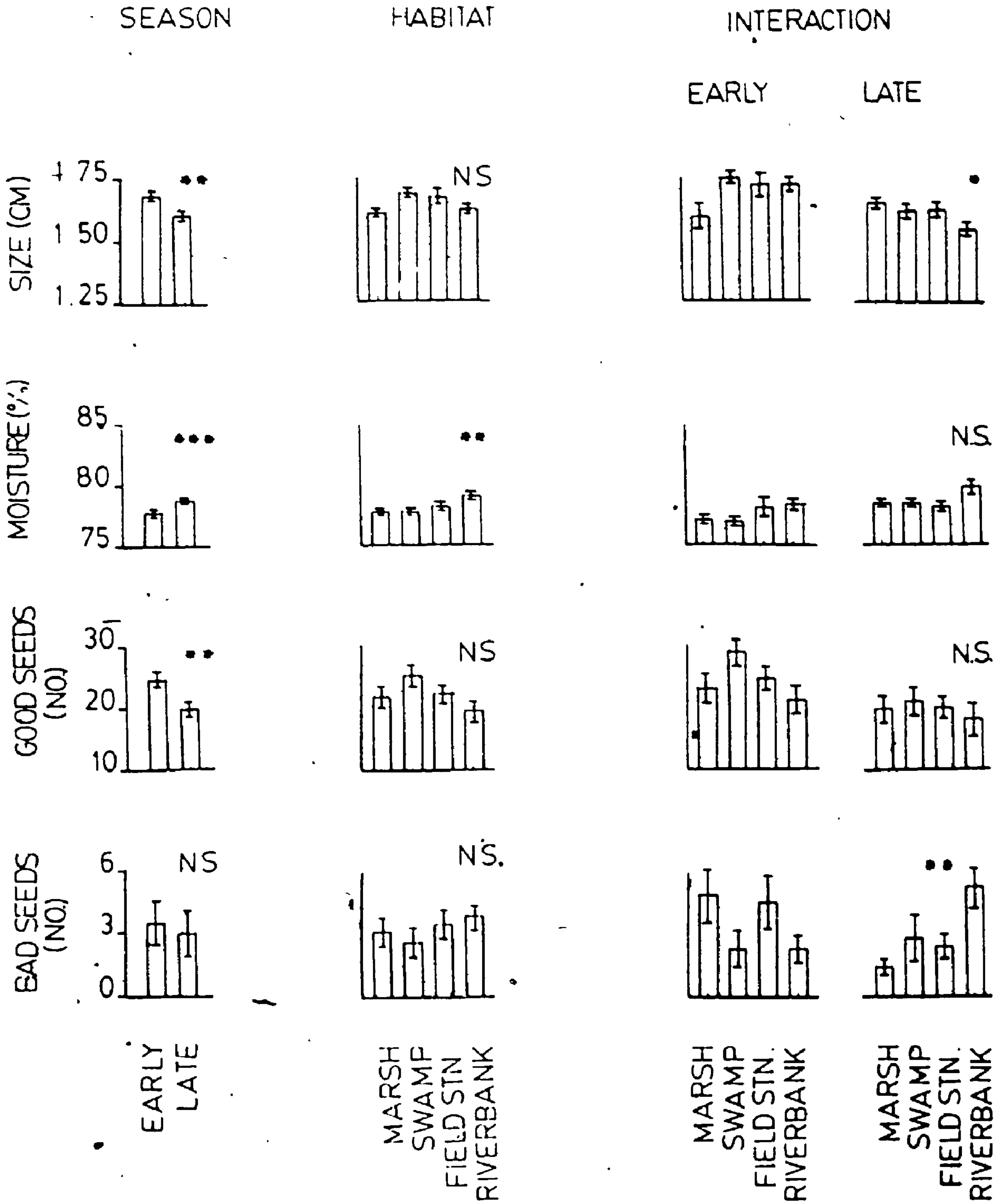
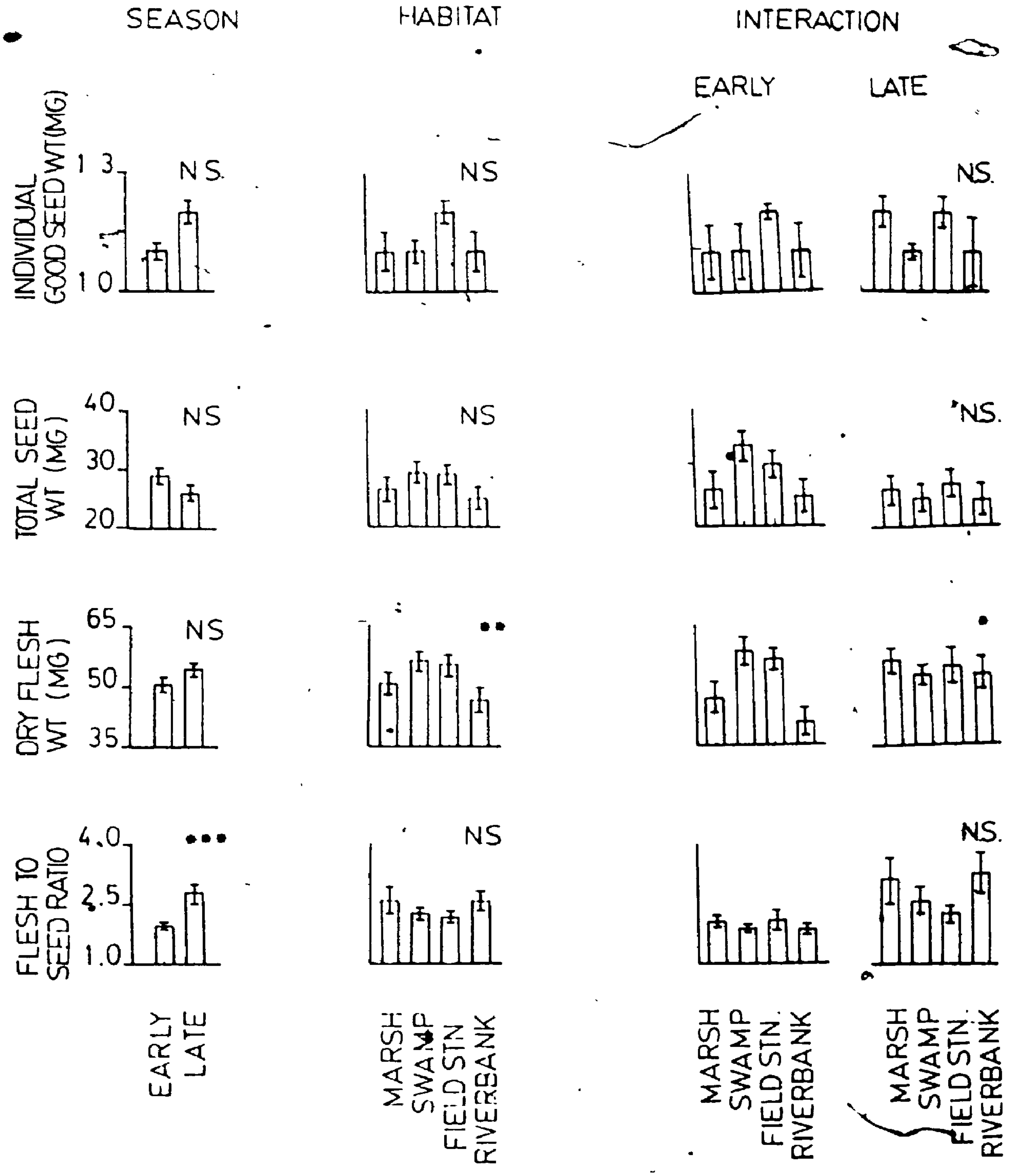

SEASON
HABITAT
INTERACTION
EARLY
LATE
SIZE (CM)
1.75
1.50
1.25
**
NS
*
MOISTURE (%)
85
80
75
***
**
N.S.
GOOD SEEDS (NO.)
30
20
10
**
NS
N.S.
BAD SEEDS (NO.)
6
3
0
NS
N.S.
**
EARLY
LATE
MARSH
SWAMP
FIELD STN
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK

Figure 3.3b The attributes of ripe fruits from the common garden: seasonal and habitat patterns. B. Mean values (± one standard deviation) of individual good seed weight, total seed weight, dry flesh weight, flesh to seed dry weight ratio.

* p(F)<.05 ** p(F)<.01 *** p(F)<.001

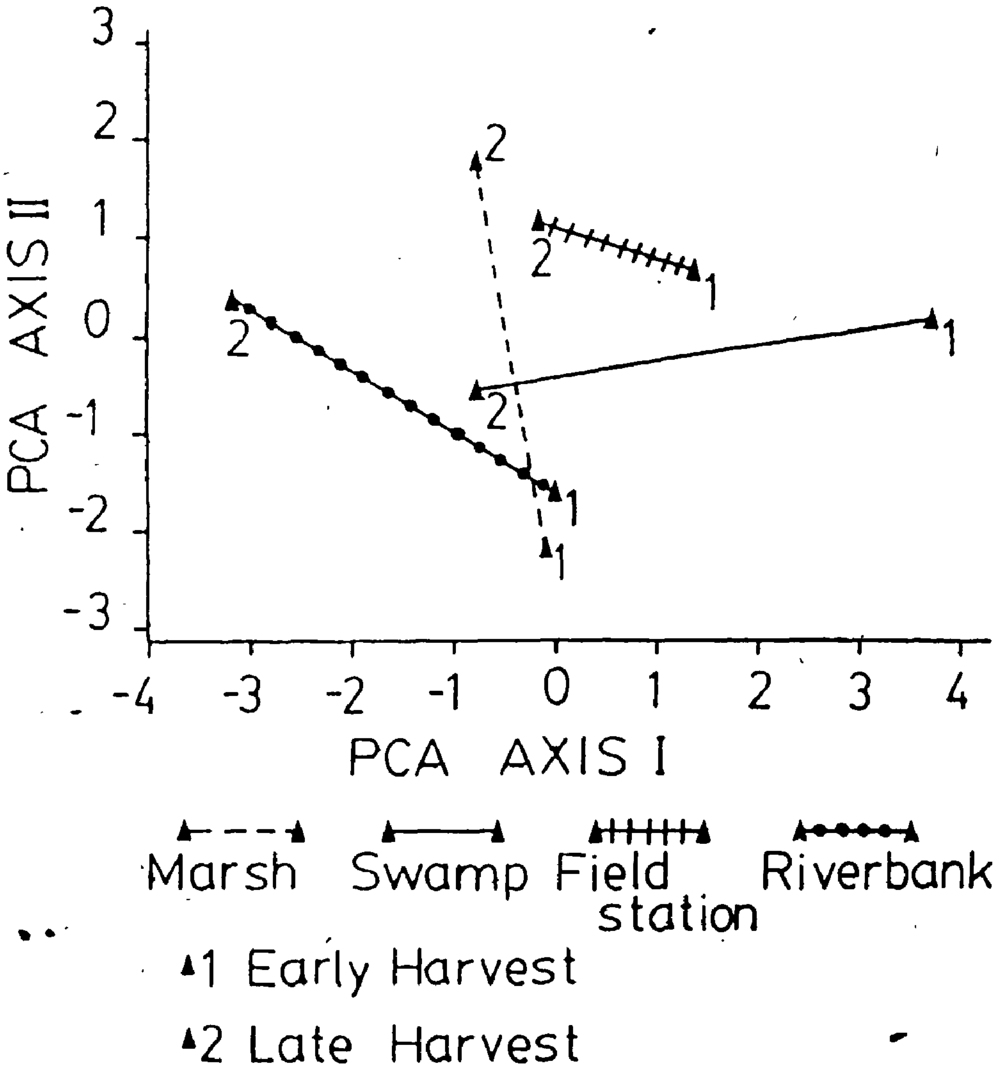

SEASON
HABITAT
INTERACTION
EARLY
LATE
INDIVIDUAL GOOD SEED WT (MG)
1.3
1.0
N.S.
NS
NS.
TOTAL SEED WT (MG)
40
30
20
NS
NS
NS.
DRY FLESH WT (MG)
65
50
35
NS
**
*
FLESH TO SEED RATIO
4.0
2.5
1.0
***
NS
NS.
EARLY
LATE
MARSH
SWAMP
FIELD STN
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK
MARSH
SWAMP
FIELD STN.
RIVERBANK

earlier fruits being somewhat larger than the later ones ($\bar{X}$= 1.69 cm versus $\bar{X}$= 1.61 cm). The later fruits also contained fewer good seeds ($\bar{X}$= 19.8 versus $\bar{X}$= 24.4) and had higher flesh-to-seed dry weight ratios ($\bar{X}$= 2.90 versus $\bar{X}$= 1.96).

The interaction components of the analyses proved significant for only two of the variables that showed a significant main effect (Figure 3.3). Three of the habitats showed the small decrease in propagule size in the second harvest, with only the fruits taken from the plants originating from the swamp habitat showing an absolute increase. Habitat rankings in terms of dry flesh weight seemed to be most strongly pronounced amongst the fruits from the early harvest.

Figure 3.4 shows the projection of the habitat representatives in the common garden for both harvests on the first two principal component axes. Habitat separations are at best weakly expressed on either axis. Both axes, rather, separated the harvest effects. The early harvest result for each of the habitat groups scored more highly on the first axis, which accounted for 50% of the total variation, and the trend towards larger, drier fruits with lower fruit-to-seed dry weight ratios and more good seeds at the first harvest was supported by the high component scores for these variables. The second axis accounted for 22% of the total variance, and, for the most part, the fruit from the second harvest scored more highly on this axis than their first harvest counterparts. Although the average weight of a good seed and dry flesh weight had high positive scores on this axis, they had not been significantly distinctive in the univariate analyses. The

Figure 3.4 Principal component analysis of the attributes of ripe fruits from the common garden. Projection of habitat of origin and harvest on Axis I and Axis II. <u>Component loadings</u>: Axis I (50% of variation) -- size (.43), moisture (-.42), number of good seeds (.46), number of bad seeds (-.17), individual good seed weight (.02), Flesh weight (.16), total seed weight (.45) and flesh-to-seed dry weight ratio (-.39); Axis II (24% of variation) -- size (.06), moisture (.25), number of good seeds (-.07), number of bad seeds (-.21), individual good seed weight (.61), Flesh weight (.58), total seed weight (-.21) and flesh-to-seed dry weight ratio (.33)


PCA AXIS II
3
2
1
0
-1
-2
-3
PCA AXIS I
-4
-3
-2
-1
0
1
2
3
4
2
2
1
2
1
2
1
1
1
Marsh
Swamp
Field station
Riverbank
▲1 Early Harvest
▲2 Late Harvest

flesh-to-seed dry weight ratio scored highly on this second axis as well, again echoing the trend towards higher ratios in the second harvest observed for fruits from the natural populations.

3.3.2 Persistent ripe fruit

The persistant ripe fruits, which could be collected only from the marsh, swamp and field station populations, differed little from the ripe fruits collected during the first and second harvests in the same habitats (Figure 3.5). They contained slightly less water ($\bar{X}$= 78.8%) than the ripe fruits of the second harvest ($\bar{X}$= 79.4%) and contained slightly more than those of the early collection ($\bar{X}$= 77.9%). The only other significant difference was between the flesh-to-seed dry weight ratio of the ripe fruits of the early ($\bar{X}$= 1.25) and late ($\bar{X}$= 1.70) harvests; the ratio for the persistant ripe fruits ($\bar{X}$= 1.29) was again intermediate but much closer to that of the early fruits.

3.3.3 Fruit development

The greatest separation amongst the unripe, ripening and ripe fruits collected from the natural habitats was between the ripe and unripe fruits (Figure 3.6); the values for ripening fruit were generally intermediate. Ripe ($\bar{X}$= 78.4%) and ripening ($\bar{X}$= 78.7%) fruits contained slightly less water than the unripe fruits ($\bar{X}$= 81%), and had fewer bad seeds (ripe $\bar{X}$= 1.8; ripening $\bar{X}$= 2.4; unripe $\bar{X}$= 4.9) and heavier good seeds (ripe $\bar{X}$= 1.2 mg; ripening $\bar{X}$= 1.2 mg; unripe $\bar{X}$= 1.1 mg). In contrast, the unripe fruits had a greater flesh-to-seed dry weight ratio ($\bar{X}$= 2.17) than the ripe fruits ($\bar{X}$= 1.56) but not the ripening fruits ($\bar{X}$= 1.67). The unripe ($\bar{X}$= 1.69 cm) and ripening ($\bar{X}$=1.64

Figure 3.5 Mean values (± one standard deviation) of attributes of early, late and persistent ripe fruits from the field habitats.

* p(F)<.05 ** p(F)<.01 *** p(F)<.001

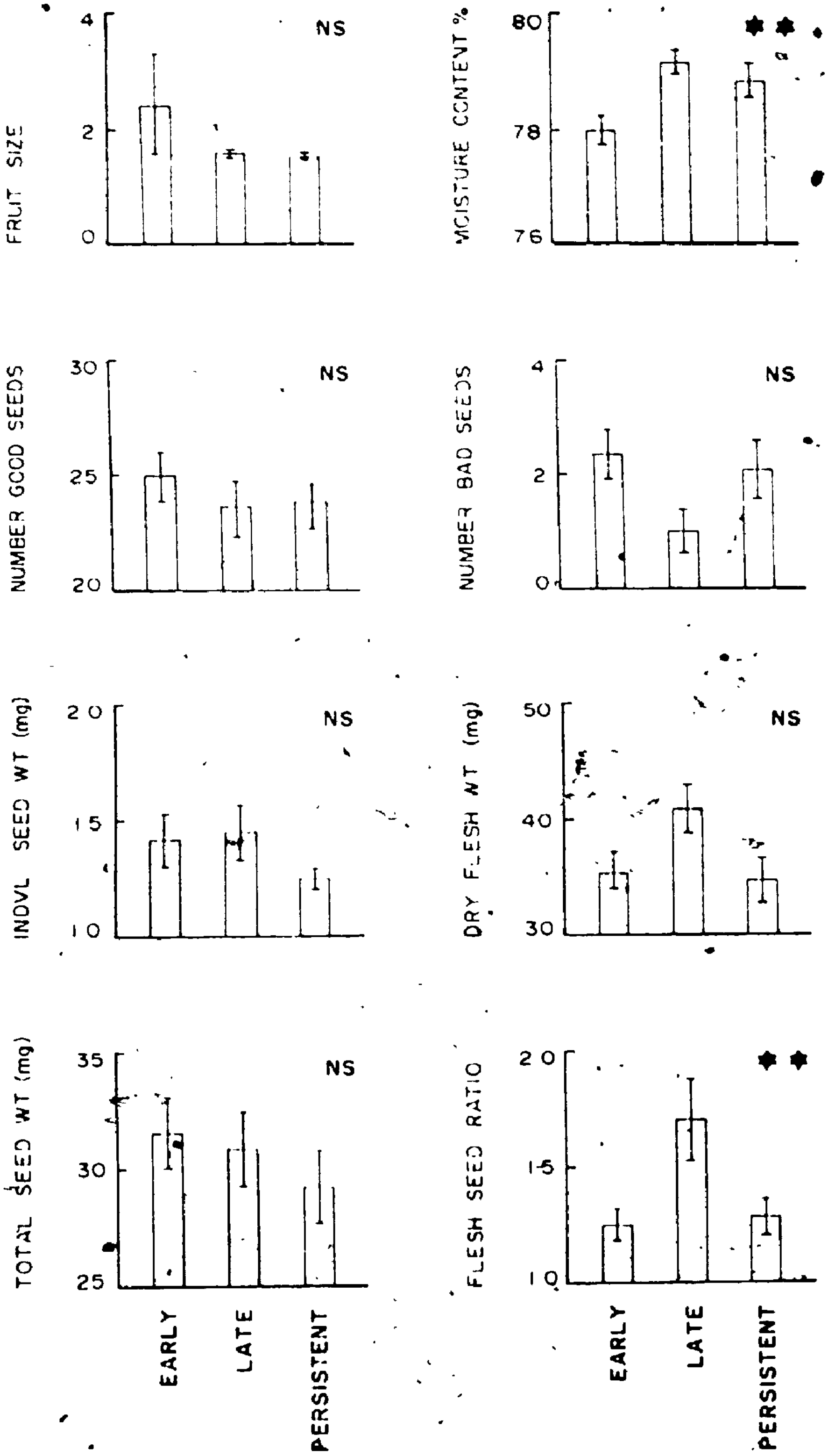
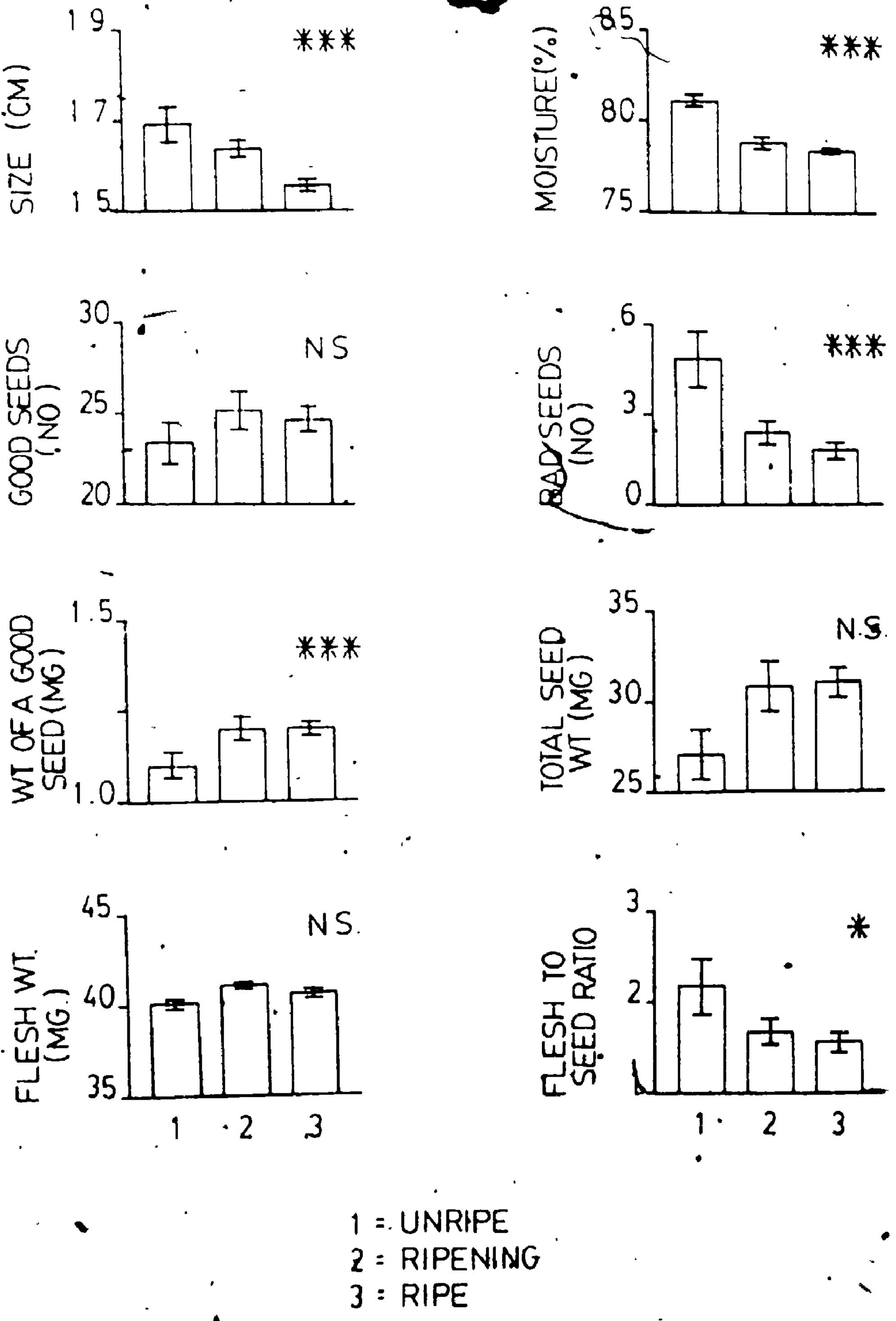

FRUIT SIZE
0
2
4
NS
MOISTURE CONTENT %
76
78
80
* *
NUMBER GOOD SEEDS
20
25
30
NS
NUMBER BAD SEEDS
0
2
4
NS
INDVL SEED WT (mg)
1 0
1 5
2 0
NS
DRY FLESH WT (mg)
30
40
50
NS
TOTAL SEED WT (mg)
25
30
35
NS
FLESH SEED RATIO
1 0
1 5
2 0
* *
EARLY
LATE
PERSISTENT
EARLY
LATE
PERSISTENT

Figure 3.6 Mean values (± one standard deviation) of attributes of unripe, ripening and ripe ~~fruits from~~ the field habitats.

