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Defining critical habitat requirements for a Canadian 'species at risk' Opuntia humifusa.

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Defining Critical Habitat Requirements for a Canadian 'Species at Risk' *Opuntia humifusa*

by

Maimoona Sahar Moeen

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ABSTRACT

"Critical habitat" is defined in the Species at Risk Act as any habitat in which a species at risk is capable of maintaining self-sustaining populations. Growth and survival of endangered *O. humifusa,* the Eastern Prickly pear cactus, was compared in field and glasshouse experiments. Conditions (light, soil organic matter, moisture, pH, and macronutrients) differed significantly among habitats at Point Pelee National Park (PPNP). The survival of transplanted seedlings in four habitats at PPNP (back beach, primary successional savanna, secondary successional savanna and deciduous forest) indicated that only two of these habitats (the savannas) would be suitable for O. humifusa over the longer term. Shading and macronutrient treatments in the greenhouse indicated growth was favoured by partial shade; nutrient enrichment enhanced growth, but in the field nutrient supplementation would accelerate secondary succession, to the detriment of *O. humifusa.*

DEDICATION

To Moeen, Hira, and Hajra

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Chapter 1 – General Introduction

1.1 Niche and habitat

From an ecological and biogeographical perspective, the habitat of a species consists of those areas that are *actually* occupied and meet the requirements for a species' growth, survival, and successful reproduction (Vandermeer 1972, Higashi 1993, Brown *et al.* 1995, Gaston *et al.* 1999, Gaston 2003, Maschinski *et al.* 2004, Anthony and Connolly 2004).

The notion of 'ecological niche' is one of the most fundamental concepts of ecology, representing the suit of relationships between an individual and all aspects of its environment. Originally defined by Joseph Grinnell (1917) as "ultimate unit…..occupied by just one species or subspecies" and Charles Elton (1927), as "organism's place in the biotic environment" the niche idea was refined later by G. Evelyn Hutchinson (1957) when he distinguished the 'fundamental' niche from the 'realized' niche. It is noteworthy that now classic experiment to discover the factors which restrict the distribution of two species of *Galium* (*G. saxatile and G. sylvestris*) within their realized niches (i.e., adaptation to acidic soils and calcareous soils, respectively) had already been carried out by Tansley in 1917, a full 40 years before Hutchinson's definition of the realized niche was actually introduced.

Hutchinson (1957) famously defined the 'fundamental niche' as an "n- dimensional hypervolume", where n equals the number of environmental and functional variables required to characterize the conditions under which a species will survive and reproduce. The simplest interpretation of this view is that a species occurs everywhere that conditions are suitable and nowhere else (Pulliam 2000). Hutchinson defined the smaller 'realized niche' as that portion of the fundamental niche *actually* occupied by a species; for example, a species will be excluded from those portions of the 'niche space' that are occupied by a dominant competitor.

The fundamental niche can perhaps be best viewed as encompassing the full range of environmental conditions within which a species can successfully survive and reproduce in the absence of deleterious interactions including competition, predation, and parasitism (Kearney and Porter 2004). Within any community, a species free from interference from another species could occupy the full range of variables to which it is adapted. This is the idealized fundamental niche. However the realized niche is more commonly and practically viewed as the circumscribed physical space after exclusion by competitors, predators, and parasites (see Bruno *et al.* 2003).

Hutchinson discussed the Volterra-Gause principle of competitive exclusion in the context of the habitat and the niche of species (Statzner *et al.* 2001). According to Hutchinson (1957), as a result of competitive exclusion a species may frequently be absent from portions of its fundamental niche. Hutchinson (1957) proposed the concept that spatial and temporal habitat variability reduces the probability of competitive exclusion among species because the non-intersection of niches increases with increasing habitat variability (see Statzner *et al.* 2001). It is generally held that environmental heterogeneity accounts for coexistence when there is niche-differentiation (Comins and Noble 1985, Chesson 2000a, b). Niche theory thereby provided a solution to the coexistence problem, based on differentiation in resource use among co-existing species and associated reduction in the intensity of interspecific competition (MacArthur and Levins 1967, Tilman 1980, Schwilk and Ackerly 2005). Hutchinson (1957) also emphasized that habitat variability has to be expressed at the scale of the organism being considered; for example, short-lived and long-lived birds perceive the same seasonal climate differently.

Hutchinson's multi-dimensional niche is a simple but rigorous concept (Pulliam 2000) that led to a 'revolution' in niche theory (Vandermeer 1972). Application of Hutchinson's n-dimensional niche directs attention toward the critical environmental variables that affect a species and the ranges of those variables that permit survival and reproduction (Pulliam 2000). However, it is clear that a species' niche is not something that can be defined entirely in terms of physical environmental factors, but that its boundaries may be set by competition from other species in regions of niche overlap, and also by predators and parasites (Silvertown 2004).

Hutchinson used the word niche to refer to the environmental requirements of a species, emphasizing that 'species, not environments, have the niches'. Of course, all species respond not only to variation in the environment, but they may also themselves change the environment in which they occur. Evidence suggests that most cases of inter-specific competition are indirect interactions between species, mediated by the influence of one species on the limiting resources of another species (see Pulliam 2000).

1.1.1 Ecological niche breadth

The realized niche is usually measured as niche breadth and /or overlap (Glime *et al.* 1987). More precisely niche breadth is "the sum total of variety of different resources exploited by an organism" (Pianka and Parker 1975). Certain interactions between species can affect the breadth of a species' niche along one or several axes. For example, competition for resources or risk of predation could reduce the ecological breadth of a species along the resource axis or food niche axis respectively (Pianka 1973). Niche-assembly theories posit that environmental factors account for observed species' niche measurements; and measurement of species' niche breadth and overlap provide information on species-environment and species-species association (Potts *et al.* 2004). As Hutchinson's multi-dimensional niche represents an essentially unlimited number of dimensions and its environmental variables are arranged in complex way, therefore in practice the fundamental niche cannot be determined completely. Instead, ecologists generally try to determine those resource dimensions which are shared with other species and, therefore, most crucial to the outcome of interactions between species (Silvertown and Lovett-Doust 1993). The fundamental niche is, therefore, not usually quantified (however see Rydin 1987, Wang 1995) but instead merely described (see Malanson 1997).

Successful and widespread colonizing species are believed to be characterized by broad environmental tolerances (Brown and Marshall 1981, Bazzaz 1986). Due to their wide niche breadth, these species are termed "generalists" in contrast to "specialists" with narrow niche breadth characteristic of particular habitats (Sultan *et al.* 1998).

A recent study shows that there is a clear difference between species' niche breadth and species habitat association; and thus habitat heterogeneity has different effects on niche breadth and overlap (Potts *et al.* 2004). The study of these authors indicates that species niche breadths measurements do not account for where a species is found along an environmental axis; however, niche overlap values reflect where a species is found in niche space in relation to another species, and thus niche overlap measurements are concerned with habitat specialization.The results of above study indicates that greater habitat heterogeneity leads to greater habitat specialization.

1.2 Relationship between a species' niche and its occurrence in a suitable habitat

The spatial and temporal distributions of species exist as the outcome of both biotic and abiotic interactions (Brown 1984, Hanski 1998, Pulliam 2000, Gaston, 2003, Holt and Keitt 2005). Notions of the habitat and niche are closely coupled, and as Dennis *et al.* (2003) noted "accurate recognition of the habitat is a prerequisite for the determination of the niche which otherwise can only be notional". This suggests the relationship between habitat and niche is reciprocal, and determination of habitat suitability seek to bring niche and habitat parameters together.

Some have argued that local abundance of a species reflects the ways in which individuals utilize local resources (Gaston 1994), and when local adaptation occurs in different parts of a range, each locally-adapted population may have a distinct niche (Holt 2003). Thus availability or suitability for a population adapted to conditions in the core area of a range may be different from a population existing at one of the margins (Travis and Dytham 2004). To understand the ecological niche and threshold response to environmental changes, geographical range limits have been suggested as an effective point of entry (Holt and Keitt 2005).

It is generally held that habitat suitability declines from the centre of a species' range towards the edge (Hengeveld and Haeck 1982; Brown 1984; Lawton 1993; Guo *et al.* 2005; but see Murphy *et al.* 2005). The central-peripheral model of species distributions assumes that responses to environmental gradients are unimodal and symmetric (Oksanen and Minchin 2002), and that increasing the distance from the optimal site (core habitat) decreases the probability of a site fulfilling the niche requirements of that particular species. There will be decreasing number of local sites where a species can occur at all and, even within these patches, population densities will tend to decline due to the scarcity of resources, and/or as conditions approach the limits that can be tolerated physiologically (Brown 1984).

Discussing the distribution patterns of species abundance Brown (1984) suggested that local abundance reflects how well a particular site meets a species' ecological and physiological requirements along diverse niche axes. He argued that these parameters are spatially autocorrelated. Thus the closer the sites are to one another, the closer and more similar these sites should be in their capabilities for meeting the multi-dimentional needs of the species (but see Murphy *et al.* 2005).

1.2.1 Habitat suitability at the edge of species range

Many species tend to be restricted to quite specific habitats and microhabitats (e.g., Carter and Prince 1985, Thomas 1993, Yagami and Goto 2000, Gaston 2003). Such habitats occupied at the range edge may be different from those occupied elsewhere in the range (Carter and Prince 1985; Yagami and Goto 2000, Jones *et al.* 2001) and may reflect the absence of conditions that make more typical habitat difficult or impossible to occupy, or changes in conditions that render otherwise unusual habitats more favourable (Gaston 2003). For example, *Picea rubens* (red spruce) occurs at its lower elevational range limit growing as small disjunct populations in bogs, a habitat unusual for the species elsewhere in its range (Webb *et al.* 1993). Other examples include the 'habitat shifts' of species on south-facing slopes in the northern hemisphere and north-facing ones in the southern hemisphere, and 'occupation of specific microhabitats' in biogeographic transitional zones, often exhibiting high levels of species richness as a result of an array of microhabitats available (Gaston 2003).

Remnant populations of many threatened and endangered species tend to be at the edge of their geographical range (Channell and Lomolino 2000a, b) and are particularly sensitive to further environmental changes because of relatively low resilience and low carrying capacity (Maurer and Taper 2002). According to 'centre-periphery hypothesis' marginal populations are also expected to have less genetic variation than central populations due to genetic drift, founder effect, bottlenecks and inbreeding, and diminished sexuality (Levine 1970, Lawton 1993, Lesica and Allendorf 1995). It is generally assumed that marginal habitats are characterized by smaller, more isolated and more fragmented areas (Brussard, 1984, Guo *et al.* 2005); and therefore, are more prone to extinction (Lawton 1993, Vucetich and Waite 2003, Hampe and Petit 2005).

Recent empirical work (Channell and Lomolino 2000a), in particular phylogeographic surveys (Hewitt 2000, 2004, Sagarin and Gaines 2002), however, contradicts the above paradigm at broad geographical scales, suggesting that range-wide patterns of population genetic diversity are usually created by past climatic-driven range dynamics, rather than by demographic and genetic stochasticity, as proposed in the 'centre-periphery model', and as a consequence, marginal populations commonly harbour the bulk of species' genetic diversity (e.g., Petit *et al.* 2003, Hewitt 2004, Hampe and Petit 2005). Several other studies (reviewed by Lesica and Allendorf 1992, 1995) argue that in peripheral parts of the range, because of different ecological conditions (even if not sub-optimal), selection is likely to affect gene frequencies in many plant species, favouring unique genotypes. Peripheral populations are, therefore, of greater conservation priority because of their potentially distinctive genetic characteristics (Lesica and Allendorf 1995).

Local extinction in a suitable habitat can also occur due to the environmental variability or genetic stochasticity (i.e., drift), rather than just small population size and demographic stochasticity, leading to genotypes maladapted to local condition (Hanski 1994). For many species, local extinctions and recolonizations are, however, common in nature (Hanski *et al.* 1994), and organisms may frequently be absent from suitable habitat because of local extinctions and/or dispersal limitations (see Pulliam 2000).

1.2.2 Dispersal limitation, source-sink, and metapopulation dynamics

Recent concepts of source-sink dynamics, metapopulation dynamics and dispersal limitation complicate any relationship between a species' niche and its occurrence in suitable habitat (Pulliam 2000). Dispersal events may consign a species to habitats in which its niche requirements are not completely met ('sink populations' Pulliam1998, 2000) or in other cases, dispersal limitation may mean species are not always present even when niche requirements *are* met (see e.g., Cain *et al.* 1998). Limited reproduction combined with low migration rates can also limit recruitment into suitable habitats (Pulliam and Danielson 1991, Honnay *et al.* 1999) and can result in a species being absent from a large fraction of its suitable habitat. Evidently, competition, dispersal, niche size and the distribution of environmental conditions in space and time all take part in determining species distribution in relation to the distribution of suitable habitat. These reflect conditions under which species might be common in unsuitable habitat, or absent from suitable habitat (Pulliam 2000).

1.3 Critical habitat for Species at Risk

Understanding factors that cause rarity can provide critical information that will ensure the long term conservation of rare flora (Coates and Atkins 2001). To prevent extinctions and facilitate recovery of endangered species, the federal government of Canada, in cooperation with the provinces began a major campaign with two main objectives: (1) to identify Canadian species at risk; (2) to lay out a sequential series of conservation and restoration strategies, once the causes of endangerment are assessed (Kerr and Deguise 2004). This responsibility is embedded in the new Canadian Species at Risk Act (SARA) that not only identifies those species that have been evaluated and determined to be at risk, but also initiates steps that should lead to their long-term survival (SARA 2003).

Amongst conservation biologist and also in legislation, a greater emphasis is being placed on the notion of "critical habitat". In order to understand the gist of critical habitat, it is important to understand what the term 'habitat' means from the conservation and legislative perspectives. The Canadian Species at Risk Act (SARA 2003) defines the term 'habitat' as follows:

"(a) in respect of aquatic species, spawning grounds and nursery, rearing, food supply, migration and any other areas on which aquatic species depend directly or indirectly in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced; and (b) in respect of other wildlife species, the area or type of site where an individual or wildlife species naturally occurs or depends on or indirectly in order to carry out its life processes or formerly occurred and has the potential to be reintroduced."

This definition includes not only those occupied areas that a species depends upon directly to carry out its life processes (as defined from the strict ecological and biogeographic standpoint), but also the areas where a species has the potential to be reintroduced. It is noteworthy that this broad definition of habitat defined by SARA has implications for the identification of critical habitat. A critical habitat, therefore, will be the habitat that is necessary for the survival or recovery of a wildlife species at risk (SARA 2003).

1.3.1 Criteria for defining critical habitat

Several ecological perspectives help in the identification of critical habitat. Thus the individual species' evolved life history requirements, species interactions and organisms in local environments are past, but so are the perspectives from other ecological processes occurring due to particular environmental parameters. Though it is impossible to incorporate all ecosystems considerations, it is important to identify, and make provisions for the essential and potentially limiting factors. Identification of critical habitat for species at risk may require special considerations that are dependent on other species for reproduction and dispersal. A threatened plant species, for example, will be unable to reproduce and recover if their critical pollinators and seed dispersers are limiting (Csotonyi and Hilburt 2000). *Yucca glauca* (Soapweed) is a threatened plant at the northern edge of its range in southern Alberta whose range in Canada is reported to be limited by its obligate pollinator, *Tegeticula yuccasella,* the endangered Yucca Moth (Csotonyi and Hilburt 2000). For the continued existence of such 'mutual relationship', therefore, critical habitat should include the habitat requirementits of both species (Allen-Wardell *et al.* 1998).

Critical habitat is dynamic for species that depend on natural disturbances like fire, succession and storms, to maintaine their original habitat. For example, an endangered grassland species *Cypripedium candidum* (Small White Lady's Slipper) is dependent on fire to prevent the encroachment of woody species into open grassland habitat (Brownell 1981).

Another phenomenon that is likely responsible to cause shifts in species' habitat and distribution over time is climate change (Pimm, 2001, Warner *et al.* 2001, Parmesan and Yohe 2003). For example, due to current global warming range shift in 35 non-migratory European butterfly species is documented in a study by Parmesan *et al.* (1999). The authors found that geographical range of 22 species shifted northwards by 35-240 km during this century. However, only two species were found to have a southward range shift, while 10 species showed no significant shift in their geographical distribution.

It is assumed that species with smaller geographical ranges are more likely to be hampered by climatic changes given populations too small to be capable of adapting, or 'tracking' the changing climatic conditions (Pimm 2001). What proportion of species is strictly limited by climate, however, remains unclear (see Gaston 2003). Nevertheless, critical habitat that is necessary for the survival or recovery of a listed wildlife species at risk (SARA 2003) will need to be revised over time, if geographical range shifts continue to occur (Hughes 2000). Predicting these shifts in species habitat, however, is not easy, and depends on knowledge of species' dispersal ability, its potential to adapt to new climatic conditions, changes in the timing of life cycle events, and interaction with the organisms of the new habitat.