* $p(F)<.05$ ** $p(F)<.01$ *** $p(F)<.001$

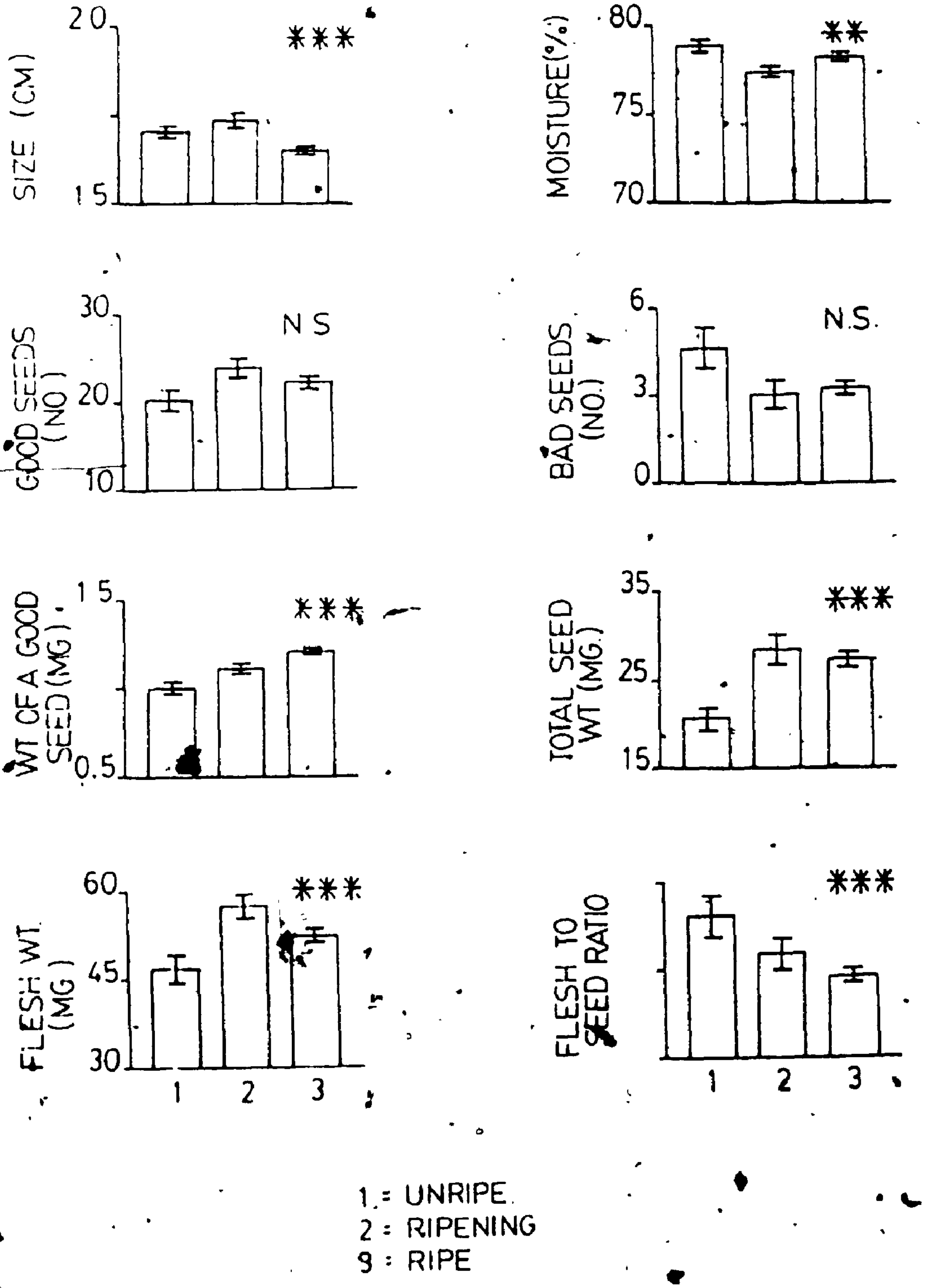

SIZE (CM)
1.9
1.7
1.5
***
MOISTURE(%)
85
80
75
***
GOOD SEEDS (NO)
30
25
20
NS
BAD SEEDS (NO)
6
3
0
***
WT OF A GOOD SEED (MG)
1.5
1.0
***
TOTAL SEED WT (MG)
35
30
25
N.S.
FLESH WT. (MG.)
45
40
35
N.S.
FLESH TO SEED RATIO
3
2
*
1
2
3
1
2
3
1 = UNRIPE
2 = RIPENING
3 = RIPE

cm) fruits were also slightly larger than the ripe fruits ($\bar{X}$=1.56 cm). It is not clear as to the factors promoted this difference in the ratio as there were no significant differences across the ripeness categories in terms of mean dry flesh weight (ripe $\bar{X}$= 40.7 mg; ripening 41.1 mg; unripe $\bar{X}$= 40.1 mg), total seed weight (ripe $\bar{X}$= 31.1 mg; ripening 30.9 mg; unripe $\bar{X}$= 27.1 mg) or the number of good seeds (ripe $\bar{X}$= 24.6; ripening 25.2; unripe $\bar{X}$= 23.4). However, given the greater number of bad seeds within an unripe fruit and the lower, but not significantly so, values for total seed weight and the number of good seeds, the high flesh-to-seed dry weight ratio for the unripe fruits might well be a reflection of the relative immaturity of their seeds and of the greater variability amongst the fruits in this category.

As with those collected in the natural habitats, ripe fruits taken from the common garden (Figure 3.7) were not as large ($\bar{X}$= 1.65) as the ripening ($\bar{X}$= 1.73 cm) and unripe ($\bar{X}$= 1.72 cm) fruits. In addition, they were not significantly drier ($\bar{X}$= 78.2%) than the unripe fruits ($\bar{X}$= 78.9%), as were the ripening fruits ($\bar{X}$= 77.3%). There were no significant ripeness effects for the number of good seeds (ripe $\bar{X}$= 22.1; ripening $\bar{X}$= 23.7; unripe $\bar{X}$=20.3) or bad seeds (ripe $\bar{X}$= 3.2; ripening $\bar{X}$= 3.0; unripe $\bar{X}$= 4.6), but both the ripe and ripening fruits had heavier individual good seed weights (ripe $\bar{X}$= 1.1 mg; ripening $\bar{X}$= 1.1 mg) and heavier total seed weights (ripe $\bar{X}$= 27.2 mg; ripening $\bar{X}$= 28.3 mg) than the unripe fruit (good seed weight $\bar{X}$= 1.0 mg; seed load $\bar{X}$=.20.1 mg). The mean flesh dry weight of the ripe fruits ($\bar{X}$= 52.3 mg) was not significantly different from that of the unripe fruits ($\bar{X}$= 47.0 mg) as was that of the ripening fruits ($\bar{X}$= 57.6 mg). Again, paralleling the pattern of the natural populations, the unripe fruits had a mean flesh-

Figure 3.7 Mean values (± one standard deviation) of attributes of unripe, ripening and ripe fruits from the common garden.

* $p(F) < .05$ ** $p(F) < .01$ *** $p(F) < .001$


SIZE (CM)
20
15
***
MOISTURE(%)
80
75
70
**
GOOD SEEDS (NO.)
30
20
10
N S
BAD SEEDS (NO.)
6
3
0
N.S.
WT OF A GOOD SEED (MG.)
1.5
0.5
***
TOTAL SEED WT (MG.)
35
25
15
***
FLESH WT. (MG.)
60
45
30
***
FLESH TO SEED RATIO
***
1
2
3
1
2
3
1 = UNRIPE
2 = RIPENING
3 = RIPE

to-seed dry weight ratio ($\bar{X}$= 3.45) greater than that of the ripe fruits ($\bar{X}$= 2.37) but not greater than that of the ripening fruits ($\bar{X}$= 2.73). Here, the evidence strongly suggests that the higher flesh-to-seed dry weight ratio of the unripe fruits arose largely as a result of lighter good seeds and lower total seed weight of the unripe fruits.

3.4 Discussion

3.4.1 Question 1. Are there seasonal shifts in the attributes of ripe propagules, particularly in flesh to seed trade-offs?

There were seasonal differences in the make-up of individual ripe fruits borne by S. dulcamara. Paricularly striking was the increase in the amount of flesh relative to the seeds. Flesh-to-seed dry weight ratios increased by a factor of 1.3 from early to late fruits in the natural habitats, and by a factor of 1.5 in the common garden. Thus, the later propagules might offer a greater relative reward, at least in the quantitative sense, which, in some views, represents a major cue to the food choices of animals (Piper 1986b, Johnsen at al. 1985). This trend towards a potentialy more rewarding flesh later in the year conforms to the claims of Herrera (1984b), Snow (1971), and to some extent, Stiles (1980 -- fall high quality fruits) for species bearing ripe fleshy propagules late in the season. In their views a more rewarding flesh later in the year might be an advantage in attracting the attention of wayward flocks of migrant birds (Willson and Melampy 1983, Herrera 1982a, Stapanian 1982b), especially if faced with possible competition from the bulk of species' that ripen fleshy propagules at this time (Stapanian 1986, Herrera 1984b, 1982a, 1982b, Stiles 1980, Thompson and Willson 1979, Morton 1973, Snow 1971).

However, Johnson *et al.* (1985) found little seasonal variation in the propagules produced by the set of species they examined, and Stapanian (1982) claimed that a contrary trend would be expected. In Stapanian's view, the more rewarding flesh, in a relative sense, would be produced earlier in the season in order to attract dispersal animals away from the abundant and preferred invertebrate prey. Stapanian claimed that an additional consequence of the relatively more rewarding flesh of early propagules was that it would be particularly prone to damage by insects and decay if not taken quickly. This last observation may also not apply to *Solanum dulcamara* as the fruits did not seem particularly prone to damage by insects or decay organisms, and ripe fruits may remain attached for considerable periods of time (pers obs), so it may not be so crucial that they be especially attractive early in the season.

3.4.2 *Question 2*. *Are there habitat differences in fruit attributes?*

The make-up of the ripe fruits varied amongst the ripe fruits produced in the four natural populations. While most of the differences were small, some were rather pronounced, especially the dry flesh weights and fruit-to-seed dry weight ratios. Flesh dry weights were lowest for the ripe fruits produced in the seasonally flooded and heavily shaded swamp habitat where growth of *S. dulcamara* appeared less vigorous (pers. obs.). The ripe fruits in this environment yielded dry flesh weights only about 59% of those in the field station or riverside habitats, and about 78% of those for the ripe fruit in the more stongly illuminated marsh. Similarly, the mean flesh-to-seed dry weight ratios were less in the marsh and swamp, being approximately 66% of the mean value for the field station fruits. they were not significantly less than the mean value at the riverside, although being only about 69% as great.

3.4.3 Question 3. Are seasonal and habitat differences expressed more strongly in the seed or fleshy component?

Most of the differences identified between the fruits of the two harvests from the natural populations seemed attributable to the fleshy rather than seed component of the propagule. The ripe fruits from the second harvest had higher flesh-to-seed dry weight ratios, were a bit larger and had more flesh, despite the propagules containing slightly more water. The only difference amongst the variables concerning the seeds alone was the small increase in the number of bad seeds contained in the later fruits. The contributions of the flesh and seed components to the differences observed between the harvests at the common garden was less clear cut. There, the fruits available during the second harvest were slightly smaller, contained more water and had fewer good seeds. Although the flesh-to-seed dry weight ratio was also higher in the second harvest, there were no significant differences in flesh dry weight, total seed weight, or the weight of anindividual good seed. Here, as in the four field habitats, the differences in fruit make-up observed across the habitats seemed also to be primarily restricted to the flesh.

If adjustments leading to increased fruit-to-seed dry weight ratios indeed rest primarily with the flesh component, the reward offered by the propagule might be enhanced, as the fleshy component might best indicate the absolute reward offerred by the propagule and be the feature upon which birds focus directly (Johnson et al. 1985, Piper 1986b). This enhancement might not accrue through adjustments in the seeds alone, as reduction in their size or numbers might merely make the propagule seem smaller. In addition, adjustments to the flesh rather than to the seeds might have less reproductive impact, as the seeds must yet run the ecological gauntlet of seed survival, germination and seedling establishment and their attributes may be additionally tuned in these respects. In poor environments where the productivity of a species is limited (as could be the case in the swamp and marsh), it might be an advantage to sacrifice some of the reward offerred by the flesh rather than reduce the seed load, as the seed load might still be dispersed by other means or by animals when the propagules finally become attractive.

While suggestive, these results reflect collections made at two harvest dates in a single year only. However, the persistant ripe fruits that may have been inititated at an intermediate period of the season possesed values for most variables that were intermediate to those of the early or late fruits. In addition, the harvest adjustments observed in the common garden further suggest that the relative contribution of the flesh component may not be clear cut. Nevertheless, the contribution of the flesh to morphological adjustments of individual fruits of S. dulcamara was substantial and an alternative to the adjustments in fruit morphologies principally arising through shifts in seed size and numbers described in other intraspecific studies (Herrera 1981a, Jordano 1982, Howe and Vande Kerckhove 1981 1980 1979).

3.4.4 Question 4. Do differences in fruit attributes reflect plastic or biotypic response?

The attributes of the ripe fruits produced in the broad suite of environments embraced by the natural populations were more variable than those produced in the common garden. For the fruits from the field populations there were significant habitat effects for five variables (fruit size, moisture content, flesh dry weight and flesh-to-seed dry weight ratios), while in the common garden there were significant effects attributable to source location of the original cuttings for only two (moisture content and flesh dry weight). Over the five habitat effects for the field populations there were fourteen significant pairwise contrasts, whilst in the common garden there were only three. If the comparison is limited to moisture content and flesh dry weight, for which significant habitat effects were observed in both the natural and common garden settings, there were ten significant pairwise contrasts in the former and three in the latter. Given the greater similarity amongst the habitat representatives in the common garden, the differences observed amongst the field populations are probably linked to phenotypic plasticity rather than to major genetic differences.

3.4.5 Question 5. What are the differences in the attributes of fruits at various stages of development?

Some of the differences in the attributes of the fruits at different stages of development were obvious, like the shift in colour from the green of the unripe fruits through the orange of the ripening to the red of the ripe fruits, or the shift in texture from the hard flesh of the unripe and ripening flesh to the soft, rather juicy flesh of the ripe fruits. But even in terms of the attributes measured in this study there were differences, especially between the ripe and unripe fruits; with the values for the ripening fruits for the most part being intermediate. Understandably, the individual unripe fruits were the most variable, since much growth in bulk occurs over the period that the fruits are green. The seeds at this unripe stage are probably the least developed, given the tendency for these fruits to contain fewer and lighter good seeds; and it may be this immaturity which promotes the greater flesh-to-seed dry weight ratios of the unripe fruits. It would not be prudent to interpret the effects of developmental stage observed here at more than a generalized level, since the berries do not represent genuine ripening sequences. For instance, the ripe fruits taken at the first harvest were unripe some weeks earlier, whilst the unripe fruits taken at the same harvest would not ripen until some weeks later. In addition, only ripe fruit were observed to have been consumed by birds. Thus, other factors, such as the shifts in texture and colour, or the drop in alkaloid levels described by Mathe <u>et al.</u> (1975), or the chemical alterations of the type typical of many fruit ripening sequences (Herrera 1982b Stiles 1980, Thompson and Willson 1979, Janzen 1977, Sherbourne 1972) might be more important in understanding the implications of the stages of propagule development to dispersal.

CHAPTER FOUR

PATTERNS OF FRUIT PRODUCTION AND DISPERSAL

4.1 Introduction

In Chapter 3, the make-up of individual propagules of Solanum dulcamara was found to be influenced by developmental stage and the season and habitat in which they were initiated. In this chapter, the variation amongst the fruits forms a backdrop to studies designed to investigate the spatial and temporal patterns of production, development and loss of individual fruits. As in Chapter Three, seasonal and habitat effects are important, but as the studies were conducted over two years some aspects of the annual pattern can also be addressed. In order to place the patterns of fruit production, development and loss into the theoretical perspectives outlined in the introductory chapter, answers to the following questions were sought:

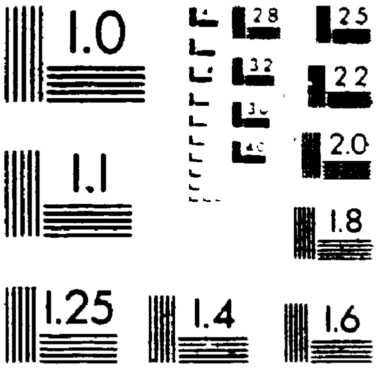
1. Are buds formed earlier in the season more likely to produce fruits than those formed later in the same year?
2. Do early fruits ripen and/or disperse more slowly than later fruits?
3. Are fruits at different stages of development equally likely to disperse, and do they disperse at the same rate.?
4. Do the patterns of development and dispersal of fruits differ across the habitats?
5. Do the patterns of production and dispersal change from year to year?

4.2 Methods

The phenological progression from bud to fruit to dispersal was monitored weekly on sets of ten inflorescences chosen in each habitat at one early and one late date in the growing seasons of 1982 and 1985. The selection of the early inflorescences, amongst the first formed in the season, was made when their numbers were sufficient to permit some choice amongst them. No inflorescences were selected that had produced fruits or had more than two actual blossoms. In 1982 the early selection was made in the last week of June, and in 1985 the first selection was made three weeks earlier. The later inflorescences were selected in the last week of July in 1982 and the first week in August in 1985. Earlier observations had indicated that inflorescences in the bud stage at this time of year were amongst the last formed in any sizable number that were still capable of producing ripe fruits. The weekly record of each bud/fruit was made until the first week of November in 1982 and the second week of November in 1985. At these later dates most of the stems were defoliated and had been exposed to a hard frost. Any fruits, buds, etc., still retained by the plant had shown little in the way of change for several weeks.

The inflorescences were selected at each point in the season in the following manner. At both the riverbank and the field station where Solanum dulcamara was distributed in widely spaced clusters of stems, ten clusters were selected randomly from the total number, and a single stem was chosen randomly from amongst those in the selected cluster until one bearing a suitable inflorescence was obtained. If more than one suitable inflorescence was borne by the selected stem the one closest to the bottom

2



of the stem was chosen. At the marsh and swamp habitats where the stems of S. dulcamara were not distributed as discrete clumps, five transects that traversed each habitat at eight metre intervals were laid down, and two points separated by at least a metre were selected randomly along each. At each point the closest suitable inflorescence within three metres was chosen. If necessary, additional points were selected until all ten separate inflorescences had been chosen.

Each bud was observed weekly. As they grew to a size where they could be marked without damage, coloured thread was tied around the pedicel of each to serve as identification. Eventually all buds that produced blossoms were marked. The lengths of thread were clipped short and essentially hidden by the open corollas, so it is unlikely that the threads interfered with pollination or strongly influenced the visual impact of the fruits as they ripened from green through orange to red.

At each time of recording, the phenological progress from bud to flower, etc., was noted, and the fruits were classified as unripe, ripening, ripe and desiccated. The week in which each marked fruit was lost from the infructescence was also recorded. These were considered as dispersed fruit. In order to get an indication of the numbers of inflorescences that might be produced by a stem in a growing season, 15 stems were selected in each habitat in the last week of August, 1985. The stems were selected following the general procedures used in choosing those for the marking of the individual buds, except for the requirement that they have an inflorescence. For these stems all inflorescences, regardless of their stage of development were counted.

From the phenological data it was possible to determine the fate of each bud -- whether it had produced a fruit, ripened, dispersed, etc. -- and the number of weeks that fruits remained in a particular state. The weekly monitoring was adequate to record the main temporal patterns, as most fruits took several weeks to change state.

The proportion of buds or fruits that realized particular fates was determined for each of the ten inflorescences selected at the beginning of each period of monitoring. For example, the proportion of unripe fruits to disperse was defined as the number of unripe fruits that dispersed divided by the total number of fruits that reached this ripening stage. For buds the transition of interest was the production of fruits, here called fruit set. For unripe fruits the proportions and numbers to disperse, desiccate, ripen further, or remain as unripe were of interest; for ripening fruits the interest was upon the proportions and numbers to disperse, desiccate, ripen or remain attached as unripe fruits; for ripe fruits the possible fates were dispersal, retention or desiccation; and desiccated fruits were either dispersed or retained until the end of the monitoring. The proportion of fruits to disperse regardless of ripeness was also calculated as the numbers of dispersant fruits produced by an inflorescence divided by the total numbers of fruits produced. In terms of temporal trends the number of weeks taken for a fruit to first be recorded as ripe -- ripening rate -- was determined, as was the retention period of those fruits dispersed when unripe, ripening, ripe or desiccated.