Requirements at the population-level examine biological considerations of critical habitat that are specific to populations such as area- specificity, species-specific minimum habitat requirements, and factors that are thought to influence these quantitative requirements (Hyden *et al.* 1985). Calculations of area requirements for the purpose of identifying critical habitat are based on the amount of habitat required for long-term population persistence, and not just on the amount required for individual occurrence or individual reproductive events (Hyden *et al.* 1985, Wenny *et al.* 1993).

The proportion of suitable habitat in a landscape necessary to maintain viable populations is invariable across species or across regions (Gibbs 1998, Fahrig 2001) and depend on landscape factors e.g., quality of the metrix or non-habitat destruction (Dytham 1995, Fahrig 2001). Landscape-scale conservation is an important perspective that calls for attention in the identification of critical habitat. Species respond not only to within-patch characteristics, but also to habitat at a landscape scale (Turner 1989, Freemark *et al.* 1995, Wiens 1995); thus it is important to consider the amount and quality of habitat in landscapes at larger scales (Flather and Sauer 1996, Villard et al.1999). As different species respond to the landscape at different scales, therefore, the choice of appropriate scale to consider for the identification of critical habitat will vary accordingly (Turner 1989, Wiens *et al.* 1993).

Loss and modification of the habitat is generally regarded as one of the main factors by which a species is designated as 'species at risk' (Ehrlich and Ehrlich 1981, Groombridge 1992, Wilson 1992, Noss *et al.* 1997, Lande 1998, Kerr and Deguise 2004). The abundance and connectivity of habitats partially determines the distribution of species that require those habitats.

On a small patch of suitable habitat, in a fragmented landscape, a species is less likely to occur, as the chance of dispersal is limited and a small sized population may be too small to maintain itself (Brown 1984, Taylor *et al.* 1993, Wiens 1996). However, bigger habitat patches can support larger populations, less likely to go extinct due to stochastic events (MacArthur and Wilson 1967, Goodman 1987, Pimm *et al.* 1988; Murphy & Noon 1991, Boyce 1992) and are less susceptible to the negative influences of edge effects such as predation and nest parasitism (Murcia 1995, Kremsater and Bunnell 1999). Critical habitat, therefore, should include elements of the landscape that are necessary to allow dispersal between these habitat patches.

The distinction between sources and sinks emphasise the need for considered evaluation of patterns of risk (Gaston *et al.* 2002). Within sink populations, local reproduction is insufficient to balance local mortality and persistence results from continued immigration of individuals from source population where local reproduction is equal or greater than the local mortality (Pulliam 1988, Dias 1996); it is, therefore, emphasized to include more productive source areas as critical habitat (Carrol *et al.* 1996, Gaston *et al.* 2002) to prevent local extinction, (Brown and Kodric-Brown 1977, Pulliam 1988, 2000). However, it has also been suggested that a positive relationship between habitat quality and density should not automatically be assumed; as there are several documented cases exist where density was found to be higher in low quality habitats (van Horne 1983, also see Pulliam 2000). Identifying potential source and sink habitats will, therefore, not only require a measure of density in that habitat, but also a measure of reproductive success (see van Horne 1983). However the value of sink habitats should not be underestimated as they may serve as important links between disjunct source areas (Noss 2002), and may increase the overall size and persistence probability of a metapopulation (Gaston *et al.* 2002).

In highly variable and resource-depleted environments (and due to both physical conditions and negative interactions), dispersal or immigration becomes of utmost importance for maintaining genetic diversity through gene flow, and avoiding the deleterious effects of inbreeding in marginal populations (Pusey and Wolf 1996), Guo *et al.* 2005). Though marginal populations may persist through vegetative reproduction (Olsen 1987), in the long run, however, immigration from central or "source" habitat is the only way to survive in such intolerable environment (Howe *et al.* 1991).

Ecological monitoring of marginal populations and /or boundary conditions on a regular basis is required in order to make an accurate prediction about species decline as a critical component of recovery planning and endangered species management (Guo *et al.* 2005). Gaston (2003) suggested that rare species should be protected at multiple sites, not simply for reason of spreading the risk of extinction, but to ensure that sufficient individuals are secured. However, as mentioned above, habitats occupied at range edges may not be representative of those occupied elsewhere, and may certainly not be exploited elsewhere in the range (Gaston 2003). The conservation of species found in such habitats, therefore, needs extra caution and some management action at those habitats; maintaining them in the same state may not be the most effective strategy, and translocating individuals to areas with similar habitat may miss valuable opportunities to more effectively increase populations and spread the risk of low numbers (Gray and Craig 1991).

Guo *et al.* (2005) used a model dividing a species range into numerous concentric rings (patches) surrounding the centre of the species' distribution, and argued that central rings were most favourable when the population size was below the carrying capacity. However habitat becomes less favourable as soon as the population size gets bigger (high birth and/or low mortality rates), and as a result the next ring becomes more favourable. Thus if the habitat suitability fluctuates through time during population development, then under severe environmental changes, the same habitats may serve as both sources and sinks at different times. Thus, protecting habitat at the edge of a species' geographical range may be important, even if the habitat is currently considered to be marginal quality; what may be considered sink (marginal) habitat today could become source habitat in the future.

1.4 Study site: Point Pelee National Park (PPNP)

Point Pelee (41° 54'N and 82° 22'W) is the most southerly point in Canada (CEAR 2005) situated just above the Canadian-American border. At 47 km² (18 mi²), Pelee Island is the largest island in Lake Erie. It is a triangular-shaped, cuspate foreland extending into the shallow, western basin of Lake Erie in Ontario (Trenhaile *et al.* 2000). The southern portion of Point Pelee is taken up by 'Point Pelee National Park'which was established in 1918 (Trenhaile *et al.* 2000). The country's smallest national park, with 1564 hectares, PPNP is a blend of savanna grasslands, Carolinian forest, and southern Great Lakes marsh, along a mobile beach front (Nature Conservancy 1990, Kraus 1991).

The land of the peninsula is about 1,000 years old, and comprised of sand and gravel base; it was formed mainly as a result of erosion and deposition of sand and other sediments due to wave action in Lake Erie (Boyle 1972). Due to the erosive effects of storm waves the land is constantly changing, especially at its extremities (Nature Conservancy 1990). The erosive effects are more pronounced during periods of high lake level, and there is high correlation between high lake levels and shoreline damage (Trenhaile *et al.* 2000). Lake ice protects the shore from wave action in winter (especially January and February), although ice scouring of the bottom makes the beach more susceptible to erosion by spring storms (Dickie and Cape 1974 reviewed in Trenhaile *et al.* 2000).

1.4.1 Climate

The climate of Southern Ontario is one of the most unpredictable in Canada. Point Pelee lies within a climatic zone classified as humid continental. Non-periodic weather changes are features of the zone that is strongly affected by seasonal clash between polar and tropical air masses The prevailing winds are from southwest (Hough 1958) at about 11-16 km/h; however, because of the location of southern Ontario on cyclonic storm paths, winds are highly variable (Environment Canada 1995).

Due to its geographical position, Point Pelee has one of the warmest and most humid climates in Canada (Battin and Nelson 1978). The peninsula experiences a long frost-free period, approximately 220 days (Reznicek and Catling 1995). Lake Erie increases humidity in the region and humidity in the Park is probably greater than that experienced by the rest of Ontario (Environment Canada 1995). The shallow waters of Lake Erie reach relatively high temperatures in the summer months, giving the islands a climate similar to more southern locations. Summer temperature ranges from 25° C to 32° C (see Table 1.1). The winter is relatively mild.

The mean temperature recorded in January is about -3°C, the warmest in Ontario (Environment Canada 1995, PPNP 2005). The growing season begins early in April and ends early in November (Battin and Nelson 1978). Point Pelee and Pelee Island record the fewest days annually receiving precipitation in the province (i.e.75). Low-lying areas adjacent to lakes receive comparatively less rainfall as compared to inland. Average annual precipitation recorded is about 81mm (PPNP 2005).

Summer temperatures	25°C - 32°C
Winter temperatures	- 3°C
Frost-free period	Approx. 200 days
Wind speed (prevailing from southwest)	11-16 km/h
Average annual precipitation	81.1 mm
Growing Period	Early April - early November

Table 1.1 An overview of the overall climatic conditions at Point Pelee

1.4.2 Geology and geomorphology

According to Trenhaile *et al.* (2000) Point Pelee contains more or less parallel southerly thickening dune ridges under a mature forest cover. Along the northwestern flank, Dunes consists entirely of aeolian material in the north, but developed over a core of coarser wave-deposited sediment, probably in the form of beach ridges, further south. The highest dunes extend up to about 8 m above mean lake level but gradually become more subdued to the south, where they pass into lower area containing small, pebble to coarse sand ridges. The ridges are generally less than a meter in height (see Trenhaile *et al.* 2000 for more details).

The Point Pelee peninsula formed mainly as a result of erosion and deposition of sand and other sediments due to wave action in Lake Erie (Boyle 1972). The underlying bedrock is Precambian, composed of gneiss, schist, and various granitic rocks; and overlain by a thick layer of Paleozoic sedimentary rocks that are composed of sandstone, limestone, dolomite and shale (Hough 1958). Soil at PPNP is mostly well-drained and consists of 0-30 cm sandy soil, and 0-7.5 cm sand (see Boyle 1972).

The soil profile reported by Boyle (1972) was poorly developed, varying in depth from 0-30 cm and were generally alkaline showing a pH of 7.5 - 8.6. According to Boyle (1972) these pH levels likely resulted from the high content of minerals such as silica, calcite, and dolomite. The A horizon was not well developed, comprised of grey to black loose sand with humus content ranged from 2% on well-drained sites to 10% on poorly drained sites (Boyle 1972). The B horizon was poorly developed, composed of slightly reddish and gravely sands; and C horizon was comprised mainly of sand and/or gravel.

Opuntia humifusa has been reported to grow in sandy substrates (Kraus 1991), with flat or south-sloped exposure areas angled less than 50 degrees at elevations between 0 and 5,500 feet above sea level (Benson 1982). Jock (1984) described the topography of Point Pelee National Park as being flat to gently undulating with a variable slope of 10% where the water table lies beneath *O. humifusa*'s 3 cm deep rooting zone.

1.5 Study species: *Opuntia humifusa* (the Eastern Prickly Pear Cactus)

Opuntia humifusa is a prostrate, spreading, and perennial succulent. It is easily recognized by its flattened and segmented green stems (cladodes), bright yellow to golden showy hermaphrodite flowers, and a pear-shaped edible fruit (Jock 1984, Voss 1985). The morphology of the stem, spines, flowers, and fruit may vary widely depending on the geographical location of *O. humifusa* (Abrahamson and Rubenstein 1976, Benson 1982). Several older synonyms of this species may be attributed to this phenotypic variability exhibited by *O. humifusa* across its geographical range (Benson 1982, Wallace and Fairbrothers 1986, Leuenberger 1993) (see Leuenberger (1993) for a complete discussion of the taxonomic history and list of synonyms).

1.5.1 Species' range and conservation status

Opuntia humifusa's natural occurrence in North America extends from extreme southwestern Ontario to south eastern Texas and along the Gulf and Atlantic coasts to Florida, north to Massachusetts (Kraus 1991, Whitehead 1995) [see Fig 1.1 and 1.2]. While the species is common through out most of its range, many northern states have assigned it special status. The species is listed as rare in Connecticut, Iowa, Massachusetts, Pennsylvania, Ohio, and Ontario (see Fig. 1.2), and has been given protected status in the state of New York (see Swain 1998). The only naturally occurring populations today are found in the rare Red Cedar savanna habitats, as well as Long Point, and Rondeau at PPNP, and at Fish Point Provincial Natural Reserve, on Pelee Island (Reznicek 1982, Levi 2001). According to a thorough census carried out in 1985, only 71 patches were found at PPNP, however currently 300 patches exist at PPNP (see Levi 2001).

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) classified *O. humifusa* as "Endangered" in 1987. The Province of Ontario has ranked *O. humifusa* as S1, meaning that it is extremely rare in its regional distribution (NHIC 2003). Such species are often regarded as especially vulnerable to extirpation. *O. humifusa* is on the national list of Canadian species at risk of extirpation as there are only two remaining natural populations of the species in Canada (COSEWIC 2003). However, the species is G5 in its global rank, which means that from a global perspective it is very common and demonstrably secure under present conditions (NHIC 2003).

1.5.2 Habitats of *Opuntia humifusa*

Based on herbarium records and published descriptions, the habitats of *O. humifusa* in can vary widely (Noelle and Blackwell 1972). *O. humifusa* is generally reported from dry sandy areas. However it also occurs in cool, damp climates and areas of low relief, such as the prairie and deciduous forest regions (Fernald 1970, Whitehead 1995). *O. humifusa* has also been reported on granite outcrop formations in New Jersey, and in disturbed Pine/Oak woodlands in North Carolina (Wallace and Fairbrothers 1986). The species is reported in old literature as commonly growing in open *Quercus* woods near Sandusky in northern Ohio (Kellerman 1901), and in sand plains (Jennings 1908) and open fields (Moseley 1899) in the same region.

The habitats of *O. humifusa* in Great Lakes region have recently been reviewed by Abella and Jaeger (2004) and, according to this review, in the Chicago region the species occurs in *Quercus* savannas, old cemeteries on sandy soils, and human-made limestone barrens (see Swink and Wilhelm 1994); all eight presently known sites of *O. humifusa* in Oak Openings Preserve (Toledo Park, Ohio) occur within 100 m of a conifer plantation.
In Ontario, reports of *O. humifusa* have been limited to sandy ridges within 25 km of the shoreline (Reznicek 1982; Klinkenberg and Klinkenberg 1984) where the moderating effects of the Great Lakes are felt year-round (Whitehead 1995). The sandpit savanna is the only natural habitat type in which *O. humifusa* occurs in Canada.

At PPNP, the four contrasting habitats (in-park reference sites) at different successional stages (see Fig. 1.3) within the sandpit environment at PPNP are:

1. The North West beach (hereafter termed the "Back beach") habitat. It is very sandy with little vegetation, and no natural *O. humifusa* plants present.
2. The West beach habitat, a "primary successional savanna", located just south of the West Beach parking lot. This is an open, red cedar savanna, where there are established natural clumps of *O. humifusa.*
3. The fields on the former DeLaurier homestead (abandoned in the 1920s), a "secondary successional savanna". This site has abundant grasses and sparse trees, including deciduous trees and shrubs as well as red cedar, but is quite open at present. Cactus plants grow there naturally.
4. Hackberry-oak-hickory deciduous forest, just south of the PPNP Visitor's Centre, with mature tree cover.

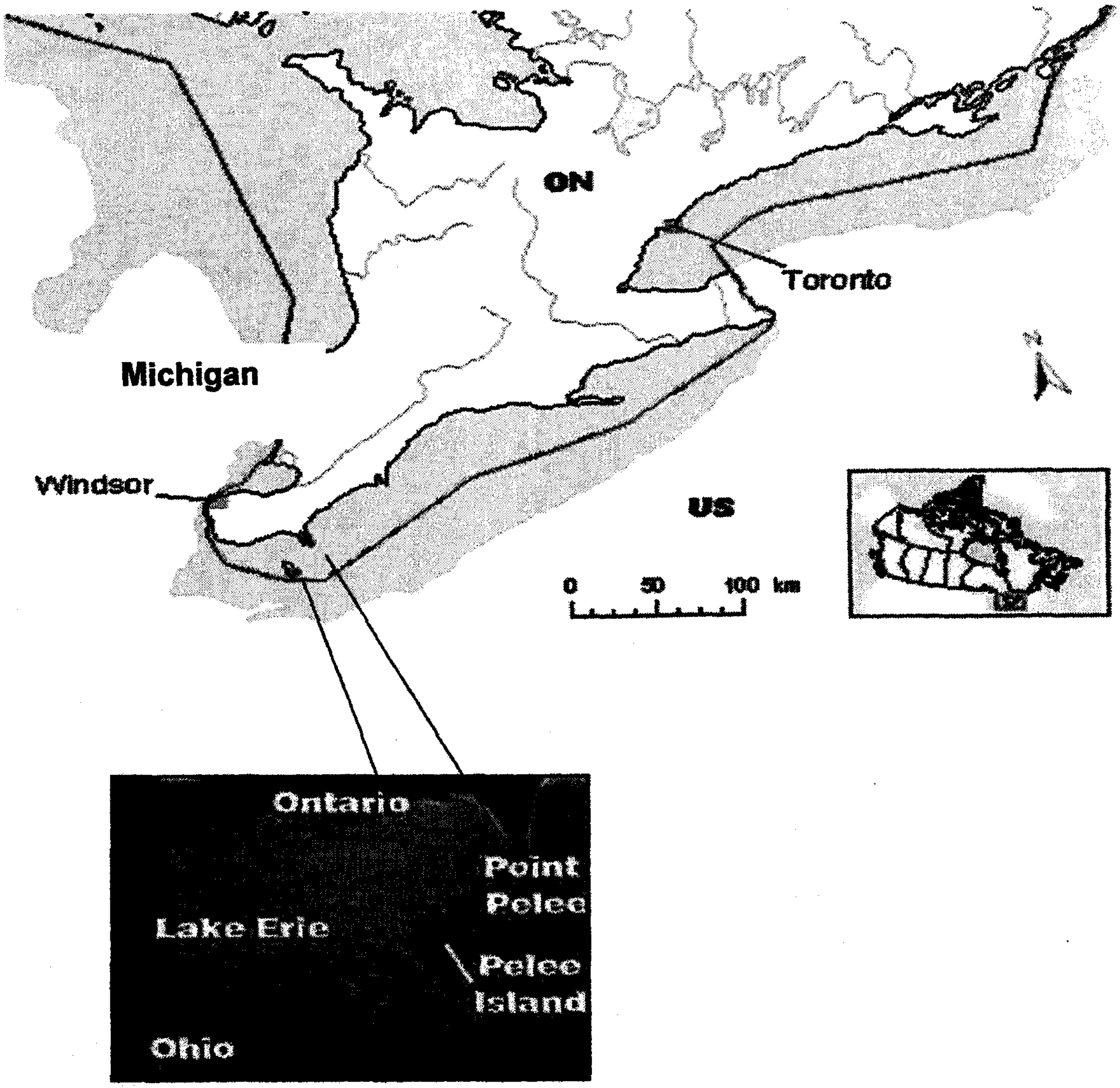

Figure 1.1 Canadian distribution of *Opuntia humifusa*

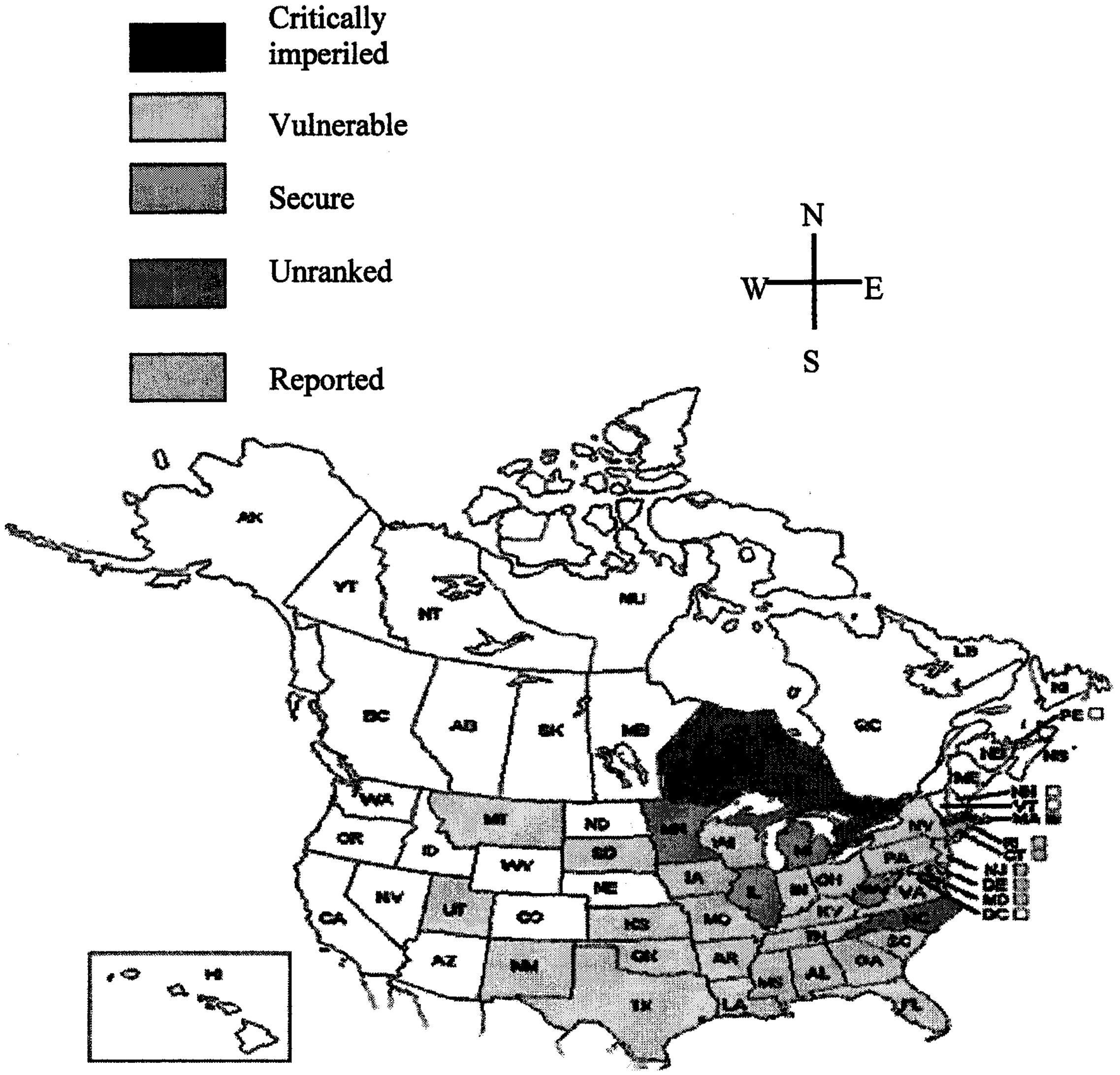

Figure 1.2 The native North American distribution and species status of *Opuntia humifusa*: Critically imperilled ON, MA; Vulnerable PA, OH, and IA; Secure NC; Unranked MN, IL, and MI, WV; Reported WI, IN, NY, MD, VA, KY, TN, SC, GA, FL, AL, MS, LA, AR, SD, TX, KS, NE, UT.

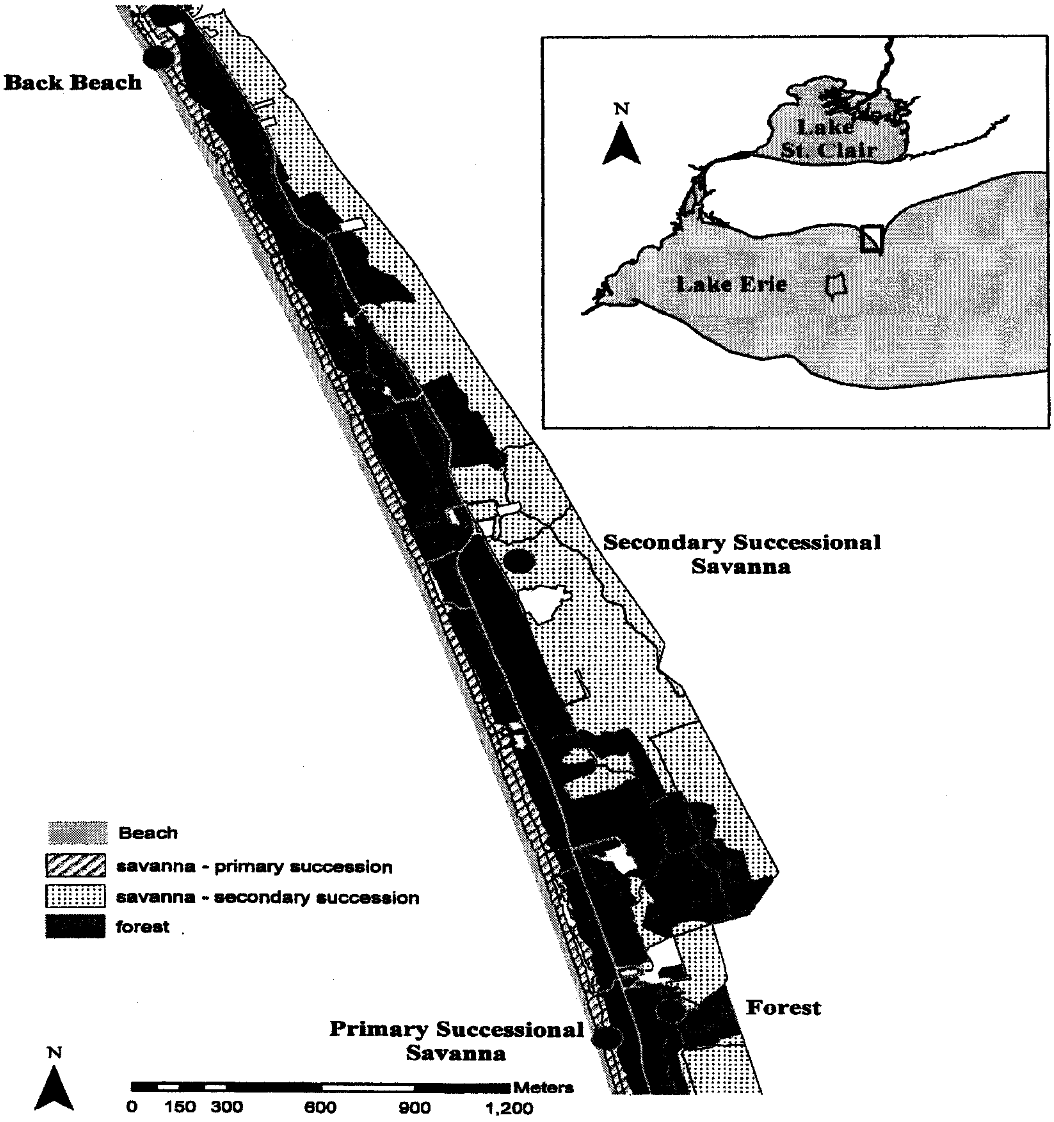

Figure 1.3 Location of the study site at Point Pelee National Park, ON, Canada. Symbols indicate where cactus samples were transplanted to each of the four succesional habitats

1.6 Research on the population biology of *Opuntia humifusa*

Dr. Lesley Lovett-Doust and her students have studied the PPNP *Opuntia humifusa* population since 1998, carrying out detailed demographic and genetic studies with the goal of developing management practices for self-sustaining populations. Objectives of their study included: (1) is *O. humifusa* capable of setting seeds apomictically? (2) are the patches monoclonal, or do they include interspersed seedlings (3) what is the genetic diversity of patches?

They identified characteristics of patches growing in each of 6 distinct regions at the park. Patches were mapped using global positioning system (GPS) and placed on GIS maps in collaboration with M.Smith, the Park's GIS specialist. Individuals showed various levels of seed production, contrasting cladode morphology, and different patch diameter-frequency distributions. Results of pollination studies suggested that *O. humifusa* was capable of setting seed apomictically (Levi 2001).

The seed stage in the plant life cycle has long been recognized as being very important since seed propagation generates genetic diversity (see Silvertown and Lovett-Doust 1993). For an endangered species, knowledge of patterns of seed viability, dormancy, germination of seeds, seedling recruitment, and seedling performance, can contribute to our understanding of the causes of rarity and assist us in designing effective conservation strategies (Holsinger and Gottlieb 1991). Little is known about the germination requirements or variability of seeds in members of the family Cactaceae (Rojas-Arechiga and Vazquez-Yanes 2000), however, a few studies suggest that the germination of several species of *Opuntia* increases with age of the seeds, suggesting some inherent primary dormancy allowing seed banks to accumulate in the soil (Mandujano *et al.* 1997 reviewed *in* Foxcroft *et al.* 2004).

At PPNP, *O. humifusa* has been found to produce a number of seed morphologies (Baskin and Baskin 1998, Levi 2001). Plenty of seeds are found in rabbit scat that is often clustered around the cactus patches in fall and in the sandy soil around the patches (Lovett-Doust 2002). Fruits and seeds of *O. humifusa* were collected from plants growing in different parts of PPNP (six sites), and compared in terms of their fruit and seed production, and the numbers and types of seed morphs. Different seed morphs of *O. humifusa* often differ in dormancy-breaking and germination requirements (Baskin and Baskin 1998). In *O. humifusa* mature seeds have been found to have a greater dormancy rate than other seed types (such as 'appended' and 'super' seeds) (Levi 2001). This suggested that the seeds were truly polymorphic in germination performance, as well as appearance.

Potter *et al.* (1984) investigated germination requirements in three common *Opuntia* species in western Texas. The authors showed that acid pre-treatment consistently increased germination of the species. An experimental study was also made of germination requirements for these very hard, stony seeds by Levi (1999) at University of Windsor. The discovery of the dormancy-breaking condition was a breakthrough in terms of pretreatments and germination conditions (Levi 1999). Levi showed that the seeds, although tough to germinate because of their stony seed coats, are viable and can germinate following cold treatment of the seeds for a minimum of six weeks, then soaking in concentrated sulphuric acid for about 90 minutes, and finally setting them to germinate in Petri plates lined with moist filter paper. The Petri dishes were then placed in a Conviron controlled environment germination chamber, under 16 hours of day light at 30° C and 8 hours of darknes at 30° C. Petri dishes were re-arranged randomly once everyday. Once the radicle was visible and protruded by 2 mm the criterion for germination was met. This allowed study of the seed cohort as well as the established plants in the population. Germination was found to be four times higher for acid-treated seeds as compared to untreated seeds. This suggests that passage through an acidic animal gut may be needed to stimulate germination.

A follow-up study comparing PPNP populations with populations from other parts of the species' range to determine overall genetic diversity, will be very helpful in this context. DNA fingerprints have been obtained from tissue samples of the large patches of this species, collected from Point Pelee National Park. The ability to accurately model ecological systems, to assess risk, and to determine the best management strategy is of critical importance in conservation efforts. Jeremy VanDerWal (Ph.D. student) and Nolan Evens (undergraduate student), are actively engaged in computer-based, quantitative modeling to predict the overall risk of extinction faced by PPNP populations of *O. humifusa*.

1.7 Present Study: niche / habitat requirements for *Opuntia humifusa*

1.7.1 Objectives

To determine habitat suitability at PPNP by testing growth and survival of cactus seedlings under contrasting conditions in both the field, and under experimental glasshouse conditions.

(1) by assessing the suitability of the four contrasting habitat types (Back Beach, West Beach, Delaurier, Deciduous forest) present in the dryland of sandspit habitats at PPNP, in terms of their suitability for growth and survival of *O. humifusa*;

(2) through experimental greenhouse studies to assess the niche-based explanation for defining the requirement of a suitable habitat for *O. humifusa* at PPNP.

Evidence in the literature suggests that the species may be limited in distribution by its seed dispersal (Santelmann 1991) or by low germination rates (Levi 2001). A species with limited dispersal ability may, therefore, leave many suitable sites unoccupied (Ozinga *et al.* 2005). It is also suggested that species of restricted distribution may be locally or globally absent from apparently suitable habitats being inefficient dispersers (Shaw and Burns 1997, Wiser *et al.* 1998), lack of a seed bank (Prins *et al.* 1998, Bakker and Berendse 1999, Blomqvist *et al.* 2003) or because of limited reproduction combined with low migration rates (Pulliam and Danielson 1991, Honnay *et al.* 1999). Wide dispersal, though, does not guarantee wide range, since not all dispersal will be to suitable habitats; however, strong dispersal ability is likely a prerequisite of large geographical range (Lloyd *et al.* 2003).

As mentioned above, *O. humifusa* has a broad distributional range in North America, where it can be found in several habitat types from prairie, deciduous forest, and semi-arid to arid environments. However, in mainland Ontario, restriction of *O. humifusa* to only two sites i.e. West beach and DeLaurier at PPNP has been linked to low germination rates (Levi 2001). There is growing evidence that some organisms are 'dispersal limited' (Cain *et al.* 1998). Maschinski *et al.* (2004) and Ozinga *et al.* (2005) also pointed out that propagules in many cases arrive at unsuitable habitats and never reach suitable habitat. In the present study it is, therefore, speculated that despite the good seed production of *O. humifusa*, seeds may not get a chance to reach neighbouring habitats suitable for seed germination as well as seedling establishment

Primack and Miao (1992) demonstrated dispersal limitation experimentally by introducing seeds of a variety of annual plants into 'unoccupied but seemingly suitable' habitat in Massachusetts. They found that several species not only established populations but thrived for at least several years, and concluded that dispersal limitations can limit the distribution of annual plant species on local scales.
There is evidence that granivores in North American deserts consume most of each year's seed crop--- estimates range from 69% (Price and Joyner 1997) to 95% (Soholt 1973) resulting in an extreme depletion of a seed crop that could limit the propagules available for dispersal and limit establishment (e.g., Quintana-Ascencio *et al.* 1998).

One way to determine if dispersal is a key factor limiting distribution is by observing the results of transplanted species to areas where that species was actually absent. To override limitations of dispersal, and allow direct assessment of site suitability for a species, a transplant experiment can provide a more accurate definition of the species' fundamental niche (e.g.), and identification of critical habitat (Mulligan and Gignac 2001). However, as some organisms may survive in new areas but cannot reproduce there, so the success of a transplant cannot be determined until at least one life cycle is completed (Silvertown and Lovett-Doust 1993).

Experimentally, it is the fate of transplants which can indicate how the habitat looks from the point of view of the plant itself. If the transplant is successful, then the 'potential range' of the species is larger than its 'actual range'. If a species does not occupy all of its potential range, the question arises: does the species lack a suitable means of dispersal to reach new areas? If the species does not survive and reproduce in the transplant areas, it can be asked whether biotic (e.g., Levin and McGraw 1998, Cabin *et al.* 2000) or abiotic factors (e.g., Gaston 1990, Sacchi and Price 1992, Escudero *et al.* 2000) exclude it from these areas. For example, in a cage/field study, the expansion of the population of an endangered limestone endemic, *Pinus subintegra*, to novel habitats was found to be limited by soil moisture capacity (Maschinski *et al.* 2004).