All factorial analyses of variance were conducted within the framework of the general linear models procedure of the SAS statistical package (SAS 1985). For the most part, the main factors were year (1982, 1985), season (early, late) and habitat (marsh, swamp, field station, and riverbank). Because of differences in the numbers of buds monitored and the varying patterns and rates of development, the designs were sometimes unbalanced, and in a few cases a cell contained no record. In all analyses the critical probability was 0.05 and the model sum of squares was partitioned with the type III option of the package. This model was chosen because the partitioning is not order dependent in the unbalanced case, and because the main effects are adjusted for their interactions, an aspect considered by Freund and Little (1981) to be useful when main effects are of importance even in the presence of interactions. In the cases where a cell was empty the type IV sum of squares option was examined, but rarely were there differences between the two in terms of rejection or acceptance of hypotheses. Subsequent pairwise contrasts within the main factors followed the Scheffé option, and again the critical probability was 0.05. All proportional data were transformed by the arcsine square root of the values and the integer data was transformed as the square root of the count plus 0.5, both transformations suggested by Steel and Torrie (1980).

4.3 Results

4.3.1 The fates of buds and fruits

The flow diagram presented in Figure 4.1 represents an overall summary of the fates of all the buds and, ultimately, fruits identified at both the early and late dates in the growing season and monitored weekly in the four field habitats in 1982 and 1985. At all branch points the width of each branch corresponds to the percentage (values in parentheses) of individuals reaching the branch point to realize a particular fate. For example, a mean of 49.6% of the 1774 monitored buds set fruit, that is, flowered, lost their petals and showed an increase in the width of their ovaries to 5 mm or more. Of the unripe fruits a mean of 28.6% were lost from the infructescences without being recorded at a more mature stage of development. Most of the unripe fruits ($\bar{X}$= 68.7%) matured to the ripening stage, marked by the shift in colour of the still firm flesh from green to orange, but a small fraction withered and dried on the infructescence and were classified as desiccated. Other than suggesting changes observed from the bud stage to the termination of the monitoring, there is no temporal component to the figure; spatial separation is meant for clarity only. Temporal changes are the subject of a later section of this chapter.

The overall summary is then subdivided into classifications showing the pattern for each of the two study years (Figure 4.2), the seasonal differences (Figure 4.3), and the pattern amongst the four habitats (Figure

Figure 4.1. Overall summary of fruit development and dispersal fates.

(percentage value)

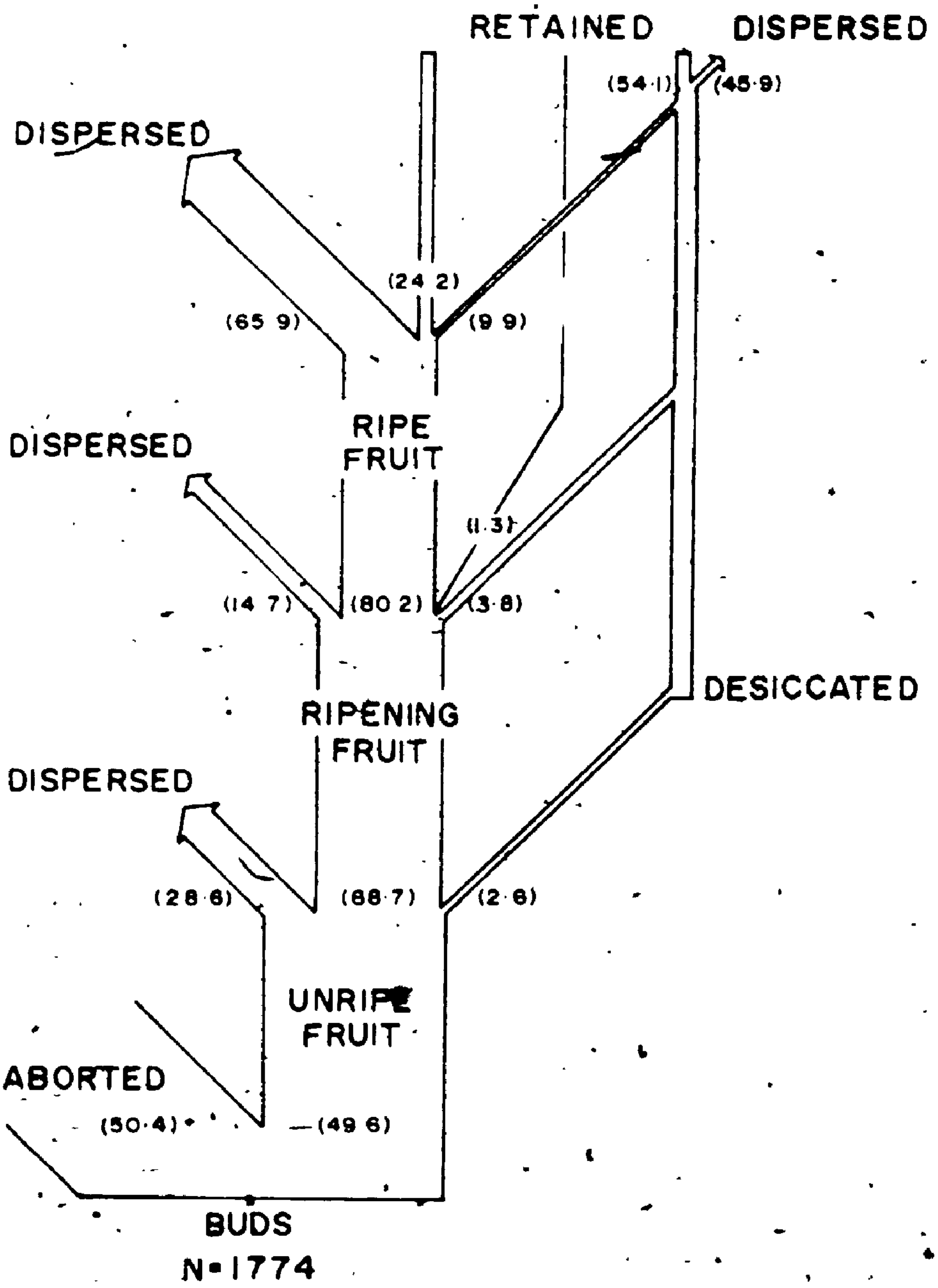
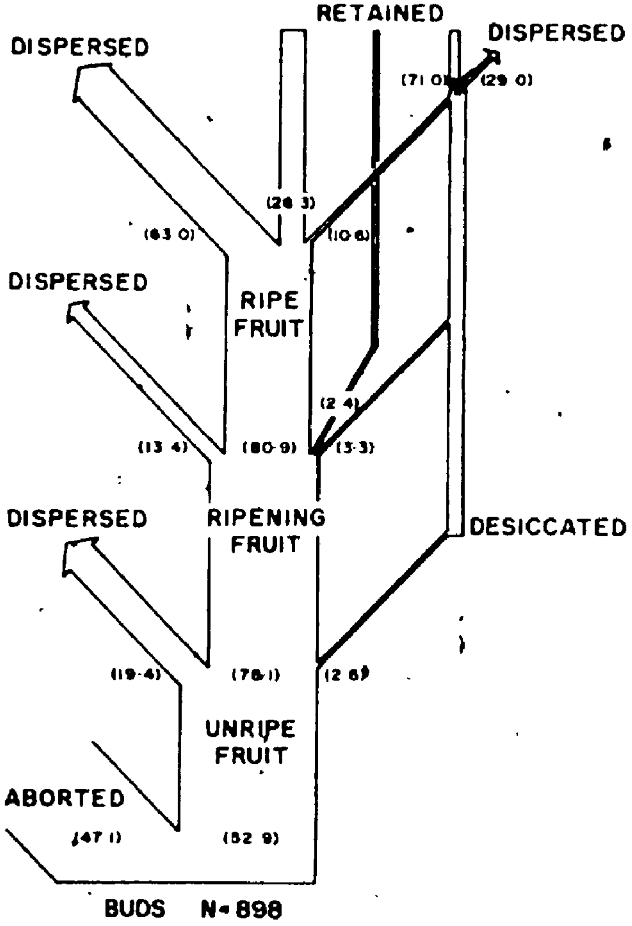
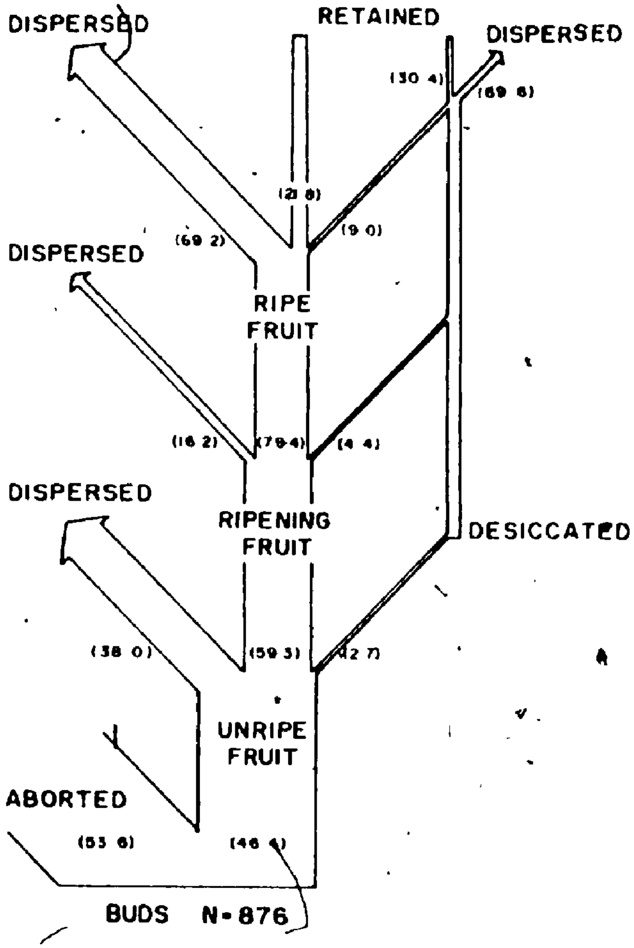

RETAINED
DISPERSED
(54·1)
(45·9)
DISPERSED
(24·2)
(65·9)
(9·9)
RIPE FRUIT
DISPERSED
(1·3)
(14·7)
(80·2)
(3·8)
DESICCATED
RIPENING FRUIT
DISPERSED
(28·6)
(68·7)
(2·6)
UNRIPE FRUIT
ABORTED
(50·4)
(49·6)
BUDS
N=1774

Figure 4.2. Yearly summaries of fruit development and dispersal fates. (percentage value)


RETAINED
DISPERSED
DISPERSED
(71 0)
(29 0)
(28 3)
(10 6)
(63 0)
DISPERSED
RIPE
FRUIT
(2 4)
(13 4)
(80 9)
(3·3)
DISPERSED
RIPENING
FRUIT
DESICCATED
(19·4)
(78·1)
(2 6)
UNRIPE
FRUIT
ABORTED
(47 1)
(52 9)
BUDS N=898

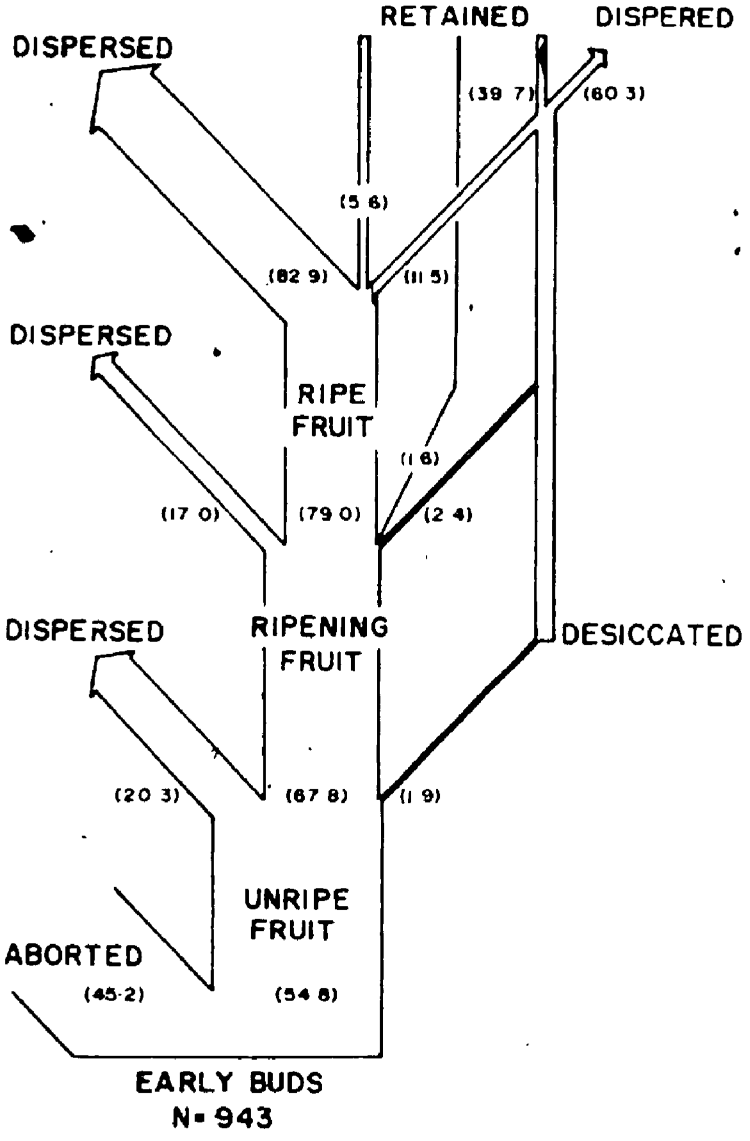
1982


DISPERSED
RETAINED
DISPERSED
(30 4)
(69 6)
(21 8)
(69 2)
(9 0)
DISPERSED
RIPE
FRUIT
(16 2)
(78·4)
(4 4)
DISPERSED
RIPENING
FRUIT
DESICCATED
(38 0)
(59 3)
(2 7)
UNRIPE
FRUIT
ABORTED
(53 6)
(46 4)
BUDS N=876

1985

Figure 4.3 Seasonal summaries of fruit development and dispersal fates.

(percentage value)


DISPERSED
RETAINED
DISPERED
(5 6)
(39 7)
(60 3)
(82 9)
(11 5)
DISPERSED
RIPE FRUIT
(1 6)
(17 0)
(79 0)
(2 4)
DISPERSED
RIPENING FRUIT
DESICCATED
(20 3)
(67 8)
(1 9)
UNRIPE FRUIT
ABORTED
(45·2)
(54 8)
EARLY BUDS
N= 943

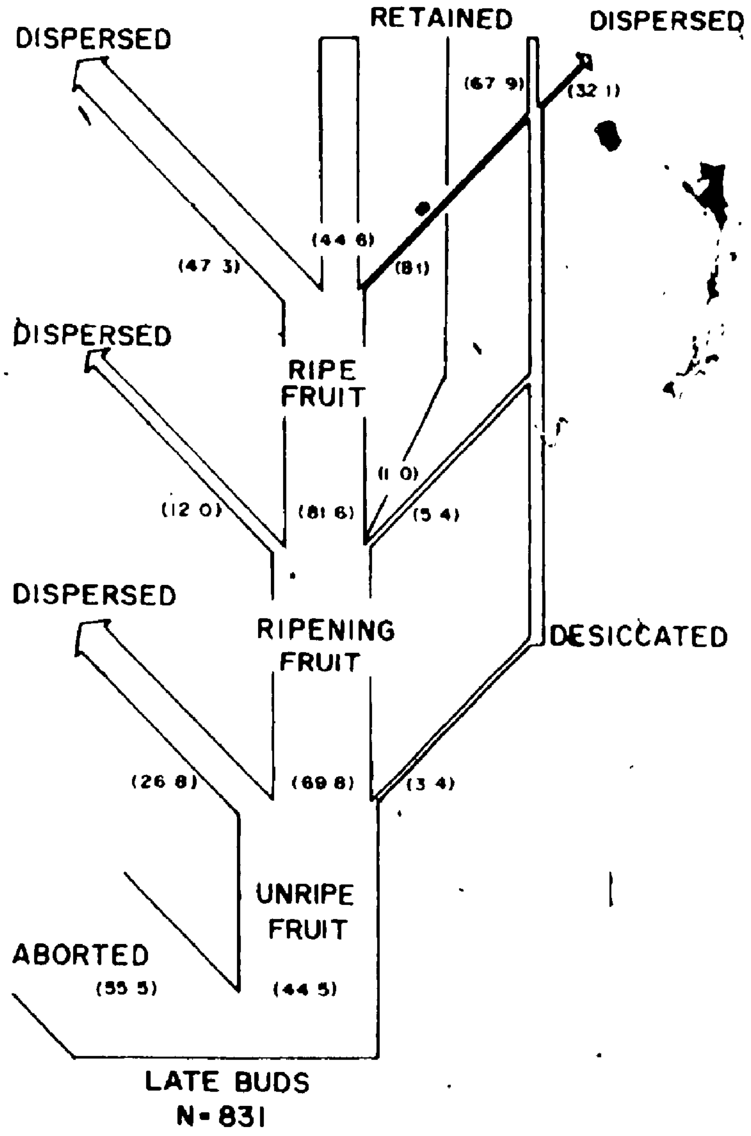
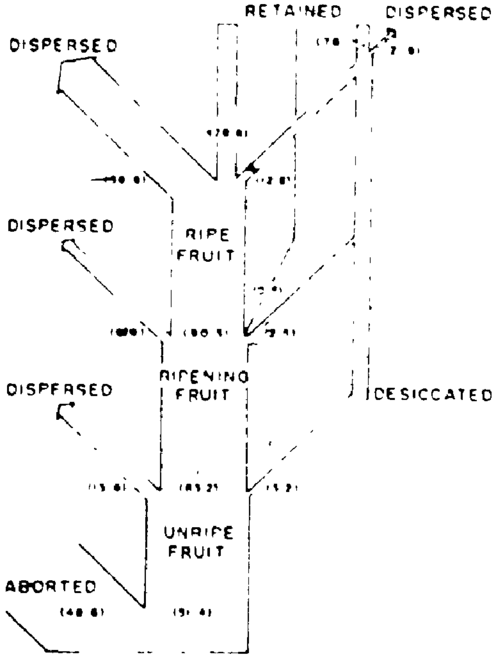
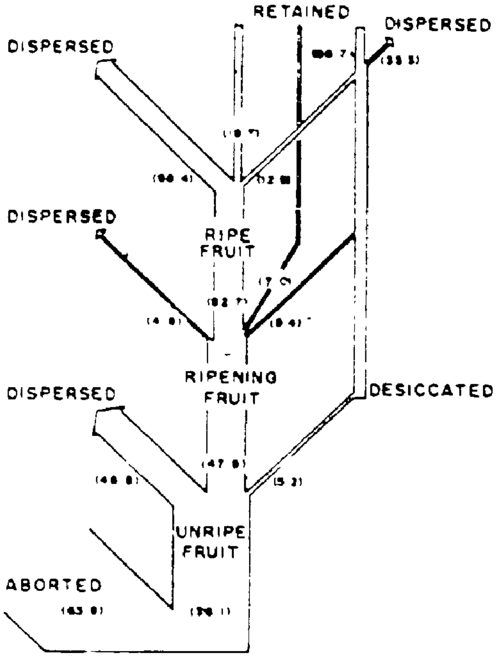

DISPERSED
RETAINED
DISPERSED
(67 9)
(32 1)
(44 6)
(47 3)
(81)
DISPERSED
RIPE FRUIT
(1 0)
(12 0)
(81 6)
(5 4)
DISPERSED
RIPENING FRUIT
DESICCATED
(26 8)
(69 8)
(3 4)
UNRIPE FRUIT
ABORTED
(55 5)
(44 5)
LATE BUDS
N= 831

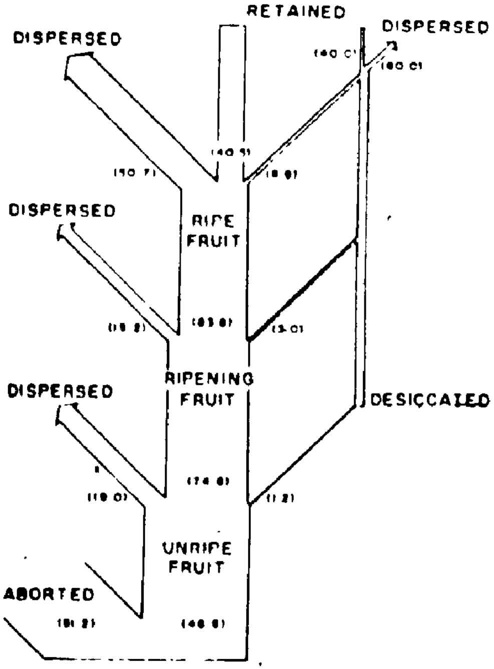
Figure 4.4. Habitat summaries of fruit development and dispersal fates. (percentage value)



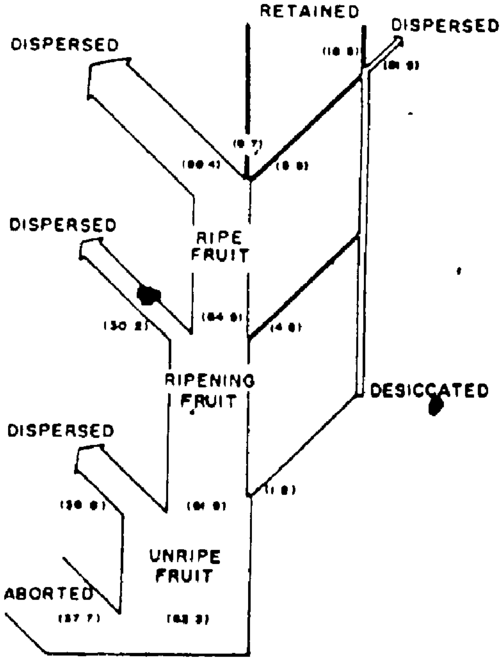
MARSH



SWAMP



FIELDSTATION



RIVERBANK

4.4). These represent summaries of the main effects of year, season and habitat as entered into the analyses of variance conducted at each branching point. Complimenting these is Table 4.1 which presents the results of these analyses for the main effects and the associated interactions.