Frequently, a species cannot complete its full life cycle if transplanted to a new area. One reason for this inability may be negative interactions with predators (Cabin *et al.* 2000), competitors (Levin and McGraw 1998, Russell and Schupp 1998) or parasites and pathogens. Or the transplant area could lack required positive effects of interdependent species, such as pollinators that are present within the actual range of a transplanted angiosperm. And if biotic factors do not set limits on the range, it is reasonable to establish the possibility of physical or chemical factors (abiotic) that may set the geographical range limits (see Gaston 1990). Maschinski *et al.* (2004) suggested monitoring the success of re-introduction trials over a long period the abiotic and biotic factors can have a dramatic effect on the establishment of plant seedlings.

Here I investigate factors preventing *O. humifusa* from further spread in other potentially suitable habitats (i.e., back beach, and woodland). I sought to determine:

1: In the absence of biotic influence (interspecific competition, or herbivory etc.) will this species be able to establish in other habitats that belong to its fundamental niche at PNP?

2: Whether the restriction of this cactus (an early colonizer species) to limited suitable habitats is linked to nutrients or light availability? Earlier successional, colonizing species are believed to be out-competed in later successional stage by larger later species for available light and soil nutrients (Tilman 1985, 1988). This could explain the distribution of *O. humifusa* based on its ability to withstand either above-ground or below-ground competition.

3: Is this cactus able to persist in later successional seres? If yes, then this could be included as part of the 'realized niche', and less management intervention would be necessary. If not, then reduced habitat breadth and abundances within transitional habitats may increase the risk of extinction.

The only way to describe accurately the fundamental niche of a species in the field is experimentally, by transplanting it into habitats in which it does not typically grow (Silvertown and Lovett-Doust 1993, Mulligan and Gignac 2001). If competitors and predators were removed, these "phytometers" or transplant experiments (including controls) may be used to determine the extent of a plant's fundamental niche. However, in the presence of all the other ecological and environmental factors (including effects of predators and interspecific interference, for example) the same experiments may also represent the limits of its realized niche. Field transplant experiments along these lines were designed to achieve present objectives assuming that they could override limitations of dispersal, providing a more accurate definition of the species' fundamental niche (Mulligan and Gignac 2001) and allowing direct assessment of site suitability for a species at risk.

Seedlings were grown under controlled conditions. The contrasting light and nutrient treatments represented the climates of four potentially suitable sites at PPNP. I started green-house experiment with a hypothesis that the interactive effect of increased nutrient availability at high irradiance level in well-drained soils may enhance the population growth of *O. humifusa*. Different nutrient treatments were superimposed on the light regimes in order to simulate differential competition for mineral nutrients, and to detect any interplay between light and nutrients in their effects on growth. Determination of separate and joint effects of different NPK levels and light intensity gradients on the growth of *O. humifusa* cladodes was actually an important attempt to get the details of the physical dimensions of the environment that may directly influence population growth.

Studies from the literature show that locally rare species (e.g., plants of south-eastern Australia) might become abundant on a particular site where their environmental niche requirements are best met (Austin *et al.* 1996). Incorporation of the greenhouse experimental study to our field experiments served as a comparison providing additional information of the role of niche variables, and allowing some more general interpretation of environment at PPNP in terms of their suitability for cactus growth, and limiting factors of the environment.

Chapter 2: Transplants of endangered *Opuntia humifusa* in sandspit habitat and effects along a successional gradient

Summary

In recent Canadian endangered species legislation "critical habitat" is regarded as any habitat in which a species at risk is capable of maintaining self-sustaining populations. Critical habitat of *Opuntia humifusa* at Point Pelee National Park likely changes during ecological succession; to identify optimal conditions, survivorship and growth of seedling transplants (N = 1440) were followed in fenced and unfenced plots at four contrasting habitats along a successional gradient: back beach, primary successional savanna, secondary successional savanna and deciduous forest. Environmental parameters (light intensity, organic matter content, soil moisture, pH, and Nitrogen, Phosphorus, and Potassium levels) differed significantly among habitats. After two years, survivorship was lowest in forest plots with no significant difference between fenced or unfenced groups (4.4% and 3.9% respectively). In the back beach, frequent sand burial caused reduced survival and diminished growth, especially in unfenced areas (61%), and basal shoots became chlorotic; plants there were less than a third the size of those in savanna habitats. Survivorship was greatest in the primary and secondary savanna habitats (mean = 91% and 94%, respectively) where plants already grow naturally. Fencing protected cactus in the secondary successional savanna from deer browsing (Mean = 94% and 91% survivorship in fenced vs. 83% and 86.6 % in unfenced plots of primary and secondary savanna respectively). Effects on growth were assessed by comparing changes in biomass, height, surface area, perimeters of cladode (shoot) and root, and root to shoot ratio. Significant differences in plant size and cladode shape were associated with

environmental conditions. At PPNP, the realized niche of *O. humifusa* closely corresponds to its critical habitat (i.e., the primary and secondary successional savanna) which is temporary in space and time.

2.1 Introduction

Rare plant species typically have quite specific requirements for survival – unique soils, habitats or restricted distributions (Gaston and Kunin 1997). Understanding the factors that most affect population viability (Pavlik 1994, Yates and Ladd 2005) or restrict the establishment and growth of such species could aid in conservation efforts by identifying suitable occupied sites for protection or restoration efforts (Schemske *et al.* 1994, Maschinski and Holter 2001, Maschinski *et al.* 2004).

From a strictly ecological and biogeographical perspective, those areas that are actually occupied and meet the requirements for a particular species' fitness (survival, growth, and reproduction) are its 'habitat' (Vandermeer 1972, Higashi 1993, Brown *et al.* 1995, Maschinski *et al.* 2004, Anthony and Connolly 2004). However, from a conservation standpoint, the term 'habitat' includes not only the areas that a species depends upon directly to carry out its life processes, but also the areas where a species has the potential to be re-introduced. Critical habitat is an important element in the development of recovery plans for species conservation. In the Canadian Species at Risk Act, it is defined as any habitat in which a species at risk is capable of maintaining self-sustaining populations (SARA 2003).

Identification of critical habitat focuses conservation efforts on locations most likely to support self-sustaining populations, provides an indication of where new populations of the species may be found, and indicates areas that would be suitable for restoration of threatened and endangered populations (Hoekstra *et al.* 2002). Theoretically, critical habitat could be defined as the species' "realized niche" (*sensu* Hutchinson 1957) – sites that are suitable with respect to both biotic environments (herbivory, competition, etc.) and abiotic (climate, soil type, etc.). Data on the autecology and synecology of rare species are necessary to compile such information (Walck *et al.* 1999).

O. humifusa, has good capability to regenerate, and has been reported to survive in a wide range of environmental conditions and to tolerate environmental disturbances (Oakwood *et al.* 1993; Edwards and Westoby 1996).While it has been suggested in the past that *O. humifusa* is intolerant of low light intensity, requires well-drained conditions, and may not tolerate disturbance in mobile sandy substrates (e.g., Klinkenberg and Klinkenberg 1985, Kraus 1991), *O. humifusa* at PPNP has been reported to exist across the sandspit from erosion and depositional beaches to closed canopy forested areas (see e.g., Ross 1971, Levi 2001).

According to Hutchinson (1957) the realized niche of a species is smaller than its fundamental niche, and a species may, therefore, frequently be absent from portions of its fundamental niche because of competition with other species (Pulliam 2000). Thus, in theory, the entire dryland portion of the sandpit is the fundamental niche (abiotically suitable habitat, without regard to biotic influences) for *O. humifusa.* However the current realized niche seems to be limited to two distinct savanna strips: one inland of, and parallel to the coastal back beach, and existing as primary successional habitat. The second is further inland, located on land that has been restored from agricultural and recreational land use, and for which the climax vegetation would be well-drained upland deciduous forest. However, swamp forest is the permanent seral stage. The inland sites are undergoing rapid secondary succession.

The current distribution of *O. humifusa* at PPNP may not reflect its environmental tolerances, as it occupies a much wider range of habitat types in the main part of its distribution in the United States (see Anthony 1954, Olson 1958, Richardson 1977, Conover and Geiger 1989). Evidence suggests that the species may be ultimately limited in distribution by its seed dispersal (Santelmann 1991) and low germination rates (Levi 2001). It is also suggested that a species with limited dispersal ability may leave many suitable sites unoccupied (Maschinski *et al.* 2004; Ozinga *et al.* 2005). A transplant experiment can overcome limitations of dispersal, and allow direct assessment of site suitability for a species, thus providing a more accurate definition of the species' realized niche (Mulligan and Gignac 2001), and identification of critical habitat.

In present study it was hypothesized that transplanted *O. humifusa* would survive in each habitat type in which the species had previously been reported (back beach, primary successional savanna, secondary successional savanna, forest) but with reduced growth and survivorship (limited by light in the forest and limited by nutrients on the Back Beach). A species' niche is described best when considerations of physical environment factors are incorporated with species' boundaries set by competition from other species in regions of niche overlap and also by predators and other biota (Silvertown and Lovett-Doust 1993). Here I report results of a 2-year field transplant study in which seedlings of *O. humifusa* were placed in each of four contrasting habitats (both within and outside their current distributions), and their survivorship and growth was monitored. The question addressed was: in the absence of the biotic influence (interspecific competition, or herbivory etc.), will this species be able to establish in other habitats that belong to its fundamental niche at Point Pelee National Park?

Seedlings were planted in both fenced and unfenced plots to investigate the impact of herbivory as well as to incorporate the impact of sand burial on the establishment, survivorship, and growth of 'species at risk'.

2.2 Materials and Methods

2.2.1 Study plots

In August 2001, six replicate plots were delineated in each of four habitats (in-park reference sites) at different successional stages:

1. The North West beach, hereafter termed the "Back Beach" habitat. It was very sandy with little vegetation, and no natural *O. humifusa* plants were present (Fig 1.3, pp. 26)
2. The West beach, a "primary successional savanna". This was an open, red cedar savanna, where there were established natural populations of *O. humifusa.*
3. The fields on the former DeLaurier homestead (abandoned in the 1920s), a "secondary successional savanna". This site had abundant grasses and sparse trees, including deciduous trees and shrubs as well as red cedar, but is quite open at present. Cactus plants grow there naturally.
4. Deciduous forest, just south of the PPNP Visitor's Centre, with mature tree cover. Cactus plants were last reported in the general area (before tree cover, c. 1980).

Locations of the four experimental plots and the extent of each of the successional habitats in the dryland portion of the PPNP sandspit are shown in Fig. 1.3.

2.2.2 Experimental transplant

In late fall of 2000, seeds were collected from established fruiting plants in the primary and secondary successional habitats at PPNP, where the cactus is naturally abundant. Seeds were removed from fruits and cold-treated (stored at 5°C) for three months. They were then acid-scarified and germinated at 30°C under a 16h day/8h night light regime over 36 days. Individual seedlings (N = 1440) were then placed in peat plugs on benches in the University of Windsor greenhouse, and left for a further 12 weeks growth , until seedlings had produced a primary cladode, approximately 3cm in height.

In each habitat location, seedlings were arranged in six plots, each containing an array of 60 plants (10 x 6), with three of the six plots being fenced, and three being completely open. Fencing comprised 3cm diameter polyethylene poles and plastic snow-fence netting. The netting did not completely exclude small herbivores, but did exclude the white-tailed deer *Odocoileus virginianus* that occur in the park. All plots were 6m x 3m, and seedlings were planted in a regularly spaced array, about 50cm apart. Within each plot, seedlings were uniquely coded and fates tracked.

Information on survival, height, number of shoots (= “cladodes” or “pads”), and any evidence of herbivore activity, were recorded on six occasions between planting and harvest. In August 2003, all plants were harvested by excavating the whole plant for subsequent analysis. Roots were carefully washed, and scaled digital images were taken of the whole plant. Plants were then dissected into roots and shoots; fresh mass of root and shoot were determined and the volume of shoots was measured by water displacement. Surface area, plant height and number of cladodes were calculated from electronic images using Sigma Scan image analysis software version 5.0 (SPSS 1999; LEAD Technologies Inc., Chicago, IL).

2.2.3 Characterization of soils and light measurements

Soils were characterized in each of the four habitats in March 2003. Ten soil samples were taken randomly from each of the transplant sites; these samples were thoroughly mixed and partitioned into sub-samples as follows. Approximately 5g was tested for water content, by comparing soil mass before and after the samples were dried to constant mass at 55°C. Organic content was determined by comparing the loss of mass on ignition (LOI) when approximately 0.75 g of soil was heated in a muffle furnace at 500°C for 2 hours.

Approximately 20g from each soil sample was used to measure the concentrations of nitrate nitrogen, total phosphorus and potassium; soil pH was determined using a LaMotte Model STH Series Combination Soil Outfit (Lamotte Co., Chestertown, MD). Light measurements were measured using a LI-COR LI-189 Radiation Sensor Photometer (LI-COR Inc., Lincoln, NB) placed at the centre of each plot.

2.3 Data Analysis

Data were analyzed using SPSS (2002) version 11.5 (LEAD Technologies Inc., Chicago, IL). Final harvest data were analyzed using a General Linear Model ANOVA, with plots nested within treatments in each of the four contrasting habitats. Where there were significant F-ratios, post-hoc comparisons of means were carried out using t-tests for paired comparisons, and Scheffé's multiple comparison tests (Zar 1984) where there were more than two means.

2.4 Results

2.4.1 Environmental conditions

The four habitats showed significant differences in terms of light intensity and all six of the observed soil parameters (Table 2.1). In most cases, the gradient of soil parameters increased with increasing successional stage: the proportion of moisture, organic matter, and the concentrations of nitrogen and phosphorus. The pH became closer to neutral, as succession proceeded from back beach, to primary succession, to secondary succession, to forest.

Light intensity was lowest in the forest, and highest in the secondary successional savanna plots. The pattern for soil potassium was different in that it was significantly higher ($p< 0.001$) in the forest and primary successional savanna (88.5 and 87 mg/kg respectively), and lower in the back beach and secondary successional savanna (60.5 and 69 mg/kg respectively).

2.4.2 Survival and growth over time

Over the two years of study, clear and significant differences emerged among plants in the four habitats, and some significant differences between fenced and unfenced plants were also apparent. By the end of two years, overall survival (irrespective of fencing) in the primary and secondary successional plots was greatest (Fig. 2.1). As a result of fencing, survival increased from 86.6% to 94 % in secondary successional savanna, 83%

to 91% in primary successional savanna, and 61% to 83% in the back beach. In contrast <4% (seven plants) survived in the forest (irrespective of fencing).

In the first 6 months of the study, plants were surviving well in the Back Beach; indeed at the end of year one there were no statistically significant differences in survivorship among the back beach and primary and secondary successional savanna areas. However by the end of the second year, survival in the back beach area was significantly lower. In the forest plots (fenced and unfenced), mortality was marked, with just 25% of the original plants still alive after seven months.

2.4.3 Effect of fencing

In the forest plots, numbers were so low by the later observation periods that no significant differences were seen between fenced and unfenced plots (Fig. 2.2). In the other three habitats, however, *Opuntia* survival was significantly greater in fenced plots (83%, 91%, and 94 % in Back Beach, primary and secondary savanna respectively).

2.4.3.1 Plant height

In all habitats there was a decrease in plant height each winter (succulent cladodes shrinking and becoming wrinkled in winter); however by 2002, and August 2003, there were statistically significant differences among plants from the four habitats, with tallest plants being found, in order of decreasing size: secondary successional savanna> primary savanna > forest > back beach. These differences also became more accentuated over time (Fig. 2.3).

Growth was slow at all locations (fenced and unfenced), but particularly slow in plants placed in the forest habitat (Fig. 2.4). By year 2, cladode number (for surviving plants) had doubled in all sites, with the greatest number of cladodes being evident in the secondary successional savanna> primary successional savanna > forest > Back Beach (all differences statistically significant by the end of year 2). In the two savanna habitats there was no significant effect of fencing on cladode number, but in the Back Beach unfenced plants produced significantly more cladodes throughout the second year (these plants were more exposed to sand burial, see below).

Table 2.1 Environmental parameters in the four successional habitats (means, with standard errors in parentheses). For each environmental parameter, results of General Linear Model ANOVA significance (P) is shown, and means for a parameter that differ significantly between plots are denoted by different superscript.