4.3.1.1 The year effect

A significant year effect was identified only for the fates of unripe fruits and for the probability of dispersal of fruits regardless of development. On average, 38.0% of the unripe fruits were lost from the infructescences in 1985, and 59.3% developed to the ripening stage. In contrast, a lower percentage ($\bar{X}$= 19.4%) of the unripe fruits produced in 1982 were dispersed, and 78.1% reached the ripening stage. There was no significant difference in the percentage of unripe fruits that desiccated, and no marked unripe fruits were found on the plants at the end of the monitoring periods. A greater percentage of all fruits, regardless of ripeness, dispersed in 1985 ($\bar{X}$= 80.0%) than in 1982 ($\bar{X}$=70.0%).

4.3.1.2 The season effect

Significant effects attributable to the season of the year in which buds were produced were identified for the proportion of buds to set fruit, the loss and retention of ripe and desiccated fruits and the dispersal of fruits regardless of development. A greater portion of the buds present early in the season set fruit (early $\bar{X}$= 54.8%; late $\bar{X}$= 44.5%). Of the fruits that ripened, a greater proportion of the early ones had dispersed by the

Table 4.1 Analysis of variance summaries of fruit development and dispersal.

* $p<.05$ ** $p<.01$ *** $p<.001$

Effects	Unripe Fruit				Ripening Fruit			
	Fruit Set	Dispersed	Desiccated	Ripening	Dispersed	Desiccated	Retained	Ripening
Year	NS[1]	**	NS	**	NS	NS	NS	NS
Season	*	NS	NS	NS	NS	NS	NS	NS
Habitat	**	***	***	***	***	NS	NS	***
Year x Season	**	NS	NS	NS	NS	NS	NS	NS
Year x Habitat	NS	NS	NS	NS	NS	NS	NS	*
Season x Habitat	NS	NS	NS	NS	NS	NS	NS	NS
Year x Season x Habitat	NS	NS	NS	NS	NS	NS	NS	NS

Effects	Ripe Fruits			Desiccated Fruits		Overall
	Dispersed	Desiccated	Retained	Dispersed	Retained	Dispersed
Year	NS	NS	NS	NS	NS	*
Season	***	NS	***	**	**	***
Habitat	***	NS	***	**	**	***
Year x Season	*	NS	**	NS	NS	*
Year x Habitat	NS	NS	NS	NS	NS	NS
Season x Habitat	NS	NS	***	*	*	**
Year x Season x Habitat	NS	NS	**	NS	NS	NS

[1] Significance of F Ratio: NS = not significant; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

end of monitoring (early $\bar{X}$= 82.9%, late $\bar{X}$= 47.3%), as had a greater proportion of the desiccated fruit (early $\bar{X}$= 60.3%, late $\bar{X}$= 32.1%). The proportion of ripe fruits retained at the end of monitoring (early $\bar{X}$= 5.6%; late $\bar{X}$=44.6%) largely echoes the difference observed in terms of ripe fruit loss, although some ripe fruit in both cases reached the desiccated stage. The fruits formed early in the season had a higher proportion disperse regardless of development (early $\bar{X}$= 87.1%, late $\bar{X}$=61.8%).

4.3.1.3 The habitat effect

Significant differences amongst the marsh, swamp, field station and riverbank habitats were identified for the proportion of buds that set fruits, the proportions of unripe fruits to disperse or mature to the ripening stage, the proportion of ripening fruits to disperse or ripen, the proportion of desiccated fruits dispersing, and for the proportion of fruit dispersing regardless of development. A greater percentage of buds produced fruits in the riverbank habitat ($\bar{X}$= 62.3%) than in the swamp ($\bar{X}$= 36.1%); fruit production at the marsh ($\bar{X}$= 51.4%) and field station ($\bar{X}$= 48.8%) was intermediate. The mean percentage of unripe fruit dispersed at the swamp ($\bar{X}$= 46.8%) was greater than the percentage dispersed at the field station ($\bar{X}$= 19.0%) and the marsh ($\bar{X}$= 13.6%), as was the value at the riverbank ($\bar{X}$= 36.8%) different from that at the marsh. The percentage of unripe fruit to reach the ripening stage was highest for the marsh habitat ($\bar{X}$= 83.2%), greater than found for the riverside ($\bar{X}$= 61.9%) and swamp ($\bar{X}$= 47.9%) habitats. The percentage of unripe fruit to reach the ripening stage was also higher at the field station habitat ($\bar{X}$= 79.8%) than at the swamp habitat. The percentage of ripening fruit to disperse at the riverbank ($\bar{X}$= 30.2%) was greater than the percentage at the marsh ($\bar{X}$=6.6%), swamp ($\bar{X}$= 4.8%) or field station (13.2%). The percentage of ripening fruit to reach the ripe stage at the riverbank ($\bar{X}$= 64.9%) also differed from the the values at the other habitats (marsh 90.3%, swamp 82.7%, field station 83.8%), although some ripening fruit remained attached at the end of the monitoring or desiccated. A greater percentage of ripe fruit dispersed at the riverside ($\bar{X}$= 88.4%) than at the marsh ($\bar{X}$= 58.6%) or field station ($\bar{X}$= 50.7%), and the mean of 68.4% at the swamp was intermediate. However, a greater proportion of the ripe fruits remained attached to the infructescences at the end of monitoring at the field station ($\bar{X}$= 40.5%) and marsh ($\bar{X}$=28.6%) than at the riverbank ($\bar{X}$= 5.7%); again the value at the swamp ($\bar{X}$= 18.7%) was intermediate and not significantly different from any other. The percent dispersal of desiccated fruits at the riverbank ($\bar{X}$=81.5%) was greater than that in the swamp ($\bar{X}$= 33.3%) or marsh ($\bar{X}$= 21.9%) but not from the intermediate value at the field station ($\bar{X}$=60.0%). Overall, the proportion of fruits to disperse at the riverbank ($\bar{X}$=92.3%) was greater than at the field station ($\bar{X}$= 62.7%) or marsh ($\bar{X}$= 66.1%) habitats; at the swamp the value was intermediate ($\bar{X}$= 78.4%).

4.3.1.4 Interactions

The interaction of year and season was a significant component of the analyses of variance models for the proportion of buds to set fruits, the dispersal and retention of ripe fruits, and dispersal regardless of development. The seasonal differences in fruit set may have rested mostly with the difference observed in 1985 when a mean of 56.7% of the early buds set fruit and a mean of 36.1% of the later buds set fruit, as the 1982 differences were slight (early $\bar{X}$= 52.8%; late $\bar{X}$= 53.0%). Neither the main effects concerning the proportions of ripe fruit to disperse or be retained were confounded, but the season effect may have been more pronounced in 1985. Similarly the seasonal effect may have been more pronounced in 1985 for the proportion of fruits dispersing regardless of dispersal.

An examination of the rankings classed at the levels of the other significant interactions -- habitat with year for the maturation of ripening fruits to ripe fruits, seasonality with habitat upon the probability of ripe fruit retention, and the dispersal of desiccated fruits or fruits regardless of ripeness, plus the three way interaction of year, habitat and seasonality upon the retention of ripe fruit -- did not suggest that the relevant main effects were confounded. In each instance the rankings were consistent with the main trends. Just in terms of rankings, however, the following are of some note: a) intraseasonal variation seemed especially pronounced in the field station habitat in 1985, as all the ripe fruit produced from the early buds dispersed whilst none of those borne later in 1985 had been dispersed by the end of the monitoring; b) none of the ripe fruit produced from the early buds in any habitat in 1985 remained attached at the end of the monitoring; c) all of the ripe fruit from the later buds in the riverbank dispersed in 1985, whilst none of their counterparts were lost at the field station. For the 12 cells recognizable at the level of the three way interaction, however, relatively few fruits were considered in some cases. In 1985 at the field station, for example, there were only eight ripe fruits produced from the 85 buds monitored later in the season.

4.3.1.5 Differences between unripe, ripening and ripe fruits

When the proportion of fruits to disperse was analysed with the stage of development as an additional factor, all the main effects were significant. The trend attributable to year, season and habitat, however, closely parallelled those observed for the considerations of dispersal regardless of development. All four developmental categories differed significantly from each other, ranking from a mean of 65.9% for ripe fruits through 45.9% for desiccated fruits and 28.6% for unripe fruits to 14.7% for ripening fruits. The interaction of season with habitat and the interaction of developmental stage with habitat were significant. However any exceptions to the main effects were as earlier described in the sections dealing with the effects of season and habitat upon the dispersal patterns observed for each developmental class.

4.3.1.6 Differences in number.

Figures 4.1 to 4.4 give an impression of differences in the numbers of buds and fruits to reach certain stages, as the number of buds individually monitored in each case is presented and the proportional scale of branch widths is also consistent with number. But to compliment this, analyses of the numbers of buds produced per inflorescence, and the numbers of unripe, ripening, ripe and desiccated fruits were also made. The results of these analyses, with year, season and habitat as factors, are presented in Table 4.2 . The year effect was significant only for the numbers of ripening and ripe fruits produced. In both cases the numbers borne on the infructescences of 1982 were greater (ripening: 1982 $\bar{X}$=4.8, 1985 $\bar{X}$= 3.1; ripe 1982 $\bar{X}$= 4.1, 1985 $\bar{X}$=2.4). The only instance of a significant season effect was for the greater number of buds to set fruits on the early infructescences ($\bar{X}$= 6.5) than on later ones ($\bar{X}$= 4.7). There were habitat differences for all the variables except the numbers of desiccated fruits produced. In terms of the number of buds and fruits the riverbank stood out from all the other habitats (buds; riverbank $\bar{X}$= 13.9, marsh $\bar{X}$= 10.4, field station $\bar{X}$= 10.1, swamp $\bar{X}$= 10.0; number of fruits: riverbank $\bar{X}$= 8.5, field station $\bar{X}$=5.1, marsh $\bar{X}$= 5.1, swamp $\bar{X}$=3.8). It was the swamp habitat, however that stood out from all the others in terms of the numbers of ripening and ripe fruits (ripening swamp $\bar{X}$=2.0, field station $\bar{X}$= 4.1, marsh $\bar{X}$= 4.3, riverbank $\bar{X}$= 5.4; ripe: swamp: $\bar{X}$= 1.7, field station $\bar{X}$=3.4, riverbank $\bar{X}$=3.9, marsh $\bar{X}$= 3.9). Although there was a significant interaction of year with season for the numbers of fruit set, the rankings were consistent over the two years, but the seasonal effect may have been more pronounced in 1985. The only other significant interaction for which a main effect was also significant was that of season and habitat for the number of buds, but in all cases the value for the riverbank remained highest in rank, a separation perhaps more pronounced amongst the later fruits.

The numbers of fruits dispersed per infructescence also varied between the years, within the season and amongst the habitats (Table 4.3). Fewer unripe and more ripe fruits were dispersed in 1982 (unripe $\bar{X}$= 1.0; ripe $\bar{X}$=2.5)

Table 4.2 Analysis of variance summaries of the numbers of buds and unripe, ripening, ripe and desiccated fruits produced per infructescence.

* $p < .05$ ** $p < .01$ *** $p < .001$

Effects	Buds	Fruits			
		Unripe	Ripening	Ripe	Desiccated
Year	NS[1]	NS	**	***	NS
Season	NS	**	NS	NS	NS
Habitat	***	***	***	***	NS
Year x Season	*	**	NS	NS	NS
Year x Habitat	NS	NS	NS	NS	NS
Season x Habitat	*	NS	NS	NS	NS
Year x Season x Habitat	NS	NS	NS	NS	NS

1. Significance of F Ratio: NS = Not significant; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

Table 4.3 Analysis of variance summary of the numbers of dispersant unripe, ripening, ripe and desiccated fruits per infructescence.

* $p<.05$ ** $p<.01$ *** $p<.001$

Effects	Dispersant Fruits			
	Unripe	Ripening	Ripe	Desiccated
Year	***[1]	NS	*	NS
Season	***	**	***	NS
Habitat	***	***	***	NS
Year x Season	***	NS	NS	NS
Year x Habitat	NS	NS	NS	NS
Season x Habitat	NS	*	NS	**
Year x Season x Habitat	NS	NS	NS	NS

[1] Significance of Ratio: NS = $p \geq .05$; *$p < .05$; **$p < .01$; ***$p < .001$

than in 1985 (unripe $\bar{X}$= 1.9; ripe $\bar{X}$=1.7). More early-formed unripe (early $\bar{X}$= 2.0, late $\bar{X}$= 1.0), ripening (early $\bar{X}$=0.8; late $\bar{X}$=0.4) and ripe (early $\bar{X}$=2.7; late $\bar{X}$= 1.5) fruits were dispersed per infructescence. More unripe fruits were lost from the infructescences at the riverbank ($\bar{X}$= 2.8) than from those at the swamp ($\bar{X}$=1.7), field station ($\bar{X}$= 0.9) or marsh ($\bar{X}$= 0.6), and from the swamp than the marsh. The number of ripening fruits to disperse was also highest at the riverbank ($\bar{X}$= 1.3), a value greater than at any other habitat (field station $\bar{X}$= 0.6; marsh $\bar{X}$= 0.3; swamp $\bar{X}$= 0.2). More ripe fruits were dispersed from the infructescences at the riverbank ($\bar{X}$= 3.5) than at either the field station ($\bar{X}$= 1.6) or swamp ($\bar{X}$= 1.0) but not the marsh ($\bar{X}$= 2.3). There was a significant interaction of year and season in terms of the number of unripe fruit to disperse, and an examination of the rankings evident at this level suggested that the seasonal difference was largely confined to 1985 when a mean of 2.9 early unripe fruits dispersed and a mean of 0.9 late fruits dispersed per infructescence; seasonal differences seemed unlikely for unripe fruit in 1982 (early $\bar{X}$= 1.0; late $\bar{X}$= 1.0). The only other significant interaction was that of season with habitat for the numbers of dispersant ripening fruits. In this case, the habitat rankings were consistent for both the early and late fruits, and the reversal of the seasonal ranking at the swamp represented the only exception to seasonal trends within the habitats, however.

The number of inflorescences borne by individual stems differed from habitat to habitat. Such production was lowest in the two seasonally flooded habitats (marsh $\bar{X}$= 0.5, swamp $\bar{X}$= 0.3). Significantly more inflorescences were produced on the stems in the field station and river bank (field station $\bar{X}$= 1.9, riverbank $\bar{X}$= 3.1)

4.3.2 Rates of ripening and fruit loss

Table 4.4 summarizes the results of the factorial analyses of variances performed on ripening rates and the retention period of dispersant fruits across the two years, the early and late inflorescences and the four natural habitats. Figure 4.5 presents the data when broken down according to the main effects. To varying extents, the main effects significantly affected the period of ripening and the retention time of dispersant fruit.

4.3.2.1 The annual effect

The fruits produced in 1985 ripened more quickly ($\bar{X}$= 5.0 weeks) than those borne in 1982 ($\bar{X}$= 5.3 weeks), and, similarly, the dispersant ripe fruits were retained for a shorter period in 1985 ($\bar{X}$= 2.3 weeks) in contrast to 1982 ($\bar{X}$= 3.4 weeks). The yearly rankings were similar for those fruits lost at the unripe or ripening stages, but the year effect was insignificant for the unripe fruits, and the difference was slight and insignificant on the basis of the Scheffé contrast for the ripening fruits.

4.3.2.2 The season effect

The only incidents of a significant difference between the early and late formed fruits concerned the period of ripening and the retention time of the dispersant ripening fruit. The fruit formed earlier in the season

Table 4.4. Analysis of variance summaries of fruit ripening rates and the retention period of dispersant fruits.

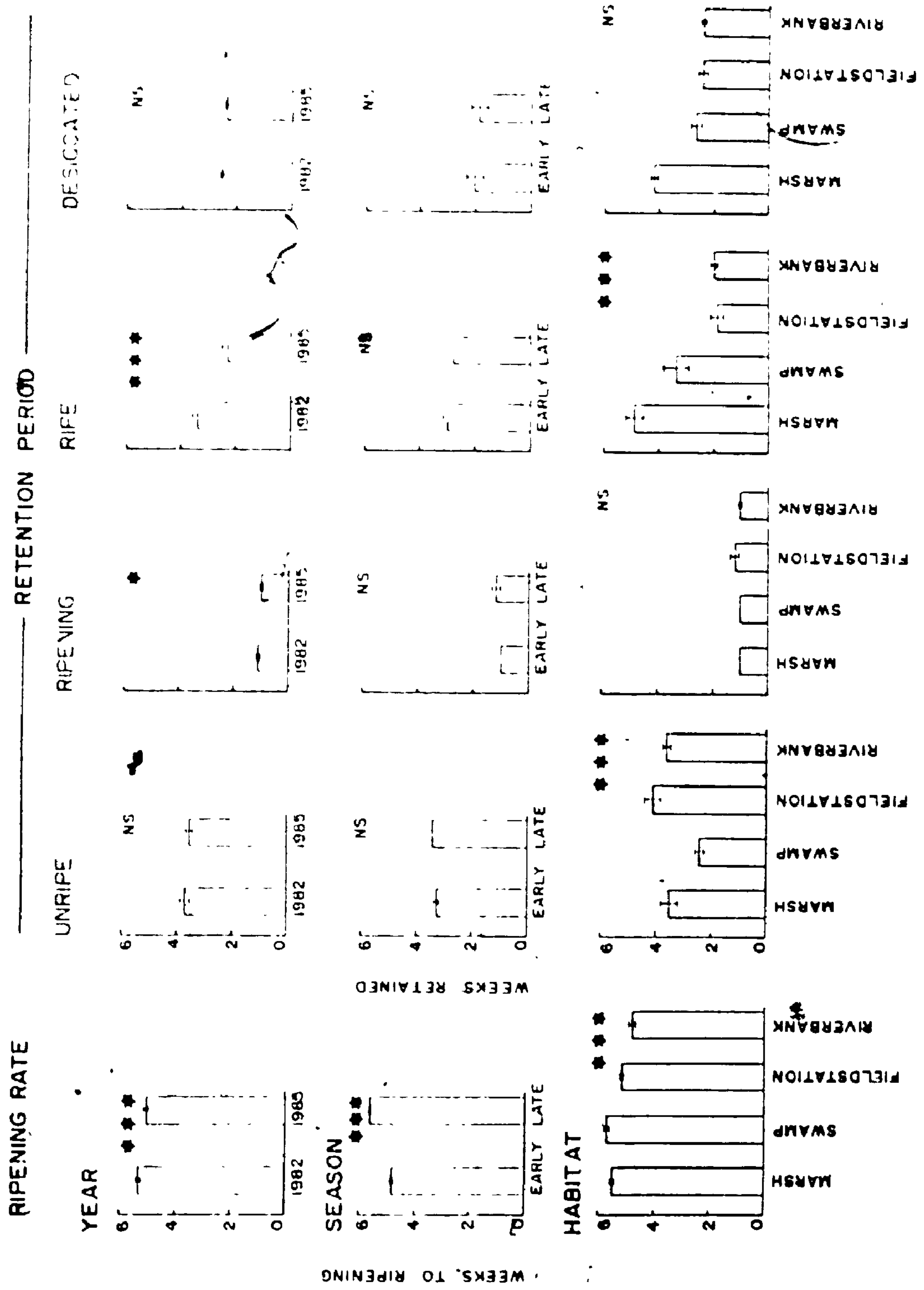
* $p < .05$ ** $p < .01$ *** $p < .001$

Effects	Ripening Rate	Retention Period of Dispersant Fruits			
		Unripe	Ripening	Ripe	Desiccated
Year	***[1]	NS	*	***	NS
Season	***	NS	NS	NS	NS
Habitat	***	***	NS	***	NS
Year x Season	***	NS	**	**	NS
Year x Habitat	NS	NS	*	*	NS
Season x Habitat	*	NS	NS	***	NS
Year x Season x Habitat	NS	NS	***	***	NS

[1] Significance of F Ratio: NS = $p > .05$; $^{*}p < .05$; $^{**}p \leq .01$; $^{***}p < .001$.

Figure 4.5. The effects of year, season and habitat on fruit ripening rates and the retention period of dispersant fruits. Mean values ± one standard deviation.

* $p(F) < .05$ ** $p(F) < .01$ *** $p(F) < .001$


RIPENING RATE
RETENTION PERIOD
UNRIPE
RIPENING
RIPE
DESICCATED
YEAR
SEASON
HABITAT
WEEKS TO RIPENING
WEEKS RETAINED
0
2
4
6
1982
1985
EARLY
LATE
MARSH
SWAMP
FIELDSTATION
RIVERBANK
***
*
NS

ripened more quickly ($\bar{X}$= 4.8 weeks) than did those formed later in the season ($\bar{X}$= 5.6 weeks), and all of the early fruits lost at the ripening stage were retained for no more than one week, while their later counterparts remained attached for a mean of 1.2 weeks prior to dispersal.

4.3.2.3 The habitat effect

A significant habitat effect was identified in all cases save the retention period of those desiccated fruits that dispersed. Ripening was slower in the marsh ($\bar{X}$= 5.5 weeks) and swamp ($\bar{X}$= 5.7 weeks) habitats than at the field station ($\bar{X}$= 5.2) or riverbank ($\bar{X}$=4.7 weeks), as was the ripening rate at the field station different from that at the riverbank. The unripe fruit dispersed in the swamp habitat ($\bar{X}$= 2.4 weeks) were lost more quickly than those at the riverbank ($\bar{X}$= 3.6) or field station ($\bar{X}$= 4.1 weeks); the value for the marsh ($\bar{X}$= 3.3 weeks) was intermediate and not significantly different from any other. Although there was a significant habitat effect for the retention time of dispersant ripening fruit, there were no significant Scheffé pairwise contrasts; and it can be noted that none of the dispersant ripening fruit in the marsh or swamp habitats were retained for more than a week. The ripe fruit that dispersed over the course of monitoring were retained for shorter periods in the field station ($\bar{X}$= 1.9 weeks) and riverbank ($\bar{X}$= 2.0 weeks) than in either the swamp ($\bar{X}$= 3.3 weeks) or marsh ($\bar{X}$= 4.9 weeks), and those in the swamp were attached for a shorter period than those in the marsh.