	Back Beach	Primary Succcessional Savanna	Secondary Successional Savanna	Forest	P
Light intensity (lux)	2128.8^{ab}	1823.0^{b}	2264.2^{a}	162.2^{c}	< 0.001
	(104.6)	(89.3)	(25.1)	(28.2)	
Moisture (%)	3.3^{b}	9.3^{ab}	13.0^{a}	14.6^{a}	< 0.001
	(0.2)	(2.5)	(2.6)	(1.6)	
Organic matter (%)	1.1^{c}	2.3^{bc}	3.4^{b}	4.1^{a}	< 0.001
	(0.2)	(0.3)	(0.5)	(0.4)	
Nitrogen (mg/kg)	6.0^{b}	7.0^{b}	7.0^{b}	23.0^{a}	< 0.05
	(0.7)	(0.8)	(0.8)	(8.7)	
Phosphorus (mg/kg)	27.5^{c}	56.3^{b}	97.5^{a}	97.5^{a}	< 0.001
	(6.4)	(4.3)	(2.5)	(2.5)	
Potassium (mg/kg)	60.5^{b}	87.0^{a}	69.0^{b}	88.5^{a}	< 0.01
	(2.3)	(4.7)	(4.8)	(3.1)	
pH	7.9^{a}	7.8^{ab}	7.4^{ab}	7.3^{b}	< 0.01
	(0.1)	(0.1)	(0.2)	(0.2)	

Table 2.2 Summary of significant main effects and interactions for plant growth and performance parameters, for plants transplanted to experimental plots in each of four successional habitats. Probability (P) values that are statistically significant are indicated in bold italics.

Growth parameters	Covariate of initial height	Habitat (H)	Treatment(T) fenced or unfenced, nested within habitats
Volume	***<0.001***	***<0.001***	***<0.001***
Shoot fresh mass	***<0.001***	***<0.001***	***<0.001***
Root fresh mass	***<0.001***	***<0.001***	0.073
Number of cladodes	***<0.001***	***<0.001***	***<0.001***
Mean cladode area	0.128	***<0.001***	0.104
Total cladode surface area	0.125	***<0.001***	0.227
Perimeter-area ratio of cladode	***<0.001***	***<0.001***	**0.026**
Cladode length-to-width ratio	***<0.001***	***<0.001***	***<0.001***
Total height	***<0.001***	***<0.001***	***0.003***
Chlorotic cladode surface area	***<0.001***	***0.003***	***0.048***
Root surface area	0.074	***<0.001***	0.140
Total surface area	**0.038**	***<0.001***	0.063
Total plant mass	***<0.001***	***<0.001***	<0.001
Shoot-to-root surface area ratio	0.650	0.631	0.711
Root-to-shoot surface area ratio	**0.013**	***<0.001***	0.140
Percent of surface area that is shoot	**0.020**	***<0.001***	***0.019***
Percent of surface area that is cladode	**0.002**	***<0.001***	***0.009***
Percent of surface area that is chlorotic cladode	0.161	***<0.001***	0.978
Percent of surface area that is root	**0.020**	***<0.001***	***0.019***
Percent of mass that is shoots	0.090	***<0.001***	***0.042***
Percent of mass that is root	0.090	***<0.001***	***0.042***
Root-to-shoot mass ratio	0.081	***<0.001***	***0.042***
Area-to-mass ratio for shoots	0.830	0.757	0.471
Mass-to-area ratio for shoots	***<0.001***	***<0.001***	***<0.001***

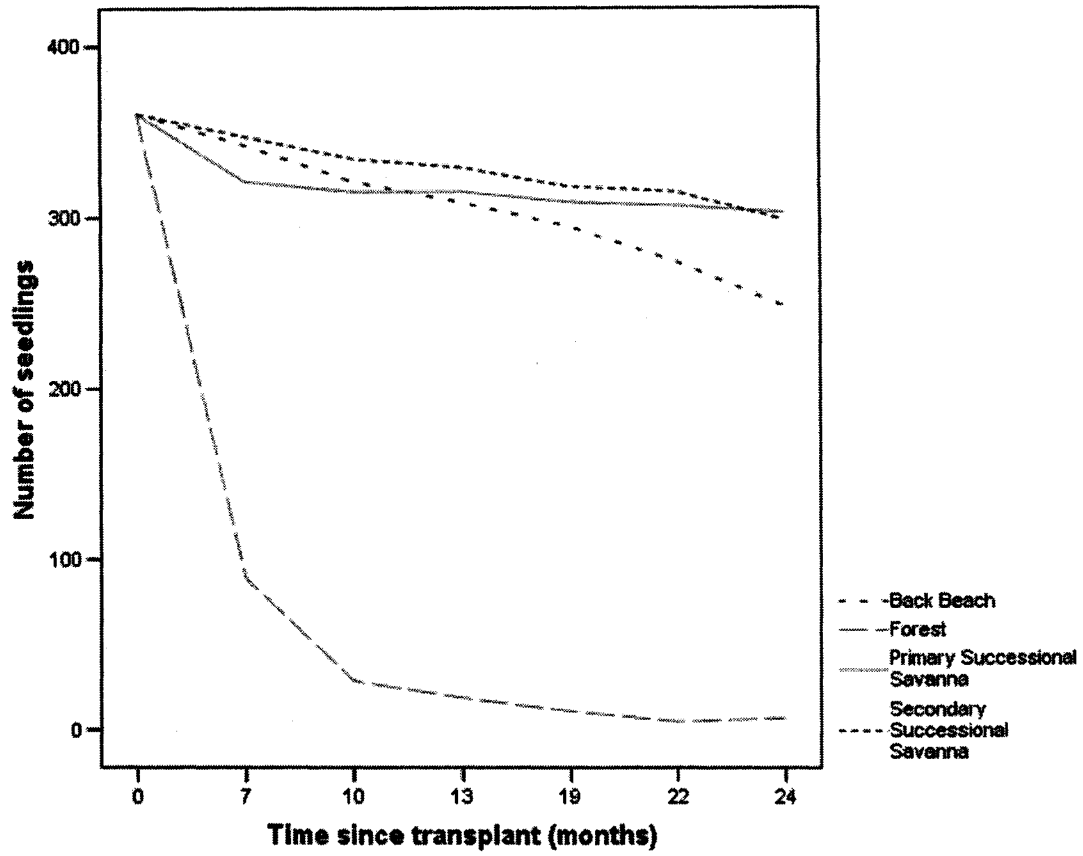

Figure 2.1 Survivorship over 24 months of cactus plants transplanted to four habitats.

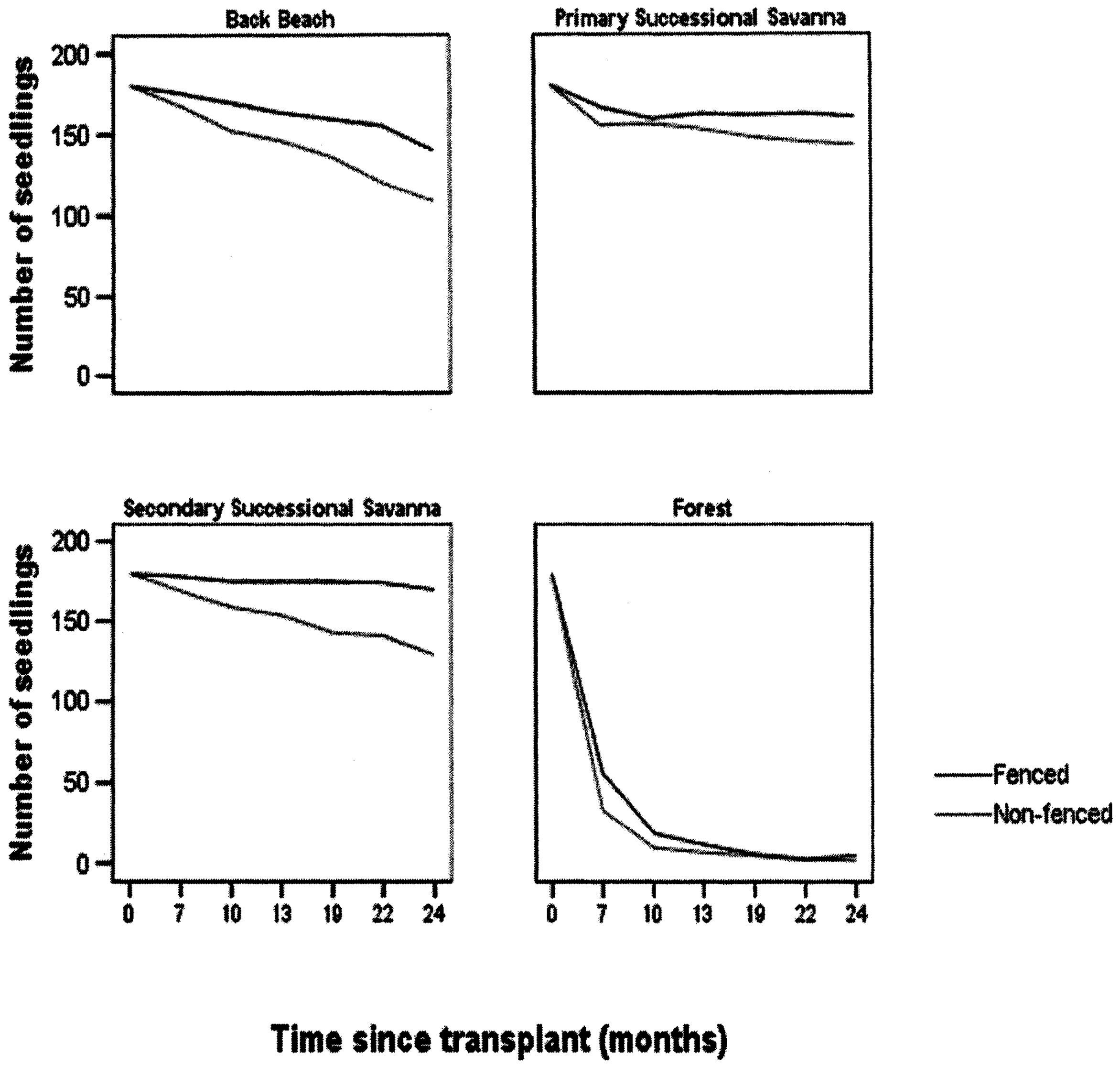

Figure 2.2 Survivorship over 24 months of cactus plants transplanted to four habitats, in fenced and unfenced plot.

2.4.4 Final harvest: growth in contrasting habitats

In Table 2.2, a summary of the significance of F-ratios derived from nested analyses of variance for each growth parameter, and for a variety of derived growth measures, is given. Initial height of each plant was included as a covariate to account for possible carryover effects of very slight initial differences in plant size. Habitat had a highly significant effect on most aspects of plant growth, and the fencing treatment affected a number of parameters. As expected, some growth measures were highly correlated, for example the associations between volume and shoot fresh mass ($r^2 = 0.991$), volume and total plant mass ($r^2 = 0.991$) and volume and total plant height ($r^2 = 0.668$). However, total cladode surface area and mean area per cladode ($r^2 = 0.986$) were associated but there was no association between total cladode surface area and number of cladodes.

Overall, plants grew larger in the secondary successional savanna, in terms of plant volume, total plant mass, shoot mass, number of cladodes per plant, mean area per cladode, cumulative cladode area, and cumulative length of cladode (Appendix A). (This latter value (cumulative length of cladode) usually equated to height, as cladodes were typically produced in a linear chain, but occasionally side-branching cladodes were produced). In most respects, plants in the primary successional savanna were significantly smaller than in the secondary successional savanna, and ranked second in size (in terms of volume, shoot mass, number of cladodes, cumulative cladode length and total plant mass) but were of similar size to plants from the secondary successional habitat in terms of mean area per cladode, and cumulative cladode area. Plants in the primary successional savanna had significantly greater mass per unit area of cladode, greater root surface area, greater root mass, and greater total plant surface area (adding roots and cladodes together).

In the Back Beach habitat plants grew relatively poorly, and were subject to frequent sand burial. There was greater chlorotic (white, buried) cladode area at that habitat. The seven survivors in the woods had the greatest perimeter-to-area ratio, and the greatest length-to-width ratio for cladodes, indicating severe etiolation.

2.4.4.1 Effect of fencing treatment

The fencing treatment caused statistically significant effects on measures of plant size, shape and biomass allocation (Table 2.2). Post hoc tests indicated that these parameters differed significantly between fenced and open plants in specific sites (Appendix B). For example, in the Back Beach, unfenced plants had significantly more cladodes, a greater-length-to-width ratio for cladodes, and had greater total height, chlorotic cladode area, total cladode area, root surface area, total plant surface area, and area-to-mass ratio for shoots. In contrast, in the secondary successional savanna, fenced plants showed greater growth in terms of shoot volume, shoot fresh mass, root fresh mass, total plant mass, proportionate mass in roots, and a greater root-to-shoot mass ratio.

In the primary successional habitat, fenced plants had slightly lower root mass, and their cladodes were more elongated (higher length to width ratio) but they did not differ significantly in any other respect. In the forest, unfenced plants had a significantly higher perimeter-to-area ratio, cladode length to width ratio, plant height, shoot to root surface area ratio, % of surface area that is shoot, or green cladode.

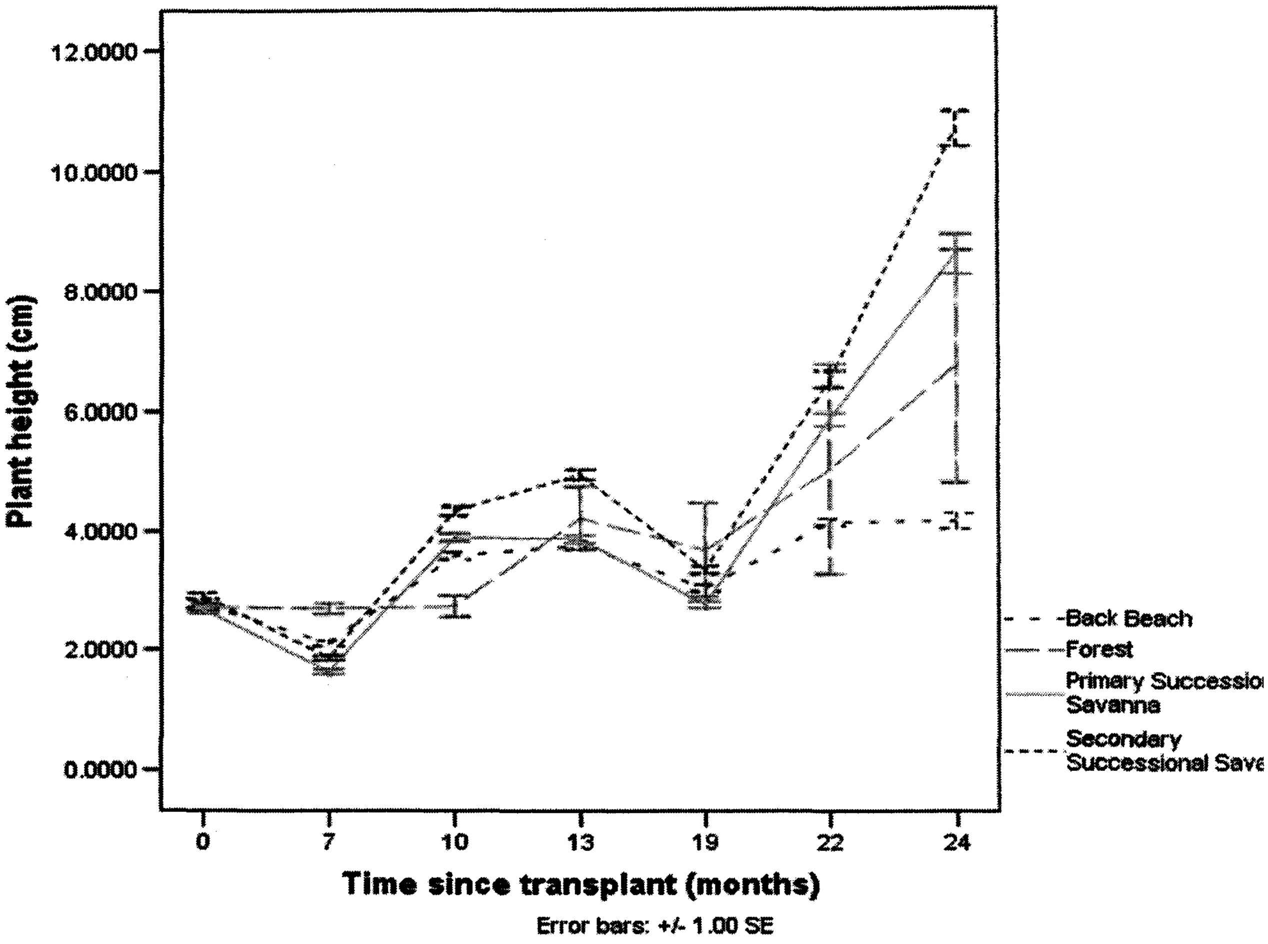

Figure 2.3 Plant height over 24 months in cactus plants transplanted to four habitats. Error bars indicate standard error.