4.3.2.4 The interactions of year, season and habitat

In a number of cases the pairwise interactions of year, season, and habitat were significant in terms of ripening rates and the retention period of dispersant fruits (Figure 4.6). For the most part, however, the interactions were a matter of degree rather than contradiction. Of particular note might be the more pronounced seasonal differences in 1982, the pronounced seasonal effect in the retention of dispersant ripe fruits at the swamp, the minimal seasonal effect on retention of dispersant ripe fruits at the marsh, and the change in rank at the swamp from the second longest retention of dispersant ripe fruits formed early in the season to the shortest retention period for later formed ripe fruits. An examination of the 12 cell rankings present at the level of the interaction of year, season and habitat in terms of the retention of dispersant ripening and ripe fruits suggested, at best, minimal contradiction beyond the trends observed for the main effects and paired interactions.

4.3.2.5 The differences between unripe, ripening and ripe fruits

Figure 4.7 depicts the significant main effects and pairwise interactions evident when the retention times of dispersant fruits were examined with the stage of development as an additional factor. The overall period of retention of fruits dispersed at the marsh habitat was greater ($\bar{X}$= 4.2 weeks) than at the others (swamp $\bar{X}$= 2.6 weeks; field station $\bar{X}$= 2.4 weeks; riverbank $\bar{X}$= 2.4). Dispersant unripe fruits were retained longer ($\bar{X}$= 3.3 weeks) than those of any other ripeness (ripening $\bar{X}$= 1.1 weeks; ripe $\bar{X}$= 2.9 weeks; desiccated $\bar{X}$= 2.1 weeks), and the retention period of dispersant

Figure 4.6 The interactions of year and season, year and habitat, and season and habitat on fruit ripening rates and the retention period of dispersant fruits. The mean values ± one standard deviation are shown.

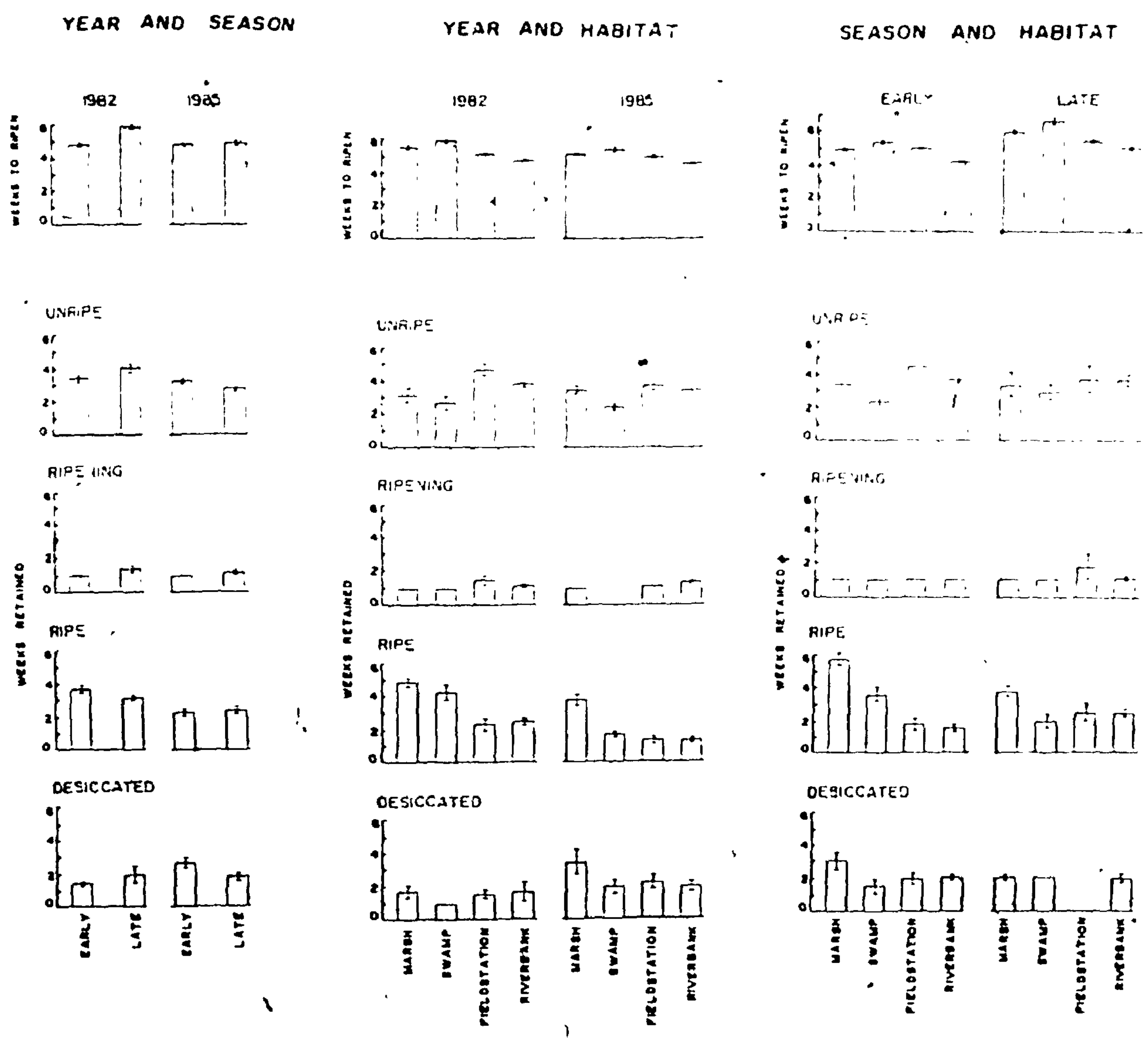
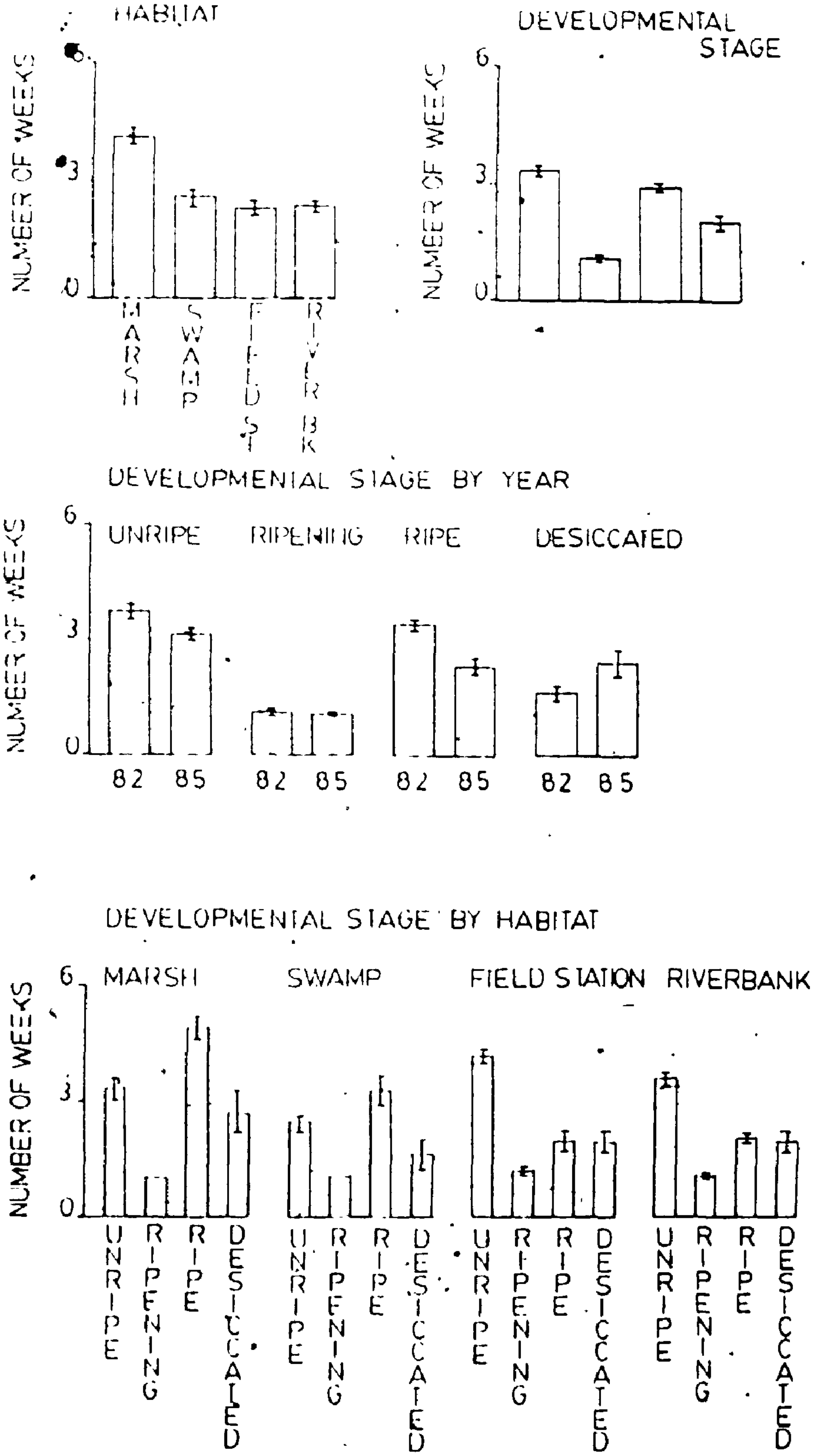

YEAR AND SEASON
YEAR AND HABITAT
SEASON AND HABITAT
1982
1985
EARLY
LATE
WEEKS TO RIPEN
WEEKS RETAINED
UNRIPE
RIPENING
RIPE
DESICCATED
0
2
4
6
EARLY
LATE
MARSH
SWAMP
FIELDSTATION
RIVERBANK

Figure 4.7 The effects of habitat, stage of development and the interactions of year and developmental stage, and habitat and developmental stage on the retention period of dispersant fruits. The mean values ± one standard deviation are shown.


HABITAT

DEVELOPMENTAL STAGE

DEVELOPMENTAL STAGE BY YEAR

DEVELOPMENTAL STAGE BY HABITAT

ripening fruits was shorter than all others. The rankings according to ripeness were consistent over both years, but the yearly trend, insignificant in this case, towards a shorter retention time in 1985 was countered only in the case of the dispersant desiccated fruits which showed a shift in ranking suggestive of a longer retention in 1985. An examination of the nature of the significant interaction of habitat and ripeness suggests that the significant main effects were not confounded to a major degree. The exceptions stood with the marsh habitat where the ranking of the unripe fruits suggested a shorter rather than longer retention period than that for the ripe fruits, and with the swamp habitat where the rankings of the ripening and ripe fruits was similarly reversed. The interaction of habitat, year and season was also significant in the analysis of variance, but the only ranking exception to the significant habitat effect was in 1982 when the later formed fruits at the riverbank had a retention period ranking longer rather than shorter than for those dispersed at the marsh. Neither were the significant habitat and ripeness trends contradicted in a major way when the rankings were examined at the scale of the significant interaction of year, season, habitat and ripeness. It is notable, however, that no desiccated fruits were dispersed from the later formed infructescences in 1982 at the swamp and field station, nor in 1985 at the marsh and field station. Similarly, no ripening fruits were dispersed from the swamp in 1985, nor from amongst those originating from the later set fruit in 1985 at the marsh. In addition, no ripe fruits were dispersed from those formed later in 1985 at the field station.

4.4 Discussion

4.4.1 Question 1. Are the buds formed earlier in the season more likely to produce fruits than those formed later in the same year?

Although the number of buds on the early and late inflorescences did not differ significantly, the early ones were more likely to produce fruit. This greater number of fruits produced by the early buds echoed a pattern noted for many plant species (Stephenson 1981) that commonly produce the early flowers lower on a stem or inflorescence in a position perhaps better able to tap resources moving up the stem. In Chapter 3, though, it was found that the ripe fruits produced later in the season were a bit bigger, had more flesh and higher flesh-to-seed dry weight ratios. So rather than being a reflection of possible resource limitations, a reduction in the numbers of fruits borne on the later infructescences may represent a means of producing relatively more rewarding fruits at a time when the bulk of species produce their fleshy propagules (Stapanian 1986, Herrera 1984b, Stiles 1980, Thompson and Willson 1979, Morton 1973, Snow 1971) and the competition for dispersers might be greatest (Herrera 1981b, Stiles 1980, Thompson and Willson 1979).

4.4.2 Question 2. Do early fruits ripen and/or disperse more slowly than later fruits?

On an intraspecific level the faster ripening rate of early fruits observed in this study contradict the predictions of Stapanian (1982), Stiles (1980) and Thompson and Willson (1979) that species which produce their fleshy propagules early in the season in eastern North America should have slower ripening rates than those species that mature their propagules later in the year. In addition to ripening more quickly the early fruits of Solanum dulcamara were more likely to disperse, especially if they reached the ripe or desiccated stage of development, and greater numbers of these early fruits dispersed. In contrast to the observation of several species by Thompson and Willson (1979) of a greater dispersal rate for species with late forming fruits, there was no difference in the period of retention of dispersant unripe, ripening or ripe fruits borne early or late in the season by Solanum dulcamara. In this sense the pattern for S. dulcamara matched that described by Sherbourne (1972) and Herrera (1984b) who were unable to recognize a seasonal trend in dispersal rates. The relatively greater reward of the later propagules, then, may play a role in maintaining the levels of dispersal in the face of potentially increased competition for dispersal agents with the bulk of plant species producing fleshy propagules at this time (Herrera 1981b, Stiles 1980).

4.4.3 Question 3. Are fruits at different stages of development equally likely to disperse and do they disperse at the same rate?

Unripe, ripening, ripe and desiccated fruits were all dispersed from the infructescences observed in this study, but the probability of dispersal and the retention period of dispersant fruits varied with the stage of development. The ripening stage was the most ephemeral and fruits at this stage were the least likely to disperse, but those that did were retained for the shortest period. Dispersant unripe fruits were retained for a longer period than any other type, and although they were not as likely to disperse as ripe or desiccated fruits, they were never-the-less lost in substantial numbers. Desiccated fruits had the second highest probability of dispersal and those that dispersed were retained for longer than the dispersant ripening fruits and shorter than the dispersant unripe fruits. The percentage of ripe fruits to disperse was highest of all and the retention period of dispersant ripe fruit was also longer than that for the ripening fruit and shorter than that of the unripe fruits.

Given that considerable proportions of the immature fruits of *Solanum dulcamara* and other species (Holthuijzen *et al.* 1987, Moermond *et al.* 1986, Willson and Thompson 1982, Foster 1977, Sherbourne 1972) may be lost from the parent and that the seeds from immature fleshy propagules of some species can germinate (Foster 1977, Lamont 1982a), it seems rash to dismiss immature propagules from models concerning the production and dispersal of species bearing fleshy propagules, as was the case for the assessment by Howe and Estabrooke (1977). The loss of immature fruits of *S. dulcamara* must be considered as potentially valid dispersal episodes unless they are known to contain no viable seeds.

4.4.4 Question 4. Do the patterns of development and loss differ across the habitats?

Differences amongst the habitats in terms of the patterns of fruit production and dispersal were more frequently encountered than differences due to year or season. Interpretation of these patterns is more difficult, however, as each habitat differed remarkably from the others in terms of physical and biotic characteristics. Each habitat will be discussed seperately below.

In general terms the production and dispersal of fruits was most efficient at the riverbank where there was little tree or ground cover and S. dulcamara tended to have a shrublike structure highly visible amongst the strewn boulders. The number of buds borne on the inflorescences at the riverbank were greater than the numbers found on those in any other habitat, and the percentage of those to set fruits was highest in rank but differed significantly only from the percentage setting fruits in the swamp. As a consequence more fruits were formed there. The fruits at the riverbank also ripened more quickly and the probability of overall dispersal was also higher than at any other habitat. Because of the greater numbers of fruits borne on the infructescences, the greater probability of dispersal regardless of ripeness, and the consistently high percentage of fruits dispersed at the various stages of development, greater numbers of unripe, ripening and ripe fruits were lost at the riverbank than elsewhere. As a further consequence of the high percentage of fruits dispersed in this habitat the initial difference in the numbers of fruits diminished with time and in terms of the numbers of ripening and ripe fruits the riverbank differred significantly only from the swamp. The riverbank did not stand out from the others in terms of the retention periods of dispersant fruits, however, as its values in this regard were usually intermediate and often significantly different from only the most extreme value. The make-up of the ripe propagules dispersed in this habitat may have contributed to the dispersal patterns, as they contained more flesh and would perhaps be more rewarding than those in the marsh and swamp. In addition, more inflorescences and likely more fruits per stem were found here than in the marsh or swamp.

At the field station where the stems of S. dulcamara clambered through the mesh of the fencelines at various locations, the patterns of fruit development and dipsersal did not stand out in any major ways from those in the other habitats. The percentages and number of buds/fruits realizing various fates, and the retention period of dispersant fruits were for the most part intermediate. In the few instances where the value for the field station was extreme in rank, it rarely differed significantly from any other value. Arguably the fruits in this habitat were the most accessible to birds, given the abundance of perch sites offered by the fences, but there was at best a weak overall tendency for dispersant fruits to be retained for shorter periods. However, the retention period of ripe fruits was lowest in rank and significantly different from the values for the marsh and swamp. As with the riverbank fruits, the make-up of the individual propagules may have contributed to some of the differences observed between the field station and the other habitats, particularly with the marsh and swamp. The dry flesh weight and flesh-to-seed dry weight ratios for ripe fruits were greater at the field station than at the marsh or swamp, and stems at the field station produced more inflorescences.

The overall productivity of S. dulcamara was probably lowest at the swamp which was flooded for much of the year, often remaining so until after the tree leaves had expanded and created a very shady environment. In terms of the number of inflorescences produced per stem this habitat ranked the lowest and differed significantly from the values at the riverbank and the field station. The ripe propagules from the swamp also had less flesh than those in any other habitat and the flesh-to-seed dry weight ratio was lower than at the riverbank or field station. The numbers of buds, the percentage of these to set fruit and the numbers of fruits produced ranked lowest at the swamp but differed significantly only from the values for the riverbank. Fewer fruits reached the ripening or ripe stage at the swamp than in any other habitat, and the numbers of ripening and ripe fruits to disperse were also lowest in rank but significantly different only from the riverbank values. The percentage of unripe fruits to disperse at the swamp was the highest in rank and significantly different from the values in the marsh and field station. Although fewer fruits reached the ripe stage of development at the swamp, the proportion of these to disperse did not differ significantly from the proportion in any other habitat, and in terms of dispersal regardless of ripeness the percentage dispersed at the swamp was second highest in rank but not significantly different than the values at the marsh or field station. Overall the retention of dispserant fruits at the swamp differed significantly only from the marsh, but the unripe dispersant fruits were retained for a shorter and dispersant ripe fruit for a longer period than at the riverbank or field station.

Although the marsh habitat was flooded much of the year, it was unshaded for most of the day, and its organic soil supported a dense tangle of rather weak stems of S. dulcamara. Although trees bounded this habitat, there were few suitable perch sites that would offer access to the fruits and the stems themselves were likely too weak to provide good support for most birds. As with the swamp, the numbers of inflorescences per stem and the amount of flesh per ripe propagule were less here than at the riverbank or field station. This habitat stood out from the rest, however, in terms of the efficiency of producing ripe fruits, since the proportion of unripe fruits to disperse in this habitat was the lowest and differed significantly from the values at the swamp and field station. Also, the proportion of ripening fruit to reach the ripe phase was highest in rank, significantly so, from all save the proportion at the field station. In addition, the probability of ripe fruit dispersing was amongst the lowest in this habitat, but in each case the value differed significantly only from the riverbank. The marsh habitat really stood out from the other habitats in terms of the retention period of dispersant ripe fruits and fruits regardless of ripeness. In both cases, the retention[illegible]iod was greatest at the marsh and significantly different from the the values at the other habitats. The longer retention of dispersant fruits might be a partial reflection of an inaccessability of the fruits in this habitat.

In general terms there were some pronounced differences between the habitats in terms of the patterns of the development and dispersal of the fleshy propagules of Solanum dulcamara, but it is difficult to place these within the context of other investigations. As in the majority of other interhabitat investigations (see section 1.2.4), fewer fruits were produced and ripened in closed habitats, here represented by the swamp, which was probably the least productive of the four habitats examined. Contrary to some observations concerning the proportions of fruits to disperse (see section 1.2.4), it does not appear that the proportion of fruits dispersed from Solanum dulcamara remains constant with crop size, at least between the habitats. The case of dispersal in the swamp is pertinent to this. Fewer inflorescences and fruits were produced by the stems in this habitat and fewer fruits reached the ripening or ripe stage, yet the overall proportion of fruits to disperse was second highest and differed significantly from only the riverbank where fruits were more numerous. This ranking was also maintained for the proportion of ripe fruits to disperse, the stage at which most studies focus (Howe and Smallwood 1982, Thompson and Willson 1979, Howe and Estabrooke 1977). At the other extreme, the riverbank, where the stems produced more inflorescences than at the marsh or swamp and the inflorescences produced more fruits than at any other habitat, a much greater overall proportion of fruits dispersed. In addition, the retention periods of dispersant fruits also varied amongst the habitats. In contrast to the observations of Willson and Melampy (1983), Morden-Moore and Willson (1982) and Thompson and Willson (1979), the retention time of fruits produced in the "closed" habitat represented by the swamp did not differ for ripe fruits or for fruits regardless of development from the values observed in the more "open" riverside and field station habitats. Furthermore, in terms of the retention period of unripe dispersant fruits, those at the swamp were retained for the shortest interval. Although the marsh habitat, like the riverbank, could be considered open, the retention times of dispersant fruits was longest there.

The observations concerning the patterns of production and loss outlined in the preceding paragraph were not put forth as definitive. Certainly, to properly evaluate the size of the crops produced under the various conditions some more elaborate means of enumeration would be required, as fruits were continuously being formed and dispersed. It was not my intention to suggest that the fruits of the various developmental stages that are dispersed from the plant do so by the same pathways or have similar implications for the subsequent performance of seeds and seedlings. Indeed, all of the observations made of bird behaviour around Solanum dulcamara indicated that only ripe fruits were consumed. Nevertheless, unripe, ripening and desiccated fruits were lost from the infructescences and these may have contained viable seeds with quite different germination properties than the seeds from ripe fruits. At present little is known about the germination characteristics of the seeds of immature fleshy propagules from any species, and the implications of the dispersal of immature fruits is also poorly understood (Thompson and Willson 1979).

4.4.5 Question 5. Do the patterns of production and loss change from year to year?

Some of the patterns of production and dispersal of the fruits varied between the two years. The fruits of 1985 ripened more quickly and the dispersant fruits, especially the dispersant ripe fruits, were retained for a shorter period than in 1982, despite the numbers of ripening and ripe fruits actually being higher in 1982. Greater numbers of unripe and fewer numbers of ripe fruits dispersed in 1985, and the proportion of fruits dispersing regardless of ripeness, but especially the proportion of unripe fruits to disperse, was greater in 1985.