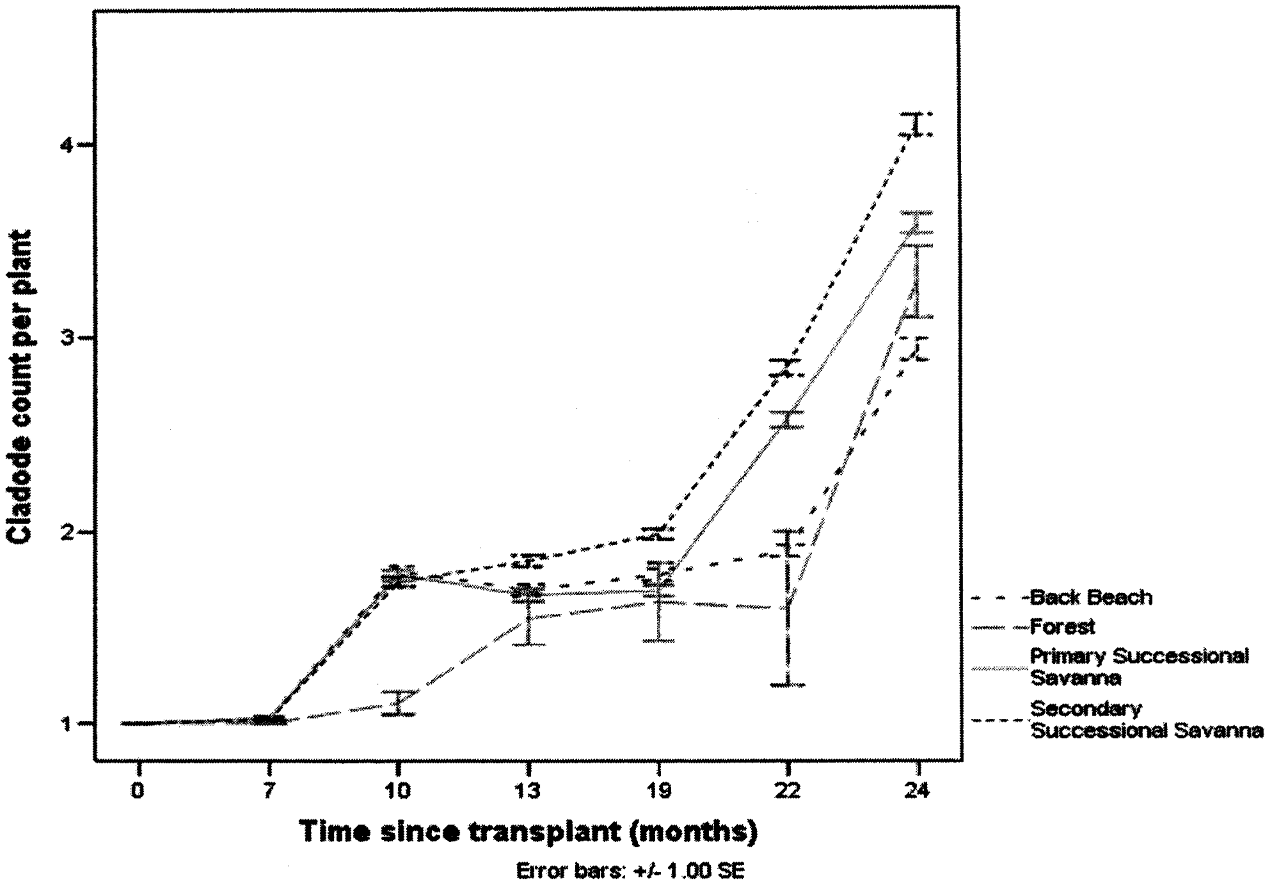

Figure 2.4 Number of cladodes (pads) per plant over time for cactus plants transplanted to four habitats. Error bars indicate standard error.

2.4.4.2 Plant shape and biomass allocation

Plant shape and absolute and proportionate distribution of biomass in different plants structures differed in several respects (Appendix A). Both the absolute amount of root tissue and the percent of biomass in root tissue were greatest for plants in the primary successional savanna. Plants in the secondary successional savanna had the greatest absolute and % biomass in shoots. Plants in the forest had a similar percent of their biomass in shoots as plants in the secondary successional savanna, ($p>0.05$), yet were only a fifth the mass of those vigorous plants.

In terms of cladode shape, the lowest perimeter-to-area and length-to-width ratios were seen in plants grown in the secondary successional savanna. These cladodes were therefore closest to being circular in outline. In contrast, the cladodes of the few plants surviving in the forest were extremely elongated, and had high ratios for both perimeter-to-area, and length-to-width with the effect being most pronounced in the unfenced plots (Appendix A, B).

2.5 Discussion

In the present study, it seems that much of the dryland habitat would support growth of *O. humifusa* with the exception of closed canopy forests. Indeed, *O. humifusa* may be dispersal-limited. While growth and survival were greatest in the areas in which *O. humifusa* persists today, the physical environment in terms of light and soil quality suggested the possibility that cactus might grow on the Back Beach, dispersal permitting.

In the greater part of this species' range, plants can flower and set seed by the end of the second year of growth (Conover and Geiger 1989), but this is not true for the Canadian population, even in the best habitat conditions available. Based on the minimum size of flowering plants of *Opuntia humifusa* in the natural field plots, plants would probably need to be at least 6-8 years old before they would be large enough to flower (Levi 2001). Delays in reproduction and limitations in fecundity will surely limit a species distribution. This has been shown for a variety of other plant species (see Holt 1972) In a transplant experiment involving the lichen *Usnea longissima* Keon and Muir (2002) found that several unoccupied habitats were in fact quite suitable for the species, and that greater growth (increase in lichen length) was sometimes associated with habitats that had been considered unsuitable. Keon and Muir (2002) concluded that the species was limited in its distribution by dispersal.

2.5.1 Forest habitat

Although previous reports indicated that cactus has occurred near the forest plots, it was last observed there some thirty years ago (Ross, 1971). It is clearly intolerant of low light, based on the observation that light levels were less than 1/10 the level in the other habitats, inducing a strong etiolation response in the cladodes. In contrast, nutrients or water are unlikely to be limiting in the forest as they are present in the forest soil in higher concentrations than in the other sites (Table 2.1). Indeed nitrogen was present in the forest at three times the concentration found in the other three habitats, where it appeared to be a limiting factor for plant growth (Table 2.1). Comparable findings have been reported when soil blocks ordinarily occupied by annual grasses and other oak understorey species were reciprocally transplanted between an oak forest and adjacent open communities (Maranon and Bartolome, 1993). In that study, there was rapid loss of light-dependent species from the formerly open soil blocks, and a severe reduction in plant diversity and biomass. An increasing emphasis on above-ground tissues and a drop in the ratio of root-to-shoot biomass in plants placed in forest plots was also seen in a study of tree saplings in shaded broadleaf forest (Van Hees and Clerkx 2003). Changes in the distribution of biomass can also provide useful clues to plastic responses to environmental limitations. Similar morphological responses to those seen in *O. humifusa* have been reported for shade-intolerant *Solidago* spp. (e.g., Bjorkman 1966, Cornelius 1990). Indeed, Walck *et al.* (1999) reported increased leaf biomass with proportionately less root biomass for light-limited treatments on *S. shortii.*

2.5.2 Back Beach habitat

Previous studies at PPNP (e.g., Levi 2001) indicated that there was no seed bank for *O. humifusa* in the Back Beach. It was, therefore, postulated that their absence from that habitat type might reflect dispersal limitation, since the site seemed otherwise suitable in terms of light intensity, presence of free-draining soils and low competition from neighbouring plants (Benson, 1982, Fig. 2.1) The Back Beach site at first appeared to be hospitable to *O. humifusa*; plants survived there in the first year as well as they did in the two successional savanna habitats (Fig. 2.1). However, unfenced plots were particularly vulnerable to movement of the unstable shifting substrate, and sand burial was associated with low and smaller survival and plant size by the end of two years. This supports an experimental study that was aimed to investigate how the New Zealand sand dune species responded to different depths of sand burial? The above study showed that few species were able to survive burial (see Sykes and Wilson 1990). The authors argued that abundant wind there often results in sand movement in the exposed sites, and thus seeds, seedlings and adult plants are regularly covered to various depths.

In an experiment using three dune species in California, Brown (1997) showed that two shrub species and a grass differed in their relative tolerance of sand burial; however as the depth of burial increased, all species shifted biomass from below-ground to above-ground tissues. In cactus, at the Back Beach, there was no change in the proportion of root tissue. Indeed the total root and shoot surface area increased when plants were buried in the unfenced areas (Appendix B) probably due to a generalized etiolation response. Plants responded to burial by elongating their main axis (growth in height and elongation of individual cladodes); lower cladodes lost their chlorophyll, reducing the net photosynthetic capacity of these plants. Provision of fencing there could reduce the impact of substrate disturbance on transplants in that site, but even fenced plants suffered significant sand burial, and their numbers declined such that there would be no survivors after 2-3 more years, if the mortality continued.

A much reduced tolerance to sand accretion in *O. humifusa* seedlings (an early colonizer) indicates that sand accumulation was an important cause of seedling mortality on the Back Beach. This supports results of a study of tropical coastal sand dune plants by Martinez (2003) which suggested that the establishment and survival of early colonizers is comparatively more hampered by the increased substrate mobility than the late colonizer grasses. Martinez (2003) argued the latter benefited by the reduced substrate shifting that occurs beneath shrubs, like *Chamaecrista*, thus decreasing the possibility of being totally covered by sand.

This would all suggest that self-sustaining populations could not be established under the back beach conditions since transplants would not live long enough to reach sufficient size to flower and bear fruit. This supports the suggestion of Klinkenberg and Klinkenberg (1985) that the beach area would probably be unsuitable for restoration plantings of *O. humifusa* due to excessive disturbance and storm action. However, as the back beach proceeds through succession to primary savanna, and substrate stability increases as vegetation develops, cactus survival is expected to increase.

2.5.3 Savanna habitats

It was initially conjectured that *O. humifusa* could show reduced survivorship in the old-field secondary successional savanna because of competition in the herb layer. However, transplants grew significantly larger in the secondary sucessional savanna compared to the primary successional savanna, which can be explained in large part by the better soil conditions. There was a more developed A horizon, with significant organic matter accumulation (Table 2.1) following several decades of agricultural use there during the mid 19th, and early 20th century, plus litter accumulation from grasses, forbs and shrubs (Nature Conservancy 2003). This land use may have provided some extra nutrients, superior water-holding capacity, and enhanced buffering from the effects of acid precipitation in this region.

In the secondary successional habitat, fencing protected the *O. humifusa* transplants from deer browsing. In fenced areas *O. humifusa* mortality was significantly lower (Fig. 2.2) and deer prints, resting areas and evidence of browsing were common outside the fenced areas, but absent from the fenced plots in the secondary successional savanna. Fencing also facilitated these plants achieving greater overall growth (in terms of total mass, shoot mass, root mass and cladode volume; Appendix B). This result is similar to the finding of Reader and Bonser (1998) who studied the effects of exclosures and neighbour removal in order to assess the effects of competition and herbivory in six herbaceous species in five old-field and one habitat. All species showed an increase in biomass when they were fenced from herbivores, and also had increased biomass when neighbours were removed.

These results also give indirect support to findings made by several other authors who suggested that plants generally respond to environmental heterogeneity (including variations in soil nutrient availability, light intensity, and density of plants within a population) by altering growth and/ or adjusting biomass partitioning to various organs (Mooney and Winner 1991, Dale and Causton 1992, Reynolds and D'Antonio 1996 reviewed *in* Meekins and McCarthy 2000).

2.5.4 Plasticity in shape

Cladode morphology differed between populations in the two savanna habitats (see Levi 2001). Plants growing naturally in the secondary successional savanna had more circular, shorter and thicker cladodes than those in the primary successional savanna. This distinction was also noted in the experimental seedlings that were transplanted to those areas whatever their source population. This suggests a strong environmental influence on this morphological character, rather than a difference based on local genetic selection. The distinctive cladode forms are not a product of localized adaptation, but are instead an environmentally-induced, plastic response. As mentioned above *O. humifusa* has an extensive geographical range and the morphology of its stem, spine, flowers, and fruit may vary widely depending on the geographical location of *O. humifusa* (Abrahamson and Rubenstein 1976, Benson 1982). Further evidence for cladode size and shape being a plastic response is that there was no association between total cladode surface area and number of cladodes; this implies that plants with abundant cladode tissue don't have *more* cladodes, but rather have larger individual cladodes.

In summary, results of the present study support the identification of the primary and secondary successional savanna habitats as critical and suitable habitats for *O. humifusa* a Canadian Endangered species. The cactus is clearly intolerant of the low light intensities available in the forest, where it is below compensation point, and dies out rapidly, despite ample levels of soil nutrients, moisture, and soil organic matter. It is therefore reasonable to assume that as secondary succession proceeds, and shrub and tree density and competition increase, *O. humifusa* will eventually be eliminated from the secondary successional savanna. Biomass allocation to roots was higher in the two successional savanna habitats; this fits with the finding that savanna species generally allocate more biomass to roots (Hoffmann and Franco 2003).

2.6 General conclusions

In the first few months of this study there were few differences between plants in the back beach and those in the primary and secondary sucessional vegetation; this led us to infer, at first, that it might be useful to plant cactus in the back beach area in order to assist establishment and expand the area identifiable as critical habitat (especially since those locations will eventually become primary successional savanna as beach accretion

on the west coast of the sandspit continues). By the end of the study it was apparent that the costs of recovering from sand burial events reduced the plants' net growth rate and, ultimately, survival. The back beach is a habitat that cannot presently support a self-sustaining population of *O. humifusa.* As the primary successional savanna becomes more closed, perennial vegetation may out-compete the cactus plants; at that point new individuals may well disperse to, and establish in, what is currently the location of back beach habitat, as that substrate becomes more vegetated and therefore more stable.
It is important to note that the present study involved the planting of seedlings that were quite well established, with healthy root systems at the time of transplantation. Their survival under favourable conditions was comparatively high. This contrasts with the observed survival of naturally germinated seedlings in populations of this species; for example Baskin and Baskin (1977) found 50% survived through their first winter, and after 5 years, no seedlings raised from seed remained alive at the site where adult cactus plants were still growing normally. Several authors have noted that seed germination is at best very slow in this species (Thornber 1911, Baskin and Baskin 1977, 1998, Levi 2001), so if any restoration is undertaken, it is clear that seedling transplants will be much more successful than simply broadcasting seeds.

Many factors likely intersect in determining the 'needs' (requirements) for species like *O. humifusa* grown in dynamic habitats. It is essential to incorporate other probabilistic colonization constraints, such as chances of seed arrival, seed and seedling desiccation patterns associated with site-specific and stochastic weather conditions (Lichter 2000), plus factors other than demography (including seed and seedling predation) in which the species is adjusted to or evolved into its critical habitat.

With limited resources available for conservation measures, it seem reasonable to place emphasis on conserving the existing cactus populations in the two savanna habitats rather than introducing populations to the unsuitable forest habitat or the unstable back beach. Both successional savanna habitats represent critical habitat for this Species at Risk in Canada, and constitute the realized niche of the species at PPNP. Since *O. humifusa* grows at PPNP in a dynamic sandpit environment that shifts in space and time, emphasis should be placed on the conservation of suitable successional savanna conditions that need not necessarily remain at the same geographic locations over time.

Chapter 3- Effects of shading and macro-nutrient levels on growth in *Opuntia humifusa*: a greenhouse factorial experiment

Summary

A greenhouse study was carried out to investigate the role of shading and macro-nutrient levels on the growth of *Opuntia humifusa*, and hypothesized that the increased nutrient availability at high irradiance level in well-drained soils may enhance population growth. Also, it had been reported that cactus grows best in full light. Yet plants are mostly located in sandpit savanna, so light optima were also being tested. *O. humifusa* plants raised from seeds, collected from two sites (West Beach and DeLaurier) at Point Pelee National Park (PPNP) were grown over eleven months in the greenhouse of University of Windsor.

Experiment was conducted with a full factorial design in which four nutrient treatments were superimposed on each of four shading regimes, in order to simulate differential supplies of mineral nutrients (NPK) and light, and to detect any interplay between light, nutrients, and site of origin of plants, and their effects on growth. Some of the contrasting light and nutrient treatments corresponded to conditions in potentially suitable habitats at PPNP (Back Beach, West Beach, DeLaurier, and Woodland) locations that may be suitable for the re-introduction and restoration of *O. humifusa.*

Estimates of cladode (pad) and root surface areas, perimeter-area ratio of cladode which measures etiolation, root- to- shoot surface area ratio, number of cladodes and plant fresh mass were determined at the outset, in December, 2003, and again eleven months later. Results of a split-plot, two-way nested analysis of variance indicated that both factors had

highly significant effects on growth, however, the effect of nutrient supply was more pronounced at the higher light levels. Site of origin of the seed that gave rise to these plants, i.e. West Beach versus DeLaurier (primary successional savanna vs. secondary successional savanna) had little effect on plant growth. Shade had a highly significant effect on all aspects of plant growth ($p < 0.001$), and so did the nutrient level except root area and cladode elongation. Greater gain in biomass and cladode area was achieved at the higher nutrient level combined with 30-50% shade. Moreover, the range of conditions in which the species may occur with respect to light and nutrients in the absence of other constraints such as competition or herbivory (i.e., fundamental niche) was quite broad as compared to its realized ecological niche at PPNP.

These results indicate that *O. humifusa* grows best under partial shade but will grow poorly under a closed canopy. It could also benefit in terms of vigour from nutrient supplement-action.