In some cases there were significant interactions between the effects of year, season, habitat and/or stage of development. Although the interactions were usually a matter of degree rather than contradiction, some of the noted exceptions indicate that strong pronouncements based on single year records, or which embrace only a very narrow suite of environments, or which concern propagules initiated only at a certain point in the season in which they are produced, should be regarded as tenuous. This may be especially so with a species like *Solanum dulcamara* that produces ripe propagules over such a long portion of the growing season.

CHAPTER 5

GERMINATION AND SEEDLING EMERGENCE

5.1 Introduction

In Chapter 3, which concerned the make-up of individual propagules, it was found that most unripe, ripening and ripe fruits contained seeds that were filled and firm to the touch and, hence, were considered as "good" seeds. In Chapter 4, where patterns of propagule production, development and loss were examined, it was found that substantial proportions of unripe, ripening, ripe and desiccated fruits were lost from the infructescences. Depending upon the mode of dispersal, the seeds may or may not remain encapsuled in the flesh after coming to rest. In order to consider such losses as possible dispersal episodes, it is requisite that the propagules contain seeds capable of germination. However, it is also important that examinations extend beyond mere viability as factors that alter the germination rates of seeds or affect seedling emergence can also have great impact on the contributions that a seed cohort might make to future generations (Cavers 1983). The focus of the field and laboratory studies described in this chapter is on some of these factors and their impact upon germination and seedling emergence. The questions of interest for this chapter are as follows:

> (1). What is the influence of the intact propagule upon the patterns of seedling emergence under various field and laboratory conditions?

(2). What is the impact of the stage of development of the propagule on germination and seedling emergence?

(3). Do fruits initiated early in the season contain seeds with different germination potentials than those in fruits initiated later in the season?

(4). Are there differences in germination or seedling emergence attributable to the habitat in which the seeds were produced?

5.2 Methods

5.2.1 Field emergence studies

The field emergence studies were conducted at the field station, marsh and swamp habitats. Because of the covering of large boulders and a high level of nearby pedestrian traffic no studies were conducted at the riverbank.

In all the studies, seeds or whole fruits were placed on the soil surface in cylinders which had been pounded into the ground. Each cyclinder was cut from a length of plastic sewer pipe and measured 10 cm in length with an internal diameter of 7.5 cm. Aside from the disturbance caused by the insertion of the cylinders, the ground cover was left undisturbed, save that herbaceous vegetation within the cylinder was clipped enough to allow the placement of a covering of fiberglass window screening across the top of each cylinder. It was intended that the screening would deter predators and block input of other seeds.

In 1981, a set of two cylinders, spaced 30 cm apart, was inserted at each of 35 locations, spaced at five metre intervals, along the fence line at the field station. Ripe fruits were collected from individuals growing naturally at that habitat in early October. The collection was pooled and divided in two. One group of fruits was squashed over screens and the flesh was rinsed free with water. The seeds were allowed to dry at room temperature and then were counted into lots of 100 and stored in a cold room (4^{o} C.), as were the intact fruits. Within three days of harvest one lot of 100 seeds was sprinkled into one of the pair of cylinders at each location. Twenty fruits randomly selected from the bulk collection of intact fruit were added to the second cylinder of each pair.

In 1982, identical plastic cylinders were inserted and protected as in 1981. At the field station 18 locations spaced 10 m apart along the 1981 transect were used. At both the marsh and the swamp habitats a rectangular grid of 20 cylinder locations was created, such that there was 10 m between each of the five rows and each of the four locations within a row was separated by five metres. At each cylinder location a set of three cylinders was inserted, one for each of the seed and fruit treatments and an additional cylinder receiving no inputs and acting as a control. Again lots of 100 seeds freshly extracted from ripe fruits collected in early October at the field station were used, but only 10 intact fruits were added to the cylinders receiving the whole fruit treatment. In the fall of 1983 an array of cylinders and treatments identical to that of 1982 was created at the field station.

During April, May and June of 1982, 1983, 1984 and 1985, the mesh was removed from each cylinder at about 10 day intervals and the emergent seedlings of <u>S. dulcamara</u> were counted, carefully pulled from the soil and discarded. The screens were replaced, those which had been damaged were noted and data from these cylinders were not included in later analyses. Observations later in the season were less frequently made, usually every two weeks. No attempts were made to monitor the cylinders at the marsh or swamp habitats during the period of flooding.

5.2.2 Greenhouse emergence trials

Greenhouse emergence trials initiated in August of 1981 were designed to investigate the influence of fruit development and burial upon the patterns of seedling emergence arising from bare seeds and seeds confined within intact fruit.

During the first week of August 1981, unripe, ripening and ripe fruits were collected along the fenceline at the field station. Fruit bearing stems were selected at random with the proviso that there be at least five metres between stems. No more than a single fruit of each developmental stage was taken from an infloresence and no more than three fruits of each type were selected per stem. The procedure was repeated until 80 fruits of each type had been collected. In the laboratory the fruits were pooled by ripeness and 50 of each type were randomly selected for treatments requiring intact fruit. The remaining fruits were crushed over wire mesh screens and rinsed with water until the flesh had been removed from the seeds. The intact fruits and the rinsed seeds (after drying for several hours at room temperature) were stored overnight in glass petri plates at 4°C.

The following day, 60 plastic flower pots, each 10 cm in diameter, were filled to within 2 cm of the top with the standard potting soil mixture used in the Plant Sciences Department (cmposition 8 parts loam, 4 parts sand, 2 parts peat, and trace elements). For each developmental class, five intact fruits were placed in each of five flower pots. Each fruit was marked with a small plastic stake, and soil was added to the pot until the fruits were buried to a depth of approximately 0.5 cm. Additional soil was added to another 15 pots until they were filled to the same level as those containing the buried fruits. The intact fruits added to these pots were positioned on the soil surface and, again, each of the five pots assigned to one of the three ripeness classes received five individually marked fruits. The treatments using bare seeds were similar to those using intact fruits, but in each case, 100 seeds were sprinkled evenly over the soil surface. During each of the seven weekly observations the emergent seedlings were counted and carefully removed, and individual records were made for each berry in the treatments using intact fruit. After 10 weeks the experiment was terminated.

5.2.3 Growth cabinet studies

The growth cabinet studies of seed germination patterns were designed to investigate the impact of berry development, seasonality and habitat under controlled conditions. Fruit collections were made in each of the four field habitats at two periods during the summer of 1985. The first harvest was conducted during the third week of July and the second was conducted during the second week of September.

During each harvest, unripe, ripening, and ripe fruits were collected. During the second harvest, an additional category of fruit comprised of berries that had desiccated on the infructecence was collected. The berries were collected from single infructescences borne on stems separated by at least five metres. No more than three fruits of each development class were taken from an inflorescence, and the process was repeated until 20 unripe, ripening and desiccated fruits, and 25 ripe fruits had been taken within each habitat. This imbalance was somewhat reflective of the relative abundance of each class, but, more importantly, allowed a more expanded view of the germination of seeds taken from ripe fruits, the class that preliminary investigations had suggested was most frequently dispersed.

In the laboratory the fruits of each developmental class were pooled, crushed and rinsed with water over screens to separate the flesh from the seeds. Fifty seeds were placed in each glass petri dishes on a double layer of filter paper (Whatman No. 2) and moistened with distilled water. Six plates were prepared for each of the unripe, ripening and desiccated classes and ten plates for the ripe class. The plates were placed randomly on shelves in a growth cabinet offering a warm (25°C) illuminated period of 14 hours alternating with with a ten hour dark period when a temperature of 10°C was maintained. The filter papers were kept moist with distilled water and seeds were removed and enumerated as their radicles emerged. Observations were made daily for 21 days and less frequently afterwards until 70 days had passed and the study was terminated. At that time all seeds had germinated or rotted.

5.2.4 Analytical Methods

All the experimental designs were fixed effects analysis of variance models and were performed using procedures offerred by the SAS statistical package (SAS 1985). When warranted, pairwise contasts were made using the Scheffé multiple contrast option. All proportional data were arc-sine square root transformed prior to analysis,and in each case the rejection probability was 0.05.

The data from the field emergence trials are presented in terms of proportions of total emergence, since the numbers of seeds contained within each intact fruit could not be determined without damaging the berry. Examination of 30 intact fruits selected randomly from the bulk collection taken in 1981 at the field station habitat did reveal an average of about 30 seeds per fruit, however, and some comparison of estimated seedling production rates could be made.

As the number of seeds added to each flower pot used in the bare seed treatments of the greenhouse emergence study was known, it was possible to determine the proportion of seeds producing seedlings. Factorial analyses of variance were conducted for each census date. The analyses for the census dates of the intact fruit treatments of this study were performed on seedling frequencies only, because the numbers of seeds within an intact fruit could not be pre-determined and most had broken apart by the end of the investigation

In the growth cabinet study, an analysis of the effects of habitat and harvest date on the germination of seeds from ripe fruit was conducted.

Germination data from the seeds of unripe and ripening fruits were added in a separate analysis where ripeness became a factor additional to harvest date and habitat. As desiccated fruits were available in sufficient numbers to warrant collection only during the second harvest, a third analysis was conducted for the second harvest data, with desiccated fruits representing an additional develpmental stage.

The general shape of the cumulative germination patterns observed in the growth cabinets for each combination of developmental stage, harvest and habitat factors were similar except for apparent differences in the total proportions of seeds germinating and the rates of germination. It was decided to focus upon these discrepancies and two dependent variables were selected for analysis total percent germination and the number of days required for 50% of the germinations to occur.

5.3 Results

5.3.1 Field emergence

In the studies conducted in the field station habitat, seedling emergence was mostly restricted to the spring months, regardless of whether bare seeds or intact fruit had been sown. By the end of May in any year most seedlings had emerged, although a very few new seedlings arose as late as mid-August. At the marsh and swamp habitats the pattern was different. In both habitats no seedlings emerged until the flood waters subsided. This occurred in the third week of June in 1983 and the third week of July in 1984. The majority of seedlings then arose over the next three weeks, but the occasional one could be found as late as mid-October. No seedlings of S. dulcamara were ever found in the control cylinders of any study.

General summaries of the yearly patterns of emergence for each study are presented in Table 5.1 for the seed treatment and Table 5.2 for the fruit treatment. Also given in the tables is the proportion of seeds to produce emergent seedlings over the entire study. For the fruit treatment total seed number was estimated on the basis of the mean value of 30 seeds per fruit determined from a subsample of ripe fruits taken in 1981 at the field station habitat.

The vast majority of seedlings to emerge from the bare seed treatment of the field studies did so in the first year following sowing. The lowest mean first year percentage of total emergence occurred in the 1981 field station study (89%), a value significantly lower than all others. In the second year the percentage emergence in the 1981 field station study again deviated significantly from the rest, but in this case its value was greater. The only seedlings to emerge in a third year of observation were also found in that study.

The percentage of bare seeds to produce seedlings also varied amongst the studies. The percentage of bare seeds producing seedlings at the field station varied from 66.7% for seed sown in 1981 to 46.8% for bare seeds sown in 1983. The percentage of seedlings arising from bare seeds sown in 1982 at the field station was greater than at either the marsh or swamp habitats.

Table 5.1 Yearly proportion of total seedling emergence in the field from the bare seed treatments.

A. <u>Bare seed treatment</u>

Year	Study				
	Labatt 81	82	83	Marsh 82	Swamp 82
One	0.891[1] a[2]	0.983 b	0.967 b	1.000 b	0.999 b
	0.117[3]	0.032	0.058	0.000	0.005
Two	0.101 a	0.017 b	0.033 b	0.000 b	0.001 b
	0.115	0.032	0.058	0.000	0.005
Three	0.008 a	0.000 a	---	0.000 a	0.000 a
	0.000	0.000	---	0.000	0.000
Four	0.000	---	---	---	---
	0.000	---	---	---	---
Proportion of seeds to produce seedlings					
	0.669[1] a[2]	0.613 ab	0.468 ab	0.374 c	0.458 c
	0.162[3]	0.163	0.214	0.250	0.248

1. Mean value.

2. Values followed by same letters within the same rows are not significantly different ($p < .05$).

3. Standard deviation.

Table 5.2 Yearly proportion of total seedling emergence in the field from the intact fruit treatments.

B. Intact fruit treatment

			Study		
Year	Labatt 81	82	83	Marsh 82	Swamp 82
One	0.317[1] a[2]	0.910 b	0.873 bc	1.000 c	0.988 c
	0.359[3]	0.161	0.209	0.000	0.052
Two	0.594 a	0.090 bc	0.127 b	0.000 c	0.012 c
	0.348	0.161	0.209	0.000	0.052
Three	0.008 a	0.000 a	---	0.000 a	0.000 a
	0.120	0.000	---	0.000	0.000
Four	0.011	---	---	---	---
	0.033	---	---	---	---
Proportion of seeds to produce seedlings[4]					
	0.425[1] a[2]	0.355 a	0.436 a	0.462 a	0.554 a
	0.182[3]	0.166	0.158	0.151	0.268

1. Mean value.

2. Values followed by same letters within the same rows are not significantly different ($p < .05$).

3. Standard deviation.

4. Values based one estimate of a mean of 30 seeds per fruit.

The emergence patterns for the whole fruit treatments in the swamp and marsh studies closely paralleled the bare seed results, with the great majority of seedlings emerging in the first year. Similarly, the emergence patterns of the 1982 and 1983 field station studies echoed those of their bare seed counterparts. In the 1981 field station study, however, more seedlings emerged from intact fruits during the second year after sowing than during the first year.

Based on the estimate of 30 seeds per fruit, the emergence success of the intact fruit treatments could be estimated. Although mean values ranged from 35.5% for the 1982 field station study to 55.4% in the swamp study, the differences were not significant. Because of the inconsistent effects of the treatments across the studies and the estimation required for the intact fruit treatments, only very general observations can be made between them. There did not appear to be major differences between seedling production from bare seeds or intact fruits at the marsh or swamp or field station in 1983, but more seedlings arose from bare seeds than from fruits in the 1981 and 1982 studies at the field station.

As mentioned earlier, the results presented above refer only to those cylinders for which the screen coverings were undamaged, as it was impossible to evaluate the subsequent loss of seeds or fruit. By far the greatest source of damage was rodents, as evidenced by the holes gnawed through the the mesh screening and the deposits of faeces. Rodent damage, which was restricted to the fruit treatment over the first winters at the field station, accounted for a loss of 18 of the 35 cylinders in the 1981 study, four of the 18 cylinders of the 1982 study, and one of the 18 set out in 1983. Additional small numbers of cylinders were lost through frost heaving or breakage of the elastic bands securing the screening. There was no evidence of losses to rodents at the marsh or swamp habitats.

5.3.2 Emergence in the greenhouse

Figure 5.1a depicts the cumulative emergence patterns for seedlings arising from bare seed in the greenhouse emergence study for each ripeness stage and depth of burial. For each census date there was a significant ripeness effect. After one week the ripe seeds had produced significantly more seedlings than either the ripening or unripe seeds. From then onwards the proportion of seedlings produced by unripe seeds was less than the others. By the final census date mean emergence was 56.8% for unripe seeds and 76.9% and 84.5% for ripening and ripe seeds, respectively. From the second week onwards, seeds which had been buried yielded more seedlings, and by the last census date a mean of 79.8% of the buried seeds had produced seedlings, in contrast to 65.7% of the surface sown seeds.

Figure 5.1b depicts the mean cumulative frequencies of seedling emergence for those intact fruits eventually producing seedlings. In contrast to the bare seeds, emergence was delayed from intact fruits; very few had produced seedlings by the third week and the first significant factor effects were not evident until week four. At that time the mean number of seedlings to emerge from ripe fruits was 9.6, compared to 4.7 for the ripening and 0.4 for the unripe. By the sixth week the ripe fruits had produced significantly more seedlings than only the unripe fruits, and at week 10 there was no significant ripeness effect. At observations from

Figure 5.1 Cumulative seedling emergence inthe greenhouse. A. Bare seed treatment. B. Intact fruit treatment.

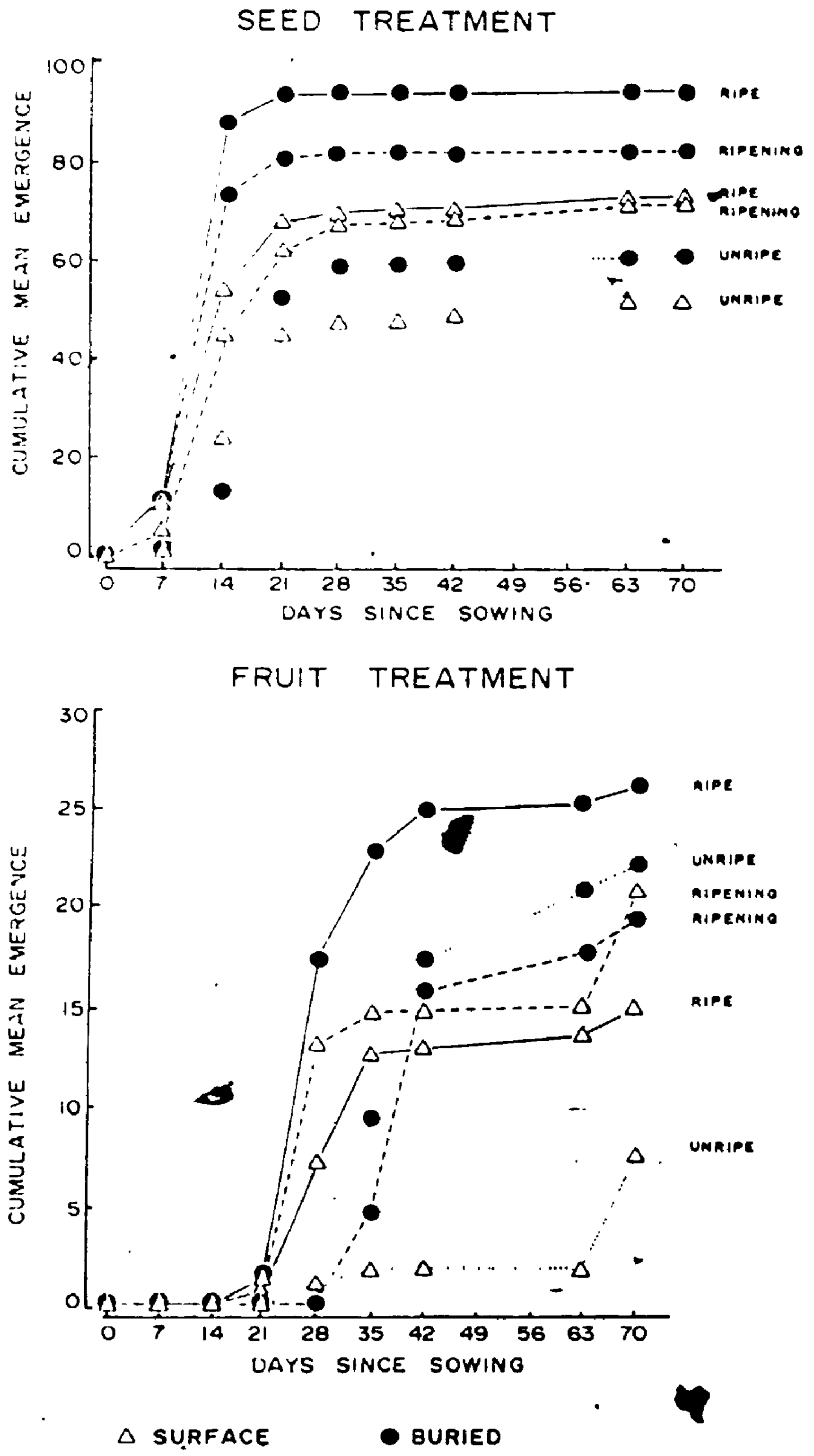

SEED TREATMENT
CUMULATIVE MEAN EMERGENCE
0
20
40
60
80
100
DAYS SINCE SOWING
0
7
14
21
28
35
42
49
56
63
70
RIPE
RIPENING
RIPE
RIPENING
UNRIPE
UNRIPE
FRUIT TREATMENT
CUMULATIVE MEAN EMERGENCE
0
5
10
15
20
25
30
DAYS SINCE SOWING
0
7
14
21
28
35
42
49
56
63
70
RIPE
UNRIPE
RIPENING
RIPENING
RIPE
UNRIPE
△ SURFACE
● BURIED

Table 5.3 Change in numbers of intact fruits producing emergent seedlings in the greenhouse.

Treatment	Ripeness	Number of days after sowing							
		7	14	21	28	35	42	63	70
Surface	Unripe n = 25	0	0	0	3	4	4	5	13
	Ripening n = 25	0	0	1	9	10	10	11	18
	Ripe n= 25	0	0	0	8	13	15	16	17
Buried	Unripe n = 25	0	0	1	4	9	14	16	17
	Ripening n = 25	0	0	0	0	10	15	16	17
	Ripe n = 25	0	1	1	15	21	21	21	21
	χ^2	0	0.0	2.0	21.8 ***	14.2 *	12.3 *	10.6	1.9

*p < .05; ***p < .001

the sixth week onwards those fruits which had been buried produced significantly more emergent seedlings. At week 10 there was a mean of 16.9 seedlings per buried fruit and a mean of 9.6 for those sown on the surface. The interaction of developmental stage and burial on seedling emergence seemed to enhance rather than confound the main effects. At weeks four and five, much of the interaction might have been attributable to the relatively low percent emergence from the buried ripening and unripe fruits. By week six the high percent emergence from buried ripe fruits and the low percent emergence from surface sown unripe fruits may have contributed most to the interaction.

Not all fruits produced seedlings during the 10 weeks of observation, and the number of fruits with emergent seedlings changed with time (Table 5.3). By the end of the investigation, however, the number of fruits producing seedlings did not differ significantly across the treatment categories. The greatest departures from expected values were consistently found for the surface sown unripe fruits and the buried ripe fruits, especially during the middle portions of the study when a particularly low number of the surface sown unripe fruits and particularly high number of buried ripe fruits had produced seedlings.

Not all fruits produced seedlings during the 10 weeks of observation, and the number of fruits with emergent seedlings changed with time (Table 5.3). By the end of the investigation, however, the number of fruits producing seedlings did not differ significantly across the treatment categories. The greatest departures from expected values were consistently found for the surface sown unripe fruits and the buried ripe fruits,

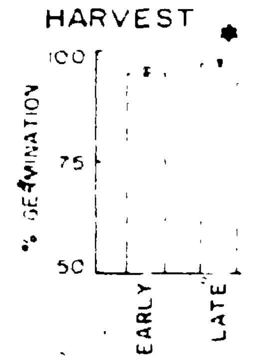
especially during the middle portions of the study when a particularly low number of the surface sown unripe fruits and particularly high number of buried ripe fruits had produced seedlings.

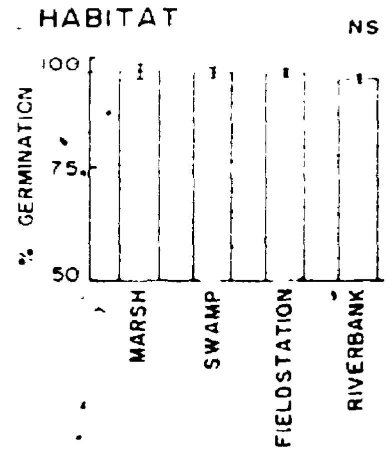
5.3.3 Germination in the growth cabinet

Displayed in Figure 5.2a+b are block diagrams depicting the proportion of seeds germinating and the number of days to 50% germination for the seeds removed from ripe fruits. In each case the results are summarized for the main effects of harvest and habitat, plus the interaction between the two. In all cases total germination exceeded 92% and the only significant effect on total germination was that of harvest date, when the mean germination of 97.4% for the second harvest was slightly higher than the mean of 95.3% for the first harvest. In terms of the number of days to 50% germination the effects of harvest and habitat were both significant. The greater impact was that of the date of harvest when the period to 50% germination was 3.6 days sooner for seeds collected at the later date. The differences amongst the habitats were less. The only significant pairwise contrast was between the seeds from the marsh habitat with the greatest mean, 12.4 days, and the seeds of the swamp habitat which took an average of only 11 days to achieve 50% germination. Although the harvest with habitat interaction was significant the impacts of the main effects were little perturbed, as the seeds from each habitat tended to germinate more quickly when collected during the second harvest and differences between habitats for each harvest were few. It seems that the effect of harvest date was least pronounced for seeds taken at the

Figure 5.2a   Mean values (± one standard deviation) for percent germination of seeds from ripe fruits in the growth cabinet.

* $p(F)<.05$ ** $p(F)<.01$ *** $p(F)<.001$


HARVEST


HABITAT

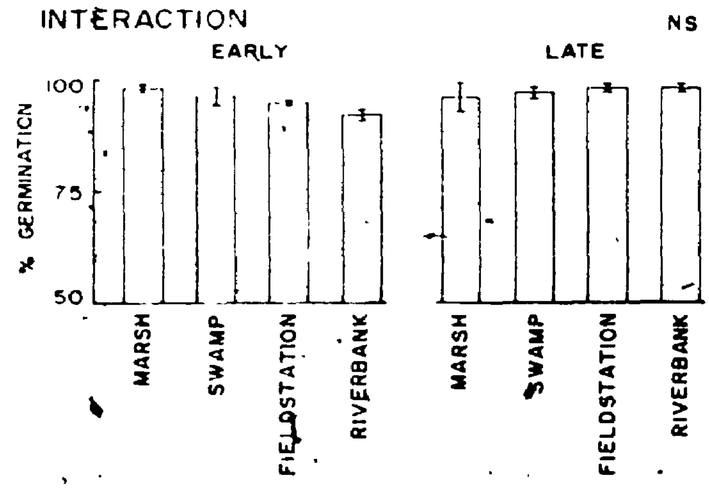
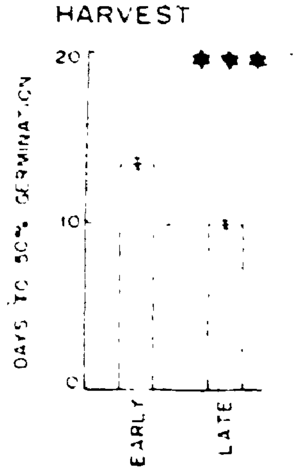
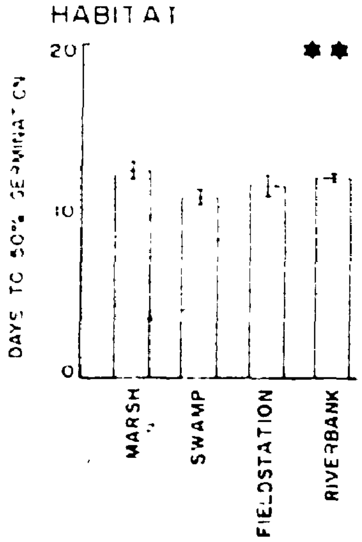

INTERACTION

Figure 5.2b Mean values (± one standard deviation) of the number of days to fifty percent of total germination of seeds from ripe fruits in the growth cabinet.

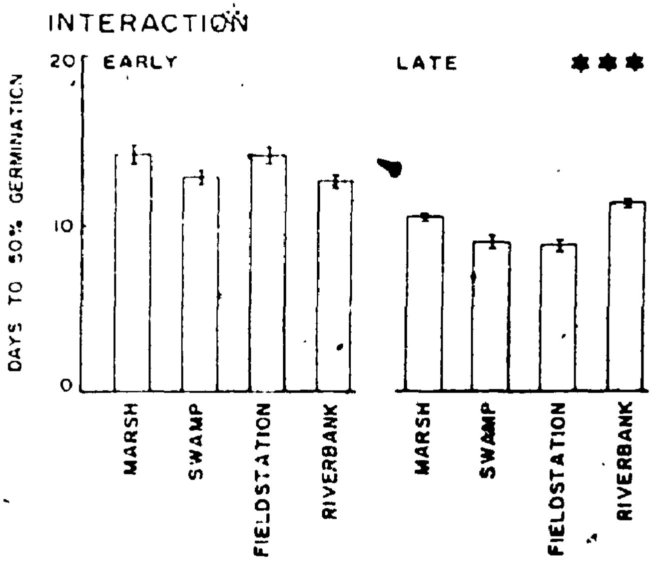
* p(F)<.05 ** p(F)<.01 *** p(F)<.001



HARVEST



HABITAT



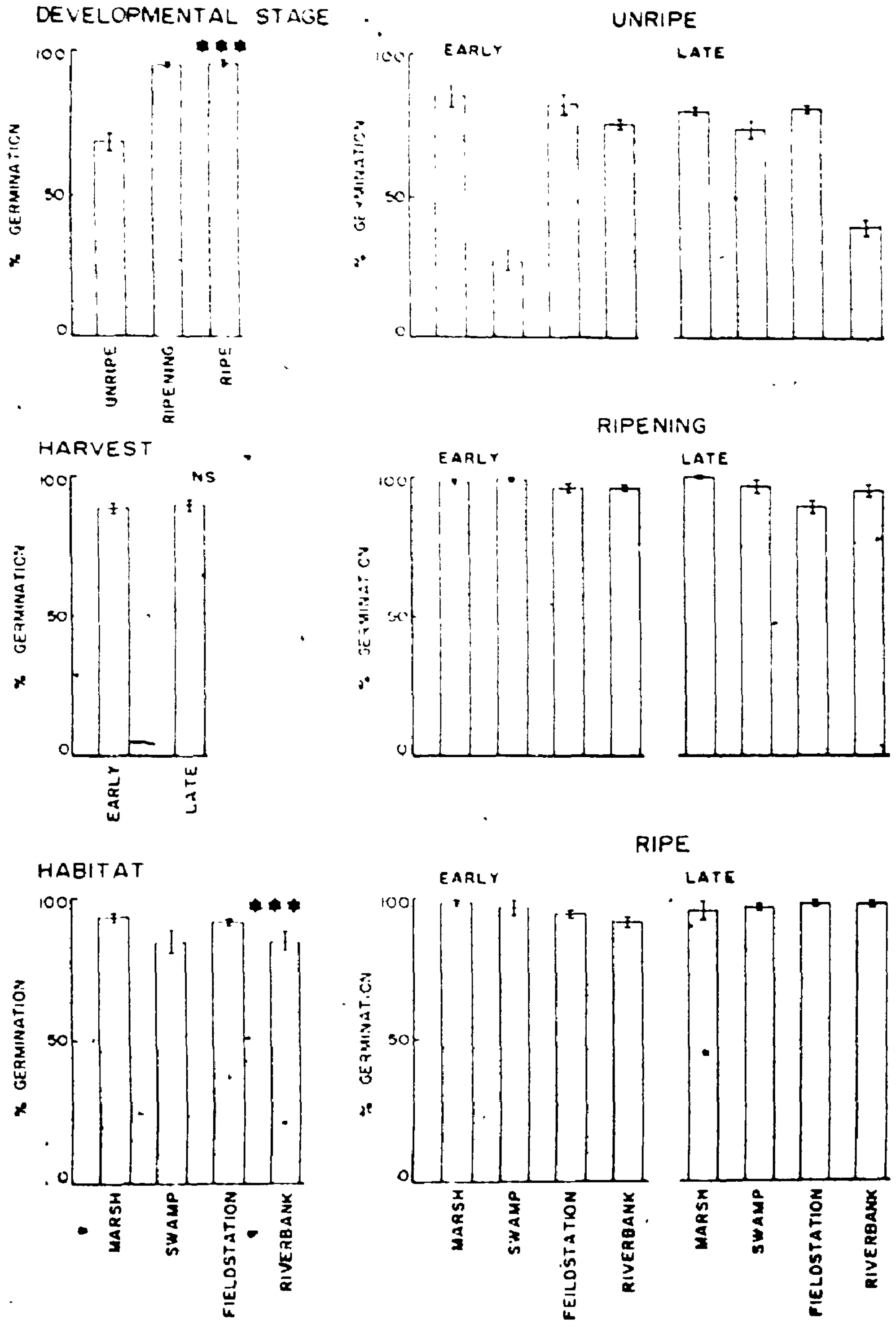
INTERACTION

riverbank habitat and most pronounced for seeds harvested at the field station.

Figure 5.3 displays block diagrams showing the proportions of seeds germinating during the course of the growth cabinet germination study after inclusion of the data from unripe and ripening fruits. In addition to summarizing the main effects Figure 5.3 provides diagrams depicting the results for the habitats and harvests of each ripeness class. The effect of fruit ripeness had the greatest impact on total percent germination; the differences were significant across all ripeness categories. A mean of 68.3% of the unripe seeds germinated, the mean value for ripening seeds was 95.9% and that for ripe seeds was 96.4%. The effect of harvest date was not significant but that of habitat was. The mean for the marsh habitat, 93.7%, was greater than all others, and the mean for the field station seeds, 91.5%, exceeded that of the riverbank seeds which had a mean percent germination of 85% over all developmental categories. All pairwise interactions and the three way interaction between ripeness, date of harvest and habitat of origin were significant, but an examination of the results broken down by habitat and harvest for each ripeness class suggested that much of the interaction was attributable to the performance of seeds taken from unripe fruits. Overall, the germination percentage for unripe seeds was less than for the others, but this trend was partially enhanced for seeds taken from the swamp habitat during the first harvest and for seeds from the riverbank taken during the second. It can be noted that, as a whole, fruit development begins later in the heavily shaded swamp habitat and ends later at the riverbank (pers. obs.); and it is possible that the

Figure 5.3 Mean values (± one standard deviation) of percent germination of seed from unripe, ripening and ripe fruits in the growth cabinet.

* $p(F) < .05$ ** $p(F) < .01$ *** $p(F) < .001$


DEVELOPMENTAL STAGE
***
100
50
0
% GERMINATION
UNRIPE
RIPENING
RIPE
UNRIPE
EARLY
LATE
100
50
0
% GERMINATION
HARVEST
NS
100
50
0
% GERMINATION
EARLY
LATE
RIPENING
EARLY
LATE
100
50
0
% GERMINATION
HABITAT
***
100
50
0
% GERMINATION
MARSH
SWAMP
FIELDSTATION
RIVERBANK
RIPE
EARLY
LATE
100
50
0
% GERMINATION
MARSH
SWAMP
FEILDSTATION
RIVERBANK
MARSH
SWAMP
FIELDSTATION
RIVERBANK

unripe fruits in both instances might have been particularly immature.

Figure 5.4 presents block diagrams as in Figure 5.3, but in this case the summaries are for the number of days to achieve 50% germination. All three main effects were significant. Each ripeness class was distinct from the others, with the rate increasing with fruit maturity. As was the case when the seeds from ripe fruit were considered alone, the seeds taken during the second harvest germinated faster, by some 2.8 days. The habitat differences were also small, with the seeds of the marsh habitat germinating more slowly than all others. The interaction between ripeness and harvest might have arisen because of the weaker trend for the less mature fruit, particularly the unripe fruits. The other significant interaction was that of harvest and habitat, but like the previous case, the second harvest seeds germinated at least as fast or faster than those from the first harvest. The trends of the main effects were generally supported at the level of the three way interaction, but theywere least pronounced amongst the unripe seeds, and within each developmental class it appeared that seeds from the riverbank habitat were least affected by the date of harvest.

The overall effects observed for the ripeness and habitat were maintained when the results for seeds from desiccated fruit (taken only during the second harvest) were analysed in conjunction with the second harvest data from the other fruit categories (Figures 5.5 and 5.6). Again there was no difference in mean total percent germination of seeds from ripening (95%) and ripe fruits (97.4%) but fewer seeds (69%) from unripe fruits germinated. The mean total germination for the seeds from desiccated fruits (85.7%) was intermediate. Across all the ripeness classes the habitat effect

Figure 5.4 Mean values (± one standard deviation) of the number of days to fifty percent germination of seeds from unripe, ripening and ripe fruits in the growth cabinet.

* $p(F)<.05$ ** $p(F)<.01$ *** $p(F)<.001$

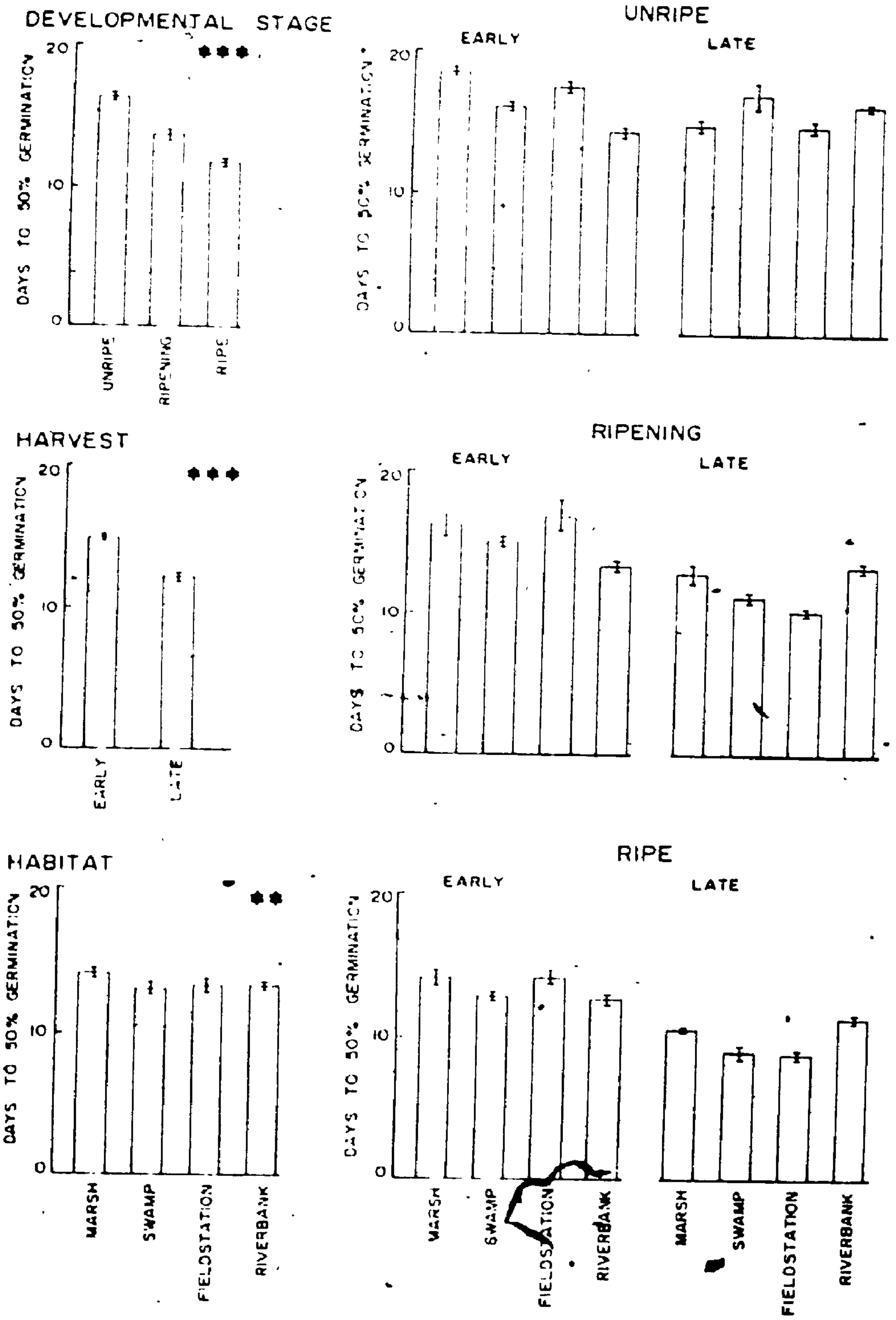

DEVELOPMENTAL STAGE
***
DAYS TO 50% GERMINATION
20
10
0
UNRIPE
RIPENING
RIPE
UNRIPE
EARLY
LATE
DAYS TO 50% GERMINATION
20
10
0
HARVEST
***
DAYS TO 50% GERMINATION
20
10
0
EARLY
LATE
RIPENING
EARLY
LATE
DAYS TO 50% GERMINATION
20
10
0
HABITAT
**
DAYS TO 50% GERMINATION
20
10
0
MARSH
SWAMP
FIELDSTATION
RIVERBANK
RIPE
EARLY
LATE
DAYS TO 50% GERMINATION
20
10
0
MARSH
SWAMP
FIELDSTATION
RIVERBANK
MARSH
SWAMP
FIELDSTATION
RIVERBANK

Figure 5.5 Mean values (± one standard deviation) of percent germination at the second harvest of seeds from unripe, ripening, ripe and desiccated fruits in the growth cabinet.

* $p(F) < .05$ ** $p(F) < .01$ *** $p(F) < .001$

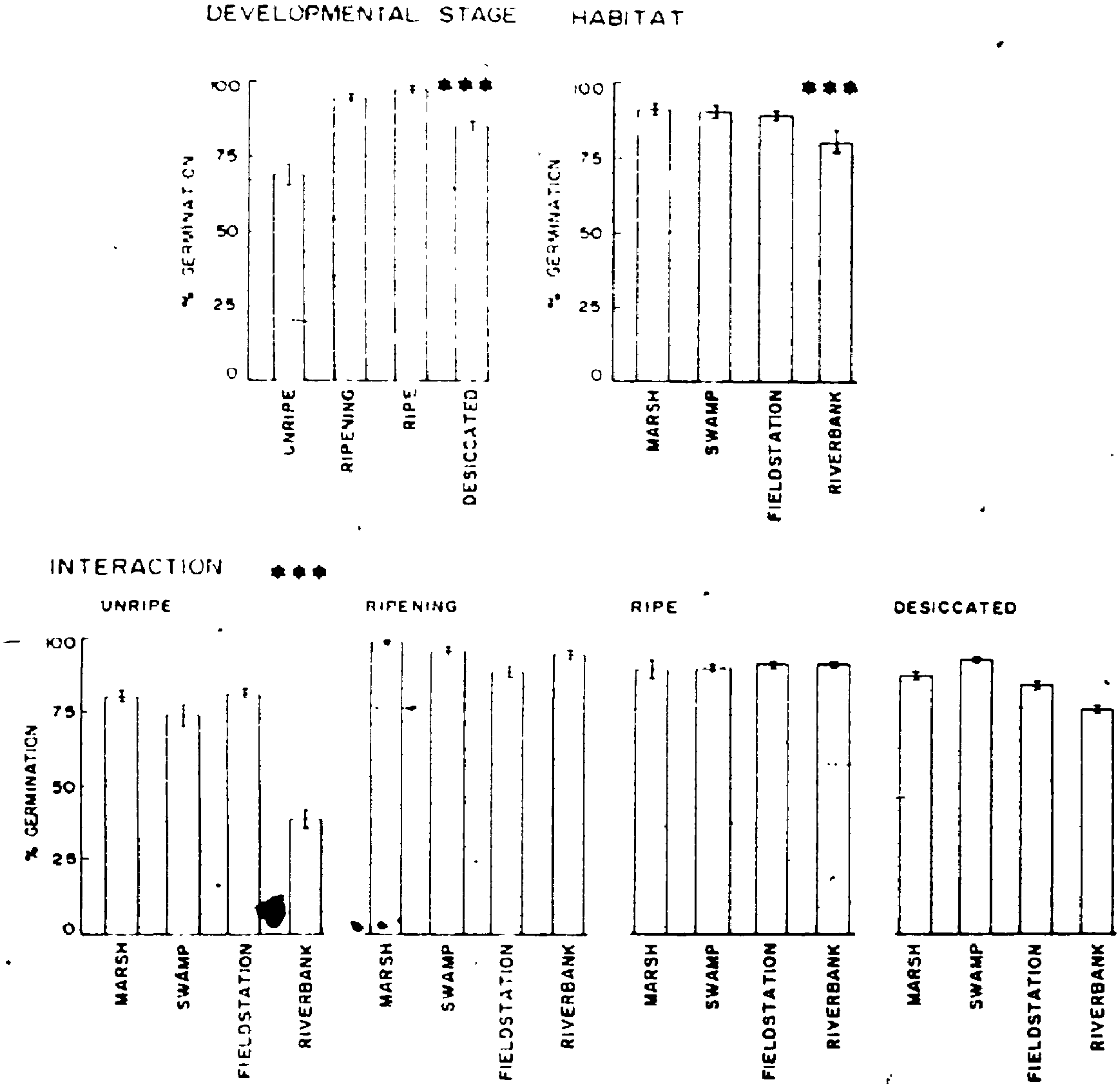
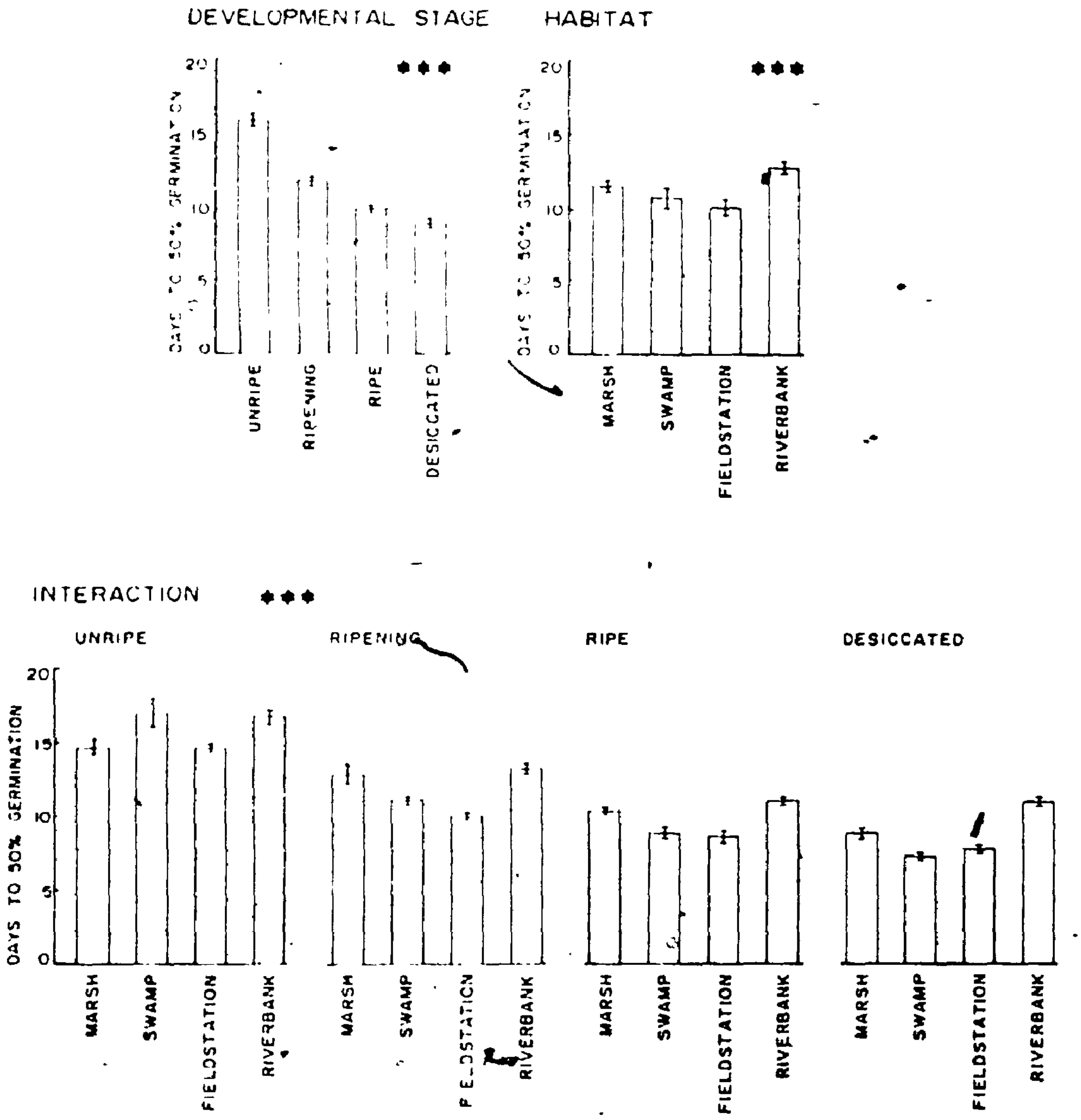