3.1 Introduction

Understanding the eco-physiological requirements of a species may help to predict both their habitat preferences within a community, as well as the species broader geographical range (Gaston 1990, Kimball *et al.* 2004).

When local adaptation occurs in different parts of a species range, locally-adapted populations may have established distinct niches (Holt 2003). Hence local abundance of a species may reflect the way in which individuals utilize local resources (Gaston 1994). It is also evident that locally rare species can become abundant at sites where their environmental niche requirements are best met (Murray and Lepschi 2004). For plants of south-eastern Australia, such sites have been shown to exist (Austin and Meyers 1996, Austin *et al.* 1996). The conservation of species with declining populations, therefore, would be facilitated by information regarding the environmental factors that limit population growth, and by identification of suitable sites for the protection and restoration of rare and endangered species (Brussard 1991, Pavlik 1994, Schemske *et al.* 1994, Maschinski and Holter, 2001, Maschinski *et al.* 2004, Yates and Ladd 2005). Recent studies also suggest that for species with limited dispersal, the major environmental variables become relatively more influential in predicting the occurrence and/or abundance of local species (see Ozinga *et al.* 2005).

The distribution ranges for many members of the family Cactaceae are significantly affected by environmental heterogeneity and species-specific physiological requirements (see review by Godinez -Alvarez *et al.* 2000). A useful framework within which to formulate the relationship between physiological process and ecological performance is that of the physiological niche: the set of environmental conditions under which a species can persist (Hutchinson 1957, Leibold 1995). Niche theories suggest that environmental factors account for most observed species' niche measurements (Potts *et al.* 2004). The realized niche is usually measured as niche breadth and /or overlap (see Glime *et al.* 1987). The fundamental niche (*sensu* Hutchinson 1957), however, has not been successfully quantified (but see Rydin 1987, Wang 1995), and thus merely described (Malanson 1997).

To determine a species' ecological niche breadth, the crucial information is the range of conditions (e.g., light, moisture, soil nutrients, soil structure, and temperature) the species may successfully occupy. These conditions represent the highest and lowest resource states that occur in sites inhabited by viable populations, rather than the mean or frequency distribution of particular environmental states (Sultan *et al.* 1988). To characterize this range accurately, it is essential to sample temporal and spatial environmental variation effectively within natural populations (Bazzaz and Sultan 1987), as well as variability among populations occupying different habitats (Quinn and Hodgkinson 1983, Baskauf and Eickmeier 1994, Blossey and Notzold 1995).

Recent studies place emphasis on quantifying the essential and potentially limiting factors in the same sites where population growth rates are measured (Pulliam 2000). Such information is particularly useful in developing successful management strategies for rare and endangered species (Brussard 1991, Schemske *et al.* 1994, Aleric and Kirkman 2005) before actually establishing what does and does not constitute suitable habitat for the survival and growth of a species (Pulliam 2000).

Many rare plant species are weedy, early successional species, and grow in habitats where vegetation remains in a transition state (Baskin and Baskin 1986, Pavlik 1994). In altered climatic and disturbance regimes, or in habitats characterized by resource limitation, tolerance of ecological and physiological factors can determine the distribution of species composition (Chesson and Huntly 1997, Emery *et al.* 2001). Leibig's 'Law of the Minimum' (Leibig 1840) or the plant biologist's version, Blackman's Law of Limiting Factors (Blackman 1905) that the performance of plants is ultimately constrained by the single resource that is most limiting (Chapin *et al.* 1987, Latham 1992). However, it is clear that plants can be limited simultaneously (co-limited) by more than one resource (see Pearson *et al.* 2003).

Light is one of the major environmental factors influencing growth and distribution in plant species (Boardman 1977, Lambers *et al.* 1998), and is a primary limiting resource in forest (Frost *et al.* 1986, Hoffmann and Franco 2003, Elemans 2004). This is also true for macro-nutrients (Nitrogen, Phosporus, and Potassium) in open savanna environment (Frost *et al.* 1986, Hoffmann and Franco 2003, Mills and Fey 2004). Tradeoffs in terms of increased efficiency of light use in lower light conditions may create partitioning along a light availability gradient, as has been found for plants in the forest canopy understorey (see Chazdon *et al.* 1996) and savanna-forest boundary (Hoffmann and Franco 2003); this principle provides a mechanistic basis for predicting effects of environmental disturbances on populations and communities.

It is generally believed that species with broad niches have traits that enable them to disperse to and occupy a greater range of habitats (Gaston and Spicer 2001, Lloyd *et al.* 2003). *Opuntia humifusa* occupies an extensive geographical range and diverse set of habitat types in the main part of its distribution in the United States. It occurs from southwestern Ontario and Wisconsin, south to eastern Texas and along the Gulf and Atlantic coasts from Florida to Massachusetts (Whitehead 1995). The species has been reported to survive in a wide range of environmental conditions, and to tolerate environmental disturbances (Oakwood *et al.* 1993, Edwards and Westoby (1996). The current, limited, distribution of *O. humifusa* at Point Pelee National Park (PPNP) likely does not reflect its environmental tolerances (see Anthony 1954, Olson 1958, Richardson 1977, Conover and Geiger, 1989). Thus a need clearly exists to asses and as well as to characterize the niche and habitat tolerance of *O. humifusa* both within PPNP and over its larger range.

Opuntia humifusa in Ontario is found in a very rare habitat type 'Lake Erie Sandspits' (Reznicek, 1982; and Reznicek, personal communication; Kraus, 1991). The only naturally-occurring populations in Canada today are found in the rare Red Cedar sandspit savanna habitats. These locations exist at Long Point, Rondeau Provincial Park, Point Pelee National Park (PPNP), and at Fish Point Provincial Natural Reserve, on Pelee Island (Reznicek 1982, Levi 2001). Due to currents and wind, the land of the peninsula is constantly changing, especially at its tip (Nature Conservancy, 1990). At present, natural locations of *O. humifusa* within Point Pelee National Park occur at the West Beach, primary successional savanna (inland of, and parallel to the coastal Back beach), and theDeLaurier homestead (further inland, abondened farmland, and secondary successional savanna for which the climax vegetation would be Eastern Deciduous Forest, Fig. 1.3).

O. humifusa has been reported across the sandpit at PPNP, in a range of locations from erosion sites and depositional beaches to closed canopy forested areas (see Whitehead 1971, Levi 2001). Therefore, it can be assumed that the entire dry land portion of the sandpit constitutes the fundamental niche (*sensu* Hutchinson 1957) for the species. However, the current *realized niche* (where *O. humifusa* is presently growing) seems to be limited to two distinct savanna strips, the primary savanna and secondary savanna.

Numerous studies on cacti, which are slow growing plant, have suggested that several abiotic factors, such as water and nutrient availability can affect their growth (see Godinez-Alvarez 2000). An experimental study on vascular epiphytes (Castro-Hernandez *et al.* 1999) and other indirect evidence (Benzing 1990, Zotz and Hietz 2001) suggest that slow growth is usually linked to brief and irregular availability of water and nutrients. Other studies also demonstrate that a high concentration of nutrients significantly increases seedling growth in cacti, including *Mammillaria magnimamma*, *Pachycereus hollianus*, and *P. pringlei* (Godinez-Alvarez and Valiente-Banuet 1998, Carrillo-Garcia *et al.* 2000, Ruedas *et al.* 2000).

In harsh or altered climates, species may be constrained by trade-offs in their capacity to compete for access to different resources (e.g., light versus nitrogen) and may be limited to specific environments (Tilman 1988). Light and nutrient may be particularly important for rare and threatened species, especially if they rely on reproduction via seeds (Rajaniemi *et al.* 2003), or are growing in transitory conditions.

As *O. humifusa* is found in the transitional habitats at PPNP, and conditions at a location likely change during ecological succession, it is particularly important to identify optimal conditions of light and nutrients for its survival and growth. Optimal partitioning models posit that plants respond to variation in the environment by partitioning biomass among various plant organs to optimize the capture of nutrients, light, water, and carbon dioxide in a manner that maximizes plant growth rate (Lovett-Doust 1980, Levin *et al.* 1989, Hilbert 1990, Dewar 1993), and that succession occurs as resource availabilities change over time and different plant traits become favoured (Lichter 2000). In other words the plants themselves modify the physical and chemical resource environment. How *O. humifusa* responds to variation in the availability of resources that represent contrasting light and nutrient environments within PPNP, and how these abiotic factors (light and nutrients) may directly influence the survival, growth and vigour of *O. humifusa* are investigated here.

A niche-based approach should help us to characterize limiting factors for patchy *O. humifusa* populations, providing a link between the physiological processes and pattern of distribution and abundance of *O. humifusa* observed along the environment gradients at PPNP.

3.2 Methods

Source plants of *Opuntia humifusa* were raised from seeds from two sites (West Beach and DeLaurier) at Point Pelee National Park (PPNP) in the greenhouse of University of Windsor. Plants, an average had a fresh mass of 1g, and comprised 1 cladode. A total of twelve hundred and eighty cladodes were propagated and planted in the moist sandy soil; each was allowed to grow until a root system was successfully developed.

The shade and nutrient experiment began on January 15, 2004 with evaluation of the starting condition of each plant. Roots were carefully washed, scaled digital images of all plants with their number tag were taken, and the fresh mass of each plant was determined. Plastic tubs (420 x 300 x 110 cm) were used. Each tub was filled with clean quartz sand to 40 cm depth. Each tub had twenty plants; ten from each site of origin, DeLaurier and West Beach were used. Tubs were numbered and each plant was marked to track its identity. Plants were arrayed (5 x 4 rows), placed approximately 8 cm apart.

Plants were allowed to acclimate under uniform light for 2 weeks before beginning the shade and nutrient treatments. Water was provided at the time of planting, and afterwards as indicated by soil moisture tests. Reverse osmosis treated (RO-pure) water was used. All survived the transplant. Water loss (via evaporation and transpiration) was significantly different for each set of plants, depending on the shade conditions. Soil moisture content was checked with moisture meter (Soil PH & Moisture Meter RRP 2002, J D Instruments UK).

3.2.1 Experimental design

Resource availability (e.g., nutrients, light and water) can vary within ecosystems due to disturbances or other land use (Fetcher *et al.* 1996); therefore, sixteen different combinations of shade and nutrient levels were provided in present experiment which included some conditions encountered in contrasting habitats at PPNP, and allowed evaluation of the effect of augmenting light, and nutrient resources. For each of the 16 different treatment combinations (4 levels shade, and 4 concentrations of nutrients), there were 4 replicate tubs, and each containing 10 plants—originating from seeds of primary successional savanna (West beach) and 10 from the secondary successional savanna (DeLaurier homestead). Tubs were arranged at random within the greenhouse

The shade treatment was provided by black polypropylene shade cloth SC-BL30, SC-BL50, SC-BL90 (IGC USA [International Greenhouse Company] On-line 2003). These fabrics provided 30%, 50%, and 90% reduction in light respectively, and could be compared with un-shaded conditions. Cloth was cut and designed according to the measurements of the tub, and then fixed 0.5 m above the tubs. Natural light was supplemented by GE LU250 bulbs (88112488 LuCalox High Pressure Sodium Lamp, 250 Watt) to provide 12:12 hour day/night cycle. Temperature ranged from 17°C to 35°C.

Four nutrient concentrations were applied based on an NPK ratio representative of the sandspit as a whole (NPK 1:10:10) (8x: 1272 mg/kg [6.02 g/ tub]; 4x: 636 mg/kg [3.01 g / tub]; 2x: 318 mg/kg [1.50 g / tub]; and 1x: 159 mg/kg [0.75 g / tub]). These were first supplied on 01 February, 2004 (2 weeks after planting), and re-applied subsequently on 01 May, and 01 August 2004.

Plants were monitored at regular intervals. The watering schedule varied to compensate for different rates of evapo-transpiration in each treatment. The schedule was: 500 ml water every 3 days to plants with 0% - 30% shade, every 6 days to plants with 50% shade, and every 10-12 days for those under 90% shade. The nine months experimental period paralleled that of the growing season of *O. humifusa* in the field at Point Pelee National Park (PPNP).

In October 2004, all plants were harvested for subsequent analysis. Fresh mass was determined for each harvested plant. The roots were carefully washed and scaled digital images of each plant, with its number tag were taken. Cladode and root surface areas, perimeter area ratio of cladode, and root to shoot surface area ratio were calculated based on analysis of the electronic images using SigmaScan Pro 5 image analysis software, version 5.0 (SPSS 1999; LEAD Technologies Inc., Chicago, IL).

3.3 Data Analysis

The data were analyzed using SPSS (2002) version 11.5 (LEAD Technologies Inc., Chicago, IL). Twenty plants (10 x 10) from two different sites (West Beach and DeLaurier) had been grown in each tub. A two-way ANOVA (split-plot nested design) was conducted to determine the interactions of different light and nutrient regimes on the growth of transplanted cladodes of *O. humifusa.* Where there were significant differences indicated by ANOVA, post-hoc comparisons of means for shade and nutrient treatments were carried out using Scheffé's multiple comparison tests (Zar 1984).

3.4 Results

Highly significant effects were seen in terms of main effects of shade on all aspects of both growth and relative growth. Nutrient levels also affected most parameters. The main effects of nutrient concentration, shade levels and site of origin, and their interactions on the growth and total plant performance are summarized in Table 3.1.

By the end of the study plants weighed an overall average of 2.5g (up from the initial average of 1g). Since initial mass was known for all plants, data were analyzed in terms of, say increase in mass or cladode number rather than crude number. Both shade and nutrient levels significantly affected plant growth. However site of origin had a significant effect only on change in fresh mass and relative root-to-shoot surface area ratio. Significant interactions (light x nutrient) were seen in all cases of plant growth except relative root-to-shoot surface area ratio.

Details of the main effects of nutrient concentration (Table 3.2), and shade levels (Table 3.3) indicate the following:

Site of origin of the plants significantly affected the fresh mass parameter ($p<0.05$). Plants from Delaurier homestead showed greater increase in fresh mass (mean value 6.6 ± 0.27 as compared to 6.2 ± 0.32 for West beach, as indicated by t-test result). The highest nutrient treatment (8x) produced the largest plants in terms of increase in fresh mass and increase in number of cladodes, as well as cladode surface area. The main effect of shade on plant growth, assessed in terms of increase in plant fresh mass and cladode number indicated 50% shade produced a statistically significant increase in plant growth (Table 3.3). Increased fresh mass and increase in number of cladode were greatest for plants grown under 8x nutrients with 30% shade (Table 3.4, Figure 3.1 & 3.2), suggesting these conditions represent optimal conditions for growth.

Cladode surface area increased significantly with increased shading, and with increasing nutrient level (Table 3.4, Figure 3.3). As a result the greatest cladode surface areas were noted under 8x nutrients combined with 90% shade. Shading affected the relative cladode area too. Greater change in area was noticeable under medium- and higher- shade treatment ($o<l<m<h$). Cladode morphology also changed in response to light conditions; cladodes became elongated under shade, and this was reflected in an increasing parimeter-area ratio with increasing shade (Table 3.5, Fig. 3.5).

Root surface area was affected by both nutrient and shade with significantly greater root area under the 2x nutrient treatment (554.60 ± 30.34) and the full light treatment (779.46 ± 32.12) in terms of main effects (Table 3.2, 3.3), and under the combinations of 4x nutrients and full light (897.43 ± 69.31) (Table 3.4, Figure 3.4). Perimeter: area ratio of cladode was greatest under 90% shade (Table 3.6, Figure 3.5). In terms of main effects, root-to-shoot surface area ratios were greatest in full light (Table 3.3) or under the (2x) nutrient treatment (Table 3.2). The ratio was, however, least where nutrients were in greatest supply (8x).

Appendix C shows the detailed ANOVA summeries and Table 3.4 displays all the means for each of the 16 different nutrient x shade treatments with their standard errors. Results of ANOVA indicate that enhancement effects of increased nutrient supply (fresh mass, cladode number) were much stronger in 70% of full light than at lower levels.