DEVELOPMENTAL STAGE
HABITAT
* * *
% GERMINATION
100
75
50
25
0
UNRIPE
RIPENING
RIPE
DESICCATED
MARSH
SWAMP
FIELDSTATION
RIVERBANK
INTERACTION
* * *
UNRIPE
RIPENING
RIPE
DESICCATED

Figure 5.6 Mean values (± one standard deviation) of the number of days to fifty percent germination at the second harvest of seeds from unripe, ripening, ripe and desiccated fruits in the growth cabinet.

* $p(F)<.05$ ** $p(F)<.01$ *** $p(F)<.001$


DEVELOPMENTAL STAGE
HABITAT
DAYS TO 50% GERMINATION
0
5
10
15
20
***
UNRIPE
RIPENING
RIPE
DESICCATED
MARSH
SWAMP
FIELDSTATION
RIVERBANK
INTERACTION ***
UNRIPE
RIPENING
RIPE
DESICCATED

on total percent germination was significant but the differences were small. The mean values of 91.8%, 91.2% and 89.8% for the marsh, swamp and field station habitats, respectively, did not differ significantly, but all were greater than the result for the riverbank habitat (80.3%). This deflection of the riverbank results was likely the result of the very low percent germination observed in this habitat for seeds from unripe fruit, 39.7%, and this finding probably represents the major contribution to the significant ripeness with habitat interaction.

Germination rates differed amongst all ripeness classes in the second harvest results. The seeds from the desiccated fruits germinated most quickly, reaching 50% after a mean of 9.0 days. Seeds from ripe fruits took an average of 9.9 days and those from ripening and unripe fruits took means of 11.9 and 15.9 days, respectively. Differences attributable to the collection habitats were again small. The mean of 13 days for the riverbank habitat seeds was greater than all others; the mean for the marsh habitat (11.6 days) was greater than the mean of 10.3 days obtained for the field station seeds. The values for the field station and swamp (10.9 days) were not significantly different, however. Although the ripeness with habitat interaction was significant in this analysis, the rankings of the ripeness patterns for each habitat were consistent with the main effect, as were the habitat rankings, in the main. The effect of ripeness was most strongly pronounced for the swamp seeds, with means ranging from 17 days for seeds from unripe fruit to a mean of 7.5 days for the seeds from the desiccated fruits.

5.4 Discussion

Mechanisms which alter the dormancy of seeds or delay the emergence of seedlings can have great impact on the patterns of germination, seedling emergence and, ultimately, the survival of new plants arising from a cohort of seeds (Cavers 1983). In the studies reported here the temporal patterns of germination and seedling emergence of Solanum dulcamara are influenced by a number of factors, namely, the presence of the intact fruit, propagule ripeness, harvest date, and habitat.

5.4.1 Question 1. What is the impact of the intact propagule upon the patterns of seedling emergence under various field and laboratory conditions?

The most dramatic impact observed was that of the fruit flesh, more precisely the intact fruit, on seedling emergence. When bare seeds of Solanum dulcamara were scattered on the surface of the soil or, as done by Roberts and Boddrell (1983), Roberts and Lockett (1977) and Adams (1927), incorporated with soil mixtures and and placed outside for the winter, the great majority of seedlings emerged in the following growing season. My studies recapitulated those observations but also showed that some bare seeds can produce seedlings in subsequent years. The effects were quite different and more variable when intact fruits were added to the field cylinders. In particular, the proportions of the seedlings to emerge in later years was higher for the intact fruit treatment. The most dramatic contrast was observed in the 1981 field station study when the majority of all the seedlings emerged in the second rather than first year, and some seedlings emerged as late as four years after sowing. In this fashion the contribution of a given year's cohort of seeds to future seedling pools might be extended over a number of years rather than being restricted to essentialy the following growing season.

In the greenhouse, seedling emergence from intact fruit was also delayed relative to the bare seed treatment. Moreover, emergence from the intact fruits was staggered over a much longer period as new fruits contributed seedlings over the course of the study. Such a staggering of emergence may have occurred in the field emergence studies as well, but it was not possible to monitor individual fruits in the field. If such were the case, however, new seedlings could emerge at various times during a single growing season and not be restricted to the environmental conditions of only a small portion of the growing season.

Too little data exists to assess the generality of the effects of intact propagules on seedling emergence over the array of species producing fleshy propagules. However, such effects may be especially important for those species like *S. dulcamara* which don't have strongly dormant seeds, because a cohort of seeds would be able to sample a suite of establishment environments existing over a number of years or over the course of a single season.

5.4.2 Question 2. What is the impact of the stage of development of the propagule on germination and seedling emergence?

The timing of seedling emergence was also affected by the stage of development of the fruits. In the middle period of the greenhouse emergence trials the numbers of fruits to have produced emergent seedlings varied amongst the ripeness categories. During this period a low number of surface sown unripe fruits produced seedlings and a high number of buried ripe fruits produced emergent seedlings. In the growth cabinet studies seeds from fruits at all stages of development were capable of germination, although those from the less mature fruits germinated more slowly, and seeds from unripe or desiccated fruits were less likely to germinate.

For S. dulcamara, Ardisia revoluta (Foster 1977), and Amyema preissii (Lamont 1982 a), at least, fruits which are lost from the parent while not fully ripe need not be considered as lost in terms of their ability to produce seedlings. Whilst immature seeds may produce fewer seedlings, the results of the greenhouse and growth cabinet studies with S. dulcamara show that the numbers can still be substantial. In addition, the slower rate of germination of immature seeds might serve to spread germination over a greater portion of a growing season, or possibly over more than one year.

The greenhouse seedling emergence trials also included a treatment in which seeds and intact fruits were buried to a depth of about 0.5 cm. As a result of burial the chances of producing a seedling were increased. It is not uncommon for similarly buried seeds, faced with an environment less sensitive to fluxes of light, temperature and moisture availability, to produce more seedlings than those sprinkled on the soil surface (Harper 1977), but the greenhouse trials described here stand, to the best of my knowledge, as the first detailed accounts of the effects of burial on seedling emergence from intact fleshy propagules.

5.4.3 Question 3. Does the season of the year in which the fruits are presented affect germination potentials?

The date of harvest also affected seed germination rates. During the growth chamber studies, the seeds from all fruit types taken in the second harvest germinated at a faster rate than their counterparts from the first harvest, especially if the fruits were ripe when collected. Although the magnitude of the harvest effects observed in the favourable germination environment of the growth chamber were small, the effect might still be important in the field. A greater dormancy of seeds produced and dispersed earlier in the year might decrease the likelihood of germination before the onset of winter. Those seeds dispersed later in the season might not need to be as dormant, since they would more likely encounter environments where ambient conditions do not promote germination. While suggestive, the harvest effect needs further investigation to be well understood, as the seeds were harvested twice only and the germination studies were restricted to growth cabinet conditions.

5.4.4 Question 4. Are there differences attributable to the habitat in which the seeds were produced?

Although the seeds from the marsh habitat tended to germinate slightly faster and in greater numbers than those from other habitats, the influence of the field habitats seemed to be quite small over all. The major exceptions to this were the unusually low percentage germination found for unripe fruits taken from the swamp habitat during the first harvest and from the riverbank during the second. There was also some indication that the seeds produced at the riverbank were less responsive to the harvest effects. Petzel (1985) also found little effect, if any, on the germination of seeds of *S. dulcamara* taken from a selection of habitats in Europe.

The results of these studies add insights to our knowledge of the ecology of fleshy propagules. Particularly important is the extension of the ecological roles played by the flesh to post-dispersal patterns of seedling emergence. Although varying from year to year and from habitat to habitat, it can in general be said that seedling emergence was delayed when seeds were confined within the intact fruits of *Solanum dulcamara*. The stage of development, too, may play an important post-dispersal role. Unripe, ripening, ripe and desiccated fruits all contained seeds capable of germination, but more seeds germinated and at faster rates when the fruits were more mature. Even during a single season of fruit production there can arise different potentials for germination, as the seeds harvested earlier in the season were slower to germinate than those collected later. For *S. dulcamara*, at least, the habitats from which seeds are taken play only a minor role in subsequent patterns of germination.

CHAPTER SIX

SUMMARY AND CONCLUSION

6.1 Introduction

A variety of annual, seasonal and habitat patterns in the production, dispersal and structure of the fleshy propagules produced by some plant species have been described in the literature (see Chapter one). The theoretical interpretations of these patterns have concentrated on implications for dispersal mediated by animals, and particularly upon the dispersal of ripe propagules. In this respect, the traditional view is that the fleshy component of the ripe propagule provides a nutritive reward to animals and serves as a "bribe" payed for the removal of seeds and their subsequent deposition. If the deposited seed is viable and rests in an environment conducive to germination and subsequent growth, dispersal has been successful and the plant, in return, has received its reward. Relatively little attention has been given to the potentially valid dispersal episodes represented by the loss of unripe, ripening or desiccated propagules from the infructescence, or to the implications of dispersal by inanimate means. Seed germination and seedling emergence patterns have also received little in the way of detailed study. The germination potentials of seeds found in non-ripe fruits and the impact of the intact propagule on seedling emergence have been particularly neglected.

In this thesis, examinations were made of aspects of the dispersal ecology of Solanum dulcamara, a perennial species that produces fleshy berries throughout most of the growing season in a disparate array of habitats near London, Ontario. The traditional focus on ripe propagules was an important theme to the investigations, but the view was widened to include a consideration of the possible dispersal implications of fruits lost from the infructescence at other stages of development and the implications of dispersal of intact fruits. To varying extents, annual, seasonal and habitat variations were examined. The following subsections present the key findings of the investigations.

6.2 The importance of fruit developmental stage at dispersal.

Although non-ripe fruits of S. dulcamara generally contained more unfilled "bad" seeds and exhibited greater variability in the weights of individual good seeds, they did contain viable seeds. Overall, 68.3% of the seeds from unripe fruits, 95.9% of the seeds from ripening fruits, 96.4% of the seeds from ripe fruits and 85.7% of the seeds from desiccated fruits germinated in the growth chamber. This pattern was echoed in the greenhouse, where 56.8% of the seed from unripe fruits, 76.9% of the seeds from ripening fruits and 84.5% of the seeds from ripe fruits produced seedlings. Consequently, any losses of unripe, ripening or desiccated fruits from an infructescence should be considered potentialy valid dispersal episodes rather than deficits to the dispersal budget.

The dispersal of non-ripe fruits was important in a quantitative sense. In fact slightly more than 50% of the fruits were not ripe when dispersed: 33.5% were unripe, 13.2% were ripening and 5.2% were desiccated. Although the nature of the dispersal pathways, be they animate or inanimate, for each fruit type was not determined, it was likely that there were differences given the great variation in fruit colour, texture and structure. In addition only ripe fruits were observed to be consumed by animals. An important outcome of different dispersal pathways would be a widening of the range of potential establishment habitats that could be reached by the seeds.

The potential contributions of each fruit type to seed dispersal varied from habitat to habitat. In the swamp, for example, where the productivity of S. dulcamara might have been the lowest, a high percentage of unripe fruits dispersed, and those unripe fruits that did disperse were retained for relatively short periods only. Since unripe fruits contained viable seeds, their loss from an infructescence would represent more than a culling of excess fruits and would indicate some possible regenerative return from investments already made towards their development.

The dispersal implications of non-ripe fruits included a temporal component. The losses of fruits at different stages of development extended the period during which fruits were dispersed from an infructescence: unripe fruits would be dispersed before those fruits that would undergo further development before dispersal. The generally slower rates of germination and seedling emergence from unripe and ripening seeds would also broaden the spectrum of establishment conditions faced by a cohort of seeds, even within a single environment.

6.3 Annual trends.

Considerable annual variation in the patterns of production and loss have been described for many species, and annual variation was a component of several of the studies described here, namely, the weekly study of bud and fruit fates and the seedling emergence trials conducted in the field habitats. In terms of the numbers of buds and fruits produced by the marked inflorescences, the only significant difference between 1982 and 1985 was the greater numbers of ripening and ripe fruits produced in 1982. Although a greater percentage of the 1985 fruits dispersed, much of the difference may have been attributable to the numerically and proportionately greater losses of unripe fruits. Fruits ripened more quickly in 1985, and dispersant fruits, especially if ripe, were retained for shorter lengths of time. In addition, there were some rather pronounced yearly differences in the patterns of seedling emergence from the intact fruit treatment of the field emergence trials.

6.4 Seasonal trends.

Seasonal differences in the attributes of fleshy propagules and in the patterns of their production and dispersal have received a great deal of attention, and a number of, often conflicting, theoretical models have been developed. Some studies in temperate environments have identified seasonal differences in the attributes of the fleshy propagules produced by species bearing ripe propagules early in the season versus the ripe propagules produced later in the season by other species. Similar contradictions in observation and theory concern the patterns of fruit production and dispersal rates.

Given the lack of congruence amongst the observations and interpretations of seasonal differences in the patterns of fleshy propagule production and dispersal, it is not surprising that the patterns observed for Solanum dulcamara conform and conflict with aspects of them all. It may also be inappropriate to expect a species like S. dulcamara that produces ripe fruits continuously throughout much of the growing season to conform very closely with models based on a sequence of species producing ripe propagules over relatively short time periods.

A trade-off in fruit numbers and qualities may have led to seasonal differences in the efficiency of seed production and dispersal. Seed production may have been more efficient early in the season. Although the seedloads of the early formed ripe fruits were similar to those of the later formed ripe fruits in terms of numbers and weights, the early fruits had less flesh and lower flesh-to-seed dry weight ratios. In addition, more fruits, and hence more seeds, were produced on the infructescences formed early in the year, despite a lack of seasonal difference in the numbers of buds found on the inflorescences. Seed production later in the season may have been less efficient. Fewer fruits were set, and those that ripened had more flesh and higher flesh-to-seed dry weight ratios than the early fruits. The production of such potentially more rewarding fruits did not, however, lead to an increase in dispersal rates. It is possible that adjustments to the fleshy component, with a possible sacrifice in overall seed production, were sufficient only to maintain the rate of dispersal at a time when interspecific competition for dispersal agents might be greatest. The ripe fruits formed in the common garden later in the season also had higher flesh-to-seed dry weight ratios that the early fruits. However it appeared that adjustments in both the flesh and seed components effected the change.

The destruction of fruits that, in some theoretical views, may arise if ripe fruits are not quickly dispersed or if ripening rates of early fruits are too rapid, was not observed for Solanum dulcamara. The early fruits actually ripened more quickly than the later fruits and rarely was there evidence of damage to the fruits by insects or decay.

If the slower rates of germination observed in the growth cabinet for seeds from fruits (especially if ripe) formed early in the season would occur in the field, fewer seedlings might emerge at a time when the growth of other plants would be near the seasonal maximum and when there might be limited opportunity for seedlings to grow to a stage capable of surviving the winter. Seeds dispersed later in the season, in contrast, would be less likely to encounter conditions conducive to germination, and the late seeds may be more reliant on a suppression of germination by the environmental conditions of fall and winter.

6.5 Habitat trends.

Major differences in the attributes of the ripe propagules (mostly confined to the fleshy component) might reflect differences in the productivity of Solanum dulcamara across the set of field habitats and a greater fitness component of the seed rather than flesh component of the propagule. The number of buds per inflorescence, the number of inflorescences per stem, and the probability of fruit set were lowest in the swamp where the shady and seasonally flooded conditions may have been the least favourable to the productivity of the species. In comparison, the greater numbers of inflorescences per stem, the higher numbers of buds per inflorescence and the high percentages of buds producing fruits suggested that the environments at the riverbank and, to some extent, the field station were more favourable to the productivity of S. dulcamara. In addition, the fruits ripened more quickly at the riverbank, and a greater percentage of fruits dispersed there than at any other habitat. Although the individual ripe propagules at the swamp and marsh, in contrast to those at the riverbank and field station, might have offered less absolute and relative reward to animals, given the adjustment to the flesh rather than the seed component, their seeds, upon which fitness more directly rests, might still be dispersed by inanimate vectors or ~~by~~ animals at a later date when alternative food supplies dwindle.

The differences in the attributes of the ripe propagules produced in the marsh, swamp, field station or riverbank habitats were likely the result of phenotypic plasticity rather than pronounced genetic differences amongst the natural populations. In contrast to the fruits from the natural habitats, the ripe fruits from the common garden showed relatively few differences that could be associated with the habitats from which the stem cuttings originated.

Only slight habitat differences in the germination patterns of seeds extracted from the various types of fruits were observed in the growth cabinet studies. It is difficult to assess whether such small differences could be considered adaptive. Certainly, more studies, especially in the field, would have to be conducted before better insights could be gained. The low overall percent germination of the seeds from the riverbank and the similarly low percent germination of the swamp seeds may have largely been a reflection of the seeds from unripe fruits. Seeds from unripe fruits taken early in the season at the swamp, where fruit development seemed to begin earlier in the year (pers. obs.), and seeds from unripe fruits collected in the second harvest at the riverbank, where new fruits were being initiated relatively late in the season (pers. obs.), may have been particularly immature and, as a consequence, less likely to germinate.

6.6 The interactions of year, season, habitat and developmental stage.

Although the studies were designed to focus on the main effects of year, season, habitat and developmental stage, interactions amongst them were identified in some analyses. When the data were broken down jointly to the level of the interacting factors, it appeared that the interactions were usually a matter of degree rather than contradiction. In most cases the rankings were consistently maintained. There were some notable exceptions, however, that suggested that strong theoretical pronouncements should not be based on single year records, or on observations from only a small suite of occuppied habitats, or from records which concern propagules produced during only a portion of the period that a species produces fruits. This may be especially so for a perennial species like Solanum dulcamara that occurs in such a wide variety of habitats and which initiates and ripens propagules over a large portion of the growing season.

6.7 The influence of the intact propagule on seedling emergence.

Dispersal of fruits by inanimate means is likely to result in seeds remaining in intact fruits. Despite reports of intact propagules being lost from many plant species, very little attention has been given to the possible influence of intact fruits upon patterns of germination and seedling emergence. My studies suggest that whether or not seeds remain in the intact propagule has important implications to the population dynamics of S. dulcamara. In the seedling emergence studies conducted in the field the chance of seedling emergence in future years was increased if intact fruits rather than bare seeds were scattered over the ground surface. In the most striking example, the 1981 trial conducted at the field station, the bulk of the seedlings actually emerged in the second rather than the first year after sowing. Seedling emergence from intact fruit in the greenhouse studies was also delayed relative to the bare seed treatments. Moreover, emergence from intact fruits was staggered over a much longer period as new fruits contributed seedlings throughout the course of the studies. These results suggest that a cohort of seeds, when confined to intact fruits, would be able to sample a wider range of establishment settings existing over a number of years or over the course of a single growing season. For species like Solanum dulcamara that do not produce seeds that are in themselves strongly dormant, such effects might be particularly important.

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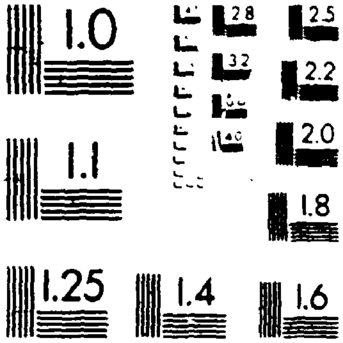

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