Table 3.1 Summary of significant main effects and interactions of nutrients (N), shade (S), and site of origin on performance parameters in *Opuntia humifusa*. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, NS = Not significant

Growth parameters	N	S	Site	NxS	NxSite	SxSite	NxSxSite
Change in:							
Plant fresh mass	* * *	* * *	*	* * *	NS	NS	NS
Cladode number	* * *	**	NS	**	NS	NS	NS
Cladode surface area	* * *	* * *	NS	*	NS	*	NS
Root surface area	*	* * *	NS	*	NS	NS	NS
Root- to-shoot surface area ratio	* * *	* * *	NS	* * *	NS	NS	NS
Perimeter-area ratio of cladode	NS	* * *	NS	* * *	NS	NS	NS
Relative change in:							
Plant fresh mass	* * *	* * *	NS	* * *	NS	NS	NS
Cladode number	* * *	* * *	NS	* *	*	NS	*
Cladode surface area	* * *	* * *	NS	*	NS	NS	NS
Root surface area	NS	* * *	NS	NS	NS	NS	NS
Root-to-shoot surface area ratio	* * *	* * *	**	NS	NS	NS	NS
Perimeter-area ratio of cladode	NS	* * *	NS	* * *	NS	NS	NS

Table 3.2 Main effects of four NPK concentration treatments in terms of mean values on plant performance parameters. Mean in the same row with the same letter do not differ significantly, those with distinct letters differ significantly at $p < 0.05$

		Nutrients				
		1x	2x	4x	8x	Significanc of effect
Change in:	Fresh mass	3.51 ± 0.12 a	4.10 ± 0.17 a	6.14 ± 0.22 b	7.34 ± 0.24 c	***
	Number of cladodes	0.99 ± 0.05 a	0.95 ± 0.05 a	1.45 ± 0.06 b	1.48 ± 0.06 b	***
	Cladode area	510.42 ± 21.56 a	572.64 ± 27.57 a	815.70 ± 31.71 b	950.60 ± 31.86 c	***
	Root area	446.91 ± 27.04 a	554.60 ± 30.34 b	520.63 ± 29.33 ab	533.77 ± 29.19 ab	**
	Root-to-shoot surface area ratio	0.36 ± 0.03 b	0.48 ± 0.04 c	0.26 ± 0.03 ab	0.17 ± 0.02 a	***
	Perimeter:area ratio of cladode	-0.14 ± 0.02 a	-0.16 ± 0.02 a	-0.18 ± 0.02 a	-0.13 ± 0.02 a	NS
Relative change in:	Fresh mass	1.04 ± 0.05 a	1.14 ± 0.05 a	1.78 ± 0.07 b	2.23 ± 0.10 c	***
	Number of cladodes	0.73 ± 0.05 a	0.73 ± 0.05 a	1.08 ± 0.06 b	1.08 ± 0.05 b	***
	Cladode area	1.22 ± 0.06 a	1.38 ± 0.08 a	2.15 ± 0.14 b	2.36 ± 0.13 b	***
	Root area	4.38 ± 0.36 a	5.85 ± 0.54 a	6.98 ± 1.15 a	5.63 ± 0.92 a	NS
	Root-to-shoot surface area ratio	1.86 ± 0.22 a	2.31 ± 0.19 b	1.72 ± 0.19 ab	1.19 ± 0.13 a	***
	Perimeter:area ratio of cladode	0.00 ± 0.04 a	-0.05 ± 0.03 a	-0.05 ± 0.04 a	-0.02 ± 0.03 a	NS

Table 3.3 Main effects of four shade levels in terms of mean values on plant performance parameters. Mean in the same row with the same letter do not differ significantly, those with distinct letters differ significantly at $p < 0.05$

		Shade (%)				
		0	30	50	90	Significance of effect
Change in:	Fresh mass	4.55 ± 0.19 a	5.37 ± 0.25 b	6.45 ± 0.21 c	4.72 ± 0.17 ab	***
	Number of cladodes	1.18 ± 0.06 ab	1.12 ± 0.06 a	1.38 ± 0.06 b	1.20 ± 0.06 ab	**
	Cladode area	399.30 ± 19.50 a	519.09 ± 27.27 b	961.54 ± 28.73 c	969.43 ± 29.52 c	***
	Root area	779.46 ± 32.12 d	674.60 ± 28.61 c	490.06 ± 23.37 b	111.79 ± 13.31 a	***
	Root-to-shoot surface area ratio	0.76 ± 0.04 d	0.53 ± 0.03 c	0.14 ± 0.02 b	-0.17 ± 0.01 a	***
	Perimeter:area ratio of cladode	-0.18 ± 0.02 a	-0.22 ± 0.02 a	-0.17 ± 0.02 a	-0.05 ± 0.02 b	***
Relative change in:	Fresh mass	1.37 ± 0.06 a	1.66 ± 0.10 b	1.85 ± 0.08 b	1.30 ± 0.05 a	***
	Number of cladodes	0.79 ± 0.05 ab	0.77 ± 0.05 a	1.06 ± 0.05 c	0.99 ± 0.06 b	***
	Cladode area	0.98 ± 0.05 ab	1.36 ± 0.11 a	2.39 ± 0.13 b	2.39 ± 0.11 b	***
	Root area	7.25 ± 0.40 b	7.16 ± 0.94 b	6.90 ± 1.19 b	1.54 ± 0.23 a	***
	Root-to-shoot surface area ratio	3.50 ± 0.22 d	2.70 ± 0.19 c	1.10 ± 0.14 b	-0.21 ± 0.08 a	***
	Perimeter:area ratio of cladode	-0.14 ± 0.03 a	-0.18 ± 0.03 a	-0.08 ± 0.03 a	0.27 ± 0.05 b	***

Table 3.4 Summary of interactive effects (nutrient x shade) on plant growth and performance parameters in terms of mean values with standard errors (±). 1x = Extra low nutrient (159 mg/kg), 2x = Low nutrient (318 mg/kg), 4x = Medium nutrient (636 mg/kg), 8x = High nutrient (1272 mg/kg).

		Change in:			
Nutrients	Shade (%)	Fresh mass	Number of cladodes	Cladode area	Root area
1x	0	3.19 ± 0.25	1.04 ± 0.10	281.05 ± 23.53	684.26 ± 62.62
	30	2.68 ± 0.22	0.66 ± 0.09	248.30 ± 23.01	578.15 ± 56.19
	50	4.43 ± 0.25	1.13 ± 0.12	699.37 ± 33.96	462.21 ± 38.93
	90	3.74 ± 0.20	1.15 ± 0.11	812.95 ± 46.08	63.02 ± 20.30
	Total	3.51 ± 0.12	0.99 ± 0.05	510.42 ± 21.56	446.91 ± 27.04
2x	0	3.44 ± 0.26	0.93 ± 0.12	246.64 ± 19.45	822.46 ± 65.43
	30	3.29 ± 0.26	0.81 ± 0.12	335.19 ± 33.67	772.24 ± 59.83
	50	5.74 ± 0.41	1.11 ± 0.08	833.07 ± 60.33	493.93 ± 51.75
	90	3.93 ± 0.30	0.96 ± 0.10	875.67 ± 55.23	129.76 ± 22.05
	Total	4.10 ± 0.17	0.95 ± 0.05	572.64 ± 27.57	554.60 ± 30.34
4x	0	4.64 ± 0.29	1.23 ± 0.10	431.76 ± 31.82	897.43 ± 69.31
	30	7.21 ± 0.59	1.35 ± 0.13	650.85 ± 58.52	582.00 ± 46.12
	50	7.52 ± 0.40	1.80 ± 0.15	1150.07 ± 61.21	486.76 ± 46.79
	90	5.21 ± 0.37	1.43 ± 0.13	1030.11 ± 62.06	116.31 ± 29.03
	Total	6.14 ± 0.22	1.45 ± 0.06	815.70 ± 31.71	520.63 ± 29.33
8x	0	6.92 ± 0.49	1.51 ± 0.12	637.76 ± 54.68	713.69 ± 57.36
	30	8.31 ± 0.52	1.66 ± 0.12	842.01 ± 63.45	765.99 ± 62.46
	50	8.11 ± 0.47	1.48 ± 0.10	1163.65 ± 52.41	517.34 ± 49.19
	90	6.03 ± 0.37	1.28 ± 0.11	1158.97 ± 64.22	138.08 ± 32.79
	Total	7.34 ± 0.24	1.48 ± 0.06	950.60 ± 31.86	533.77 ± 29.19
Total	0	4.55 ± 0.19	1.18 ± 0.06	399.30 ± 19.50	779.46 ± 32.12
	30	5.37 ± 0.25	1.12 ± 0.06	519.09 ± 27.27	674.60 ± 28.61
	50	6.45 ± 0.21	1.38 ± 0.06	961.54 ± 28.73	490.06 ± 23.37
	90	4.72 ± 0.17	1.20 ± 0.06	969.43 ± 29.52	111.79 ± 13.31
	Total	5.27 ± 0.11	1.22 ± 0.03	712.34 ± 15.08	513.98 ± 14.53

Relative change in:

Nutrients	Shade (%)	Fresh mass	Number of cladodes	Cladode area	Root area
1x	0	1.16 ± 0.14	0.66 ± 0.08	0.80 ± 0.08	7.10 ± 0.97
	30	0.63 ± 0.04	0.37 ± 0.06	0.55 ± 0.06	4.83 ± 0.70
	50	1.26 ± 0.08	0.95 ± 0.11	1.66 ± 0.11	4.29 ± 0.50
	90	1.12 ± 0.08	0.95 ± 0.11	1.88 ± 0.15	1.31 ± 0.48
	Total	1.04 ± 0.05	0.73 ± 0.05	1.22 ± 0.06	4.38 ± 0.36
2x	0	1.01 ± 0.08	0.66 ± 0.11	0.68 ± 0.08	7.10 ± 0.62
	30	1.09 ± 0.09	0.66 ± 0.11	0.93 ± 0.15	7.31 ± 0.75
	50	1.52 ± 0.11	0.83 ± 0.07	1.84 ± 0.16	7.45 ± 1.80
	90	0.95 ± 0.07	0.76 ± 0.09	2.06 ± 0.21	1.56 ± 0.40
	Total	1.14 ± 0.05	0.73 ± 0.05	1.38 ± 0.08	5.85 ± 0.54
4x	0	1.25 ± 0.09	0.78 ± 0.08	1.06 ± 0.10	7.62 ± 0.85
	30	2.31 ± 0.20	0.94 ± 0.10	1.77 ± 0.19	7.33 ± 1.03
	50	2.09 ± 0.13	1.43 ± 0.14	3.24 ± 0.41	11.56 ± 4.33
	90	1.46 ± 0.09	1.15 ± 0.13	2.55 ± 0.24	1.40 ± 0.36
	Total	1.78 ± 0.07	1.08 ± 0.06	2.15 ± 0.14	6.98 ± 1.15
8x	0	2.06 ± 0.14	1.07 ± 0.11	1.38 ± 0.12	7.16 ± 0.76
	30	2.62 ± 0.29	1.12 ± 0.11	2.20 ± 0.32	9.17 ± 3.47
	50	2.53 ± 0.21	1.04 ± 0.09	2.79 ± 0.23	4.30 ± 0.55
	90	1.69 ± 0.11	1.08 ± 0.11	3.07 ± 0.27	1.90 ± 0.56
	Total	2.23 ± 0.10	1.08 ± 0.05	2.36 ± 0.13	5.63 ± 0.92
Total	0	1.37 ± 0.06	0.79 ± 0.05	0.98 ± 0.05	7.25 ± 0.40
	30	1.66 ± 0.10	0.77 ± 0.05	1.36 ± 0.11	7.16 ± 0.94
	50	1.85 ± 0.08	1.06 ± 0.05	2.39 ± 0.13	6.90 ± 1.19
	90	1.30 ± 0.05	0.99 ± 0.06	2.39 ± 0.11	1.54 ± 0.23
	Total	1.55 ± 0.04	0.90 ± 0.03	1.78 ± 0.06	5.71 ± 0.40

3.5 Discussion

According to Grime (1979) the intensity of competition increases during succession because the abiotic disturbances that initiate succession tend not to allow early successional plants to grow sufficiently close together to compete for the major resources of light and soil nutrients. Tilman (1985, 1988) argued that intensity of competition does not change during succession rather there is a shift from competition for belowground resources early in succession to competition for light during later stages.

Although competition was not part of the present study, the gradients of light and mineral nutrient resources represent the contrasting gradients of successional habitat at PPNP i.e., Back beach, West beach (primary successional savanna), DeLaurier (secondary successional savanna), and Forest; and was aimed to determine the ecological breadth of *O. humifusa* with respect to these two key environmental factors (light and nutrient) with the goal of explaining the relative growth and distribution of this species within the Park.

Low light intensity (90% shade) simulates conditions in the climax forest where the tree canopy excludes most incident light. Since this limits assimilation (photosysnthesis) (see Aleric and Kirkman 2005), low light levels are expected to mask all effects of differences of nutrient availability on growth (Elemans 2004).

In a greenhouse study of herbaceous forest species, *Circaea lutetiana* and *Mercurialis perennis* (grow in highly shaded forest floor), and two species more common in the forest edge, *Aegopodium podagraria* and *Impatiens parviflora*, Elemans (2004) similarly found that at higher light levels, nutrient addition resulted in substantial growth in both shade-tolerant and light-demanding forest species. Likewise, in another greenhouse study the increase in *Melinus minutiflora* production in the absence of competition was attributed to a combined effect of high nutrient supply and increased light availability (Barger *et al.* 2003). The findings of Meekins and McCarthy (2000) also showed that high light level with nutrient addition had a significant influence on growth of both vegetative and reproductive *Alliaria petiolata*

In nutrient-limited environments plant success may depend on increased biomass allocation to roots, whereas, in light-limited habitats, plants may allocate proportionately more resources to leaf tissue or stem tissue, as seen in the present study (see Table 3.2, 3.3), to increase the amount of photosynthetic material available for light interception, or increase in stem height (see Chapin 1980, Smart and Barko 1980, Tilman 1988, Eickmeier and Schussler 1993, Grubb *et al.* 1996, Anderson 1996, Lentz and Cipollini 1998, Meekins and McCarthy 2000, Van Hees and Clerkx 2003, Hoffmann and Franco 2003). This suggest that plants respond to variation in the environment by partitioning biomass among various plant organs to optimize the capture of nutrients, light, water and carbon dioxide in a manner that maximizes plant growth rate (Lovett-Doust 1987, Levin *et al.* 1989, Hilbert 1990, Dewar 1993). It is suggested that in forests where light is a major limiting factor, species allocate more resources to light capture; and in savanna where nutrients and water are limiting resources, species must compete for more root intensity to capture intermittent or scarce belowground resources (Hoffmann and Franco 2003)

In the present greenhouse study, the important point is that root: shoot ratios increased significantly as light intensity increased (Table 3.5). This does not seem to be in response to nutrient supply, as the higher value of root: shoot area is seen for the combination of full light and 2x nutrient concentration. Plants in full light required more frequent watering; the greatest root area is therefore interpreted as a response to access more water, rather than to assimilate more nutrients

Opuntia humifusa is capable of acclimating to contrasting light conditions through plasticity in cladode morphology and physiology. The morphology of stem, spine, flowers, and fruit of *O. humifusa* are well known to vary widely depending on its site conditions (Abrahamson and Rubenstein 1976, Benson 1982). Several studies have reported increased leaf area ratio with decreasing light levels (Holmes and Cowling 1993, Groninger *et al.* 1996, Beaudet and Messier 1998, Sack and Grubb 2002, Aleric and Kirkman 2005). In the present study, the transplants of *O. humifusa* grown in full light had circular to ovate thick cladodes, with more biomass, and were very healthy-looking. In contrast those grown under 90% shade had long, extended and etiolated cladodes.

Plant vigour and competitive ability are affected by the efficiency with which a plant captures and utilizes available light resources (Chazdon *et al.* 1996). Meekins and McCarthy (2000) suggested that because there is greatest variability in light availability in savanna, savanna species exhibit greater plasticity than the forest species, most probably as a strategy to improve resource uptake. An example of a trait showing greater plasticity would be Specific Leaf Area (Bazzaz 1996).

Although a capacity for greater plasticity does not necessarily equate to higher fitness (Schlichting 1986), it is thought to enable species to better succeed in diverse and novel environments (Williams *et al.* 1995), and to better cope with disturbance (Callaway *et al.* 2003). The environmental tolerance of *O. humifusa* seen under greenhouse conditions suggests that is a feature of the plasticity of individuals, rather than due to any form of ecotypic specialization of entire populations under local selection pressures (see Lovett-Doust 1981, Sultan 1987).

Plants in the present study differed greatly from treatment to treatment in terms of apparent vigour, however no seedling mortality occurred throughout the study for any treatment. In the first few months of these greenhouse experiments, young plant cladodes grew well under 90% shade (though showing comparatively more growth with greatest nutrient concentrations),. They were succulent and remained alive; however, by the end of the experiment after 10 months, they had etiolated cladodes that were flaccid and prostrate. It is likely that plants grown under heavy shade would have died if the experiments had continued for a few more months.

Cladode morphology differs between natural populations in the two savanna habitats (Levi 2001). Plants growing in the secondary successional savanna tended to be erect rather than prostrate and had more circular, shorter and thicker cladodes than did those in the primary successional savanna (Levi 2001). Site of origin of the seeds that were the source of these plants (primary savanna vs. secondary savanna) affected change in fresh mass ($p< 0.05$) and relative root: shoot ratio ($p< 0.01$). The more marked effects seen in the field were shown to be attributed to the field environment, rather than genetic specialization. In the present study, cladodes were less spiny in shade in contrast to the longer, denser spines of those exposed to higher light levels.

The differences in growth and allocation patterns observed in this study suggest that interactions among abiotic environmental factors can singnificantly affect plant performance; the presence or absence of one factor can enhance or reduce the effects of others (see Meekins and McCarthy 2000).

To the degree to which plant traits may represent specific functional adaptations to environmental constraints, they may be useful predictors of the response of species to environmental factors and to competitors (Goldberg 1996, Westoby 1998, Craine *et al.* 2002, Lavorel and Garnier 2002). Plasticity in growth responses to nutrient availability has also been suggested as provide a link between plant traits, plant-plant interactions and plant environment interaction (Callaway *et al.* 2003).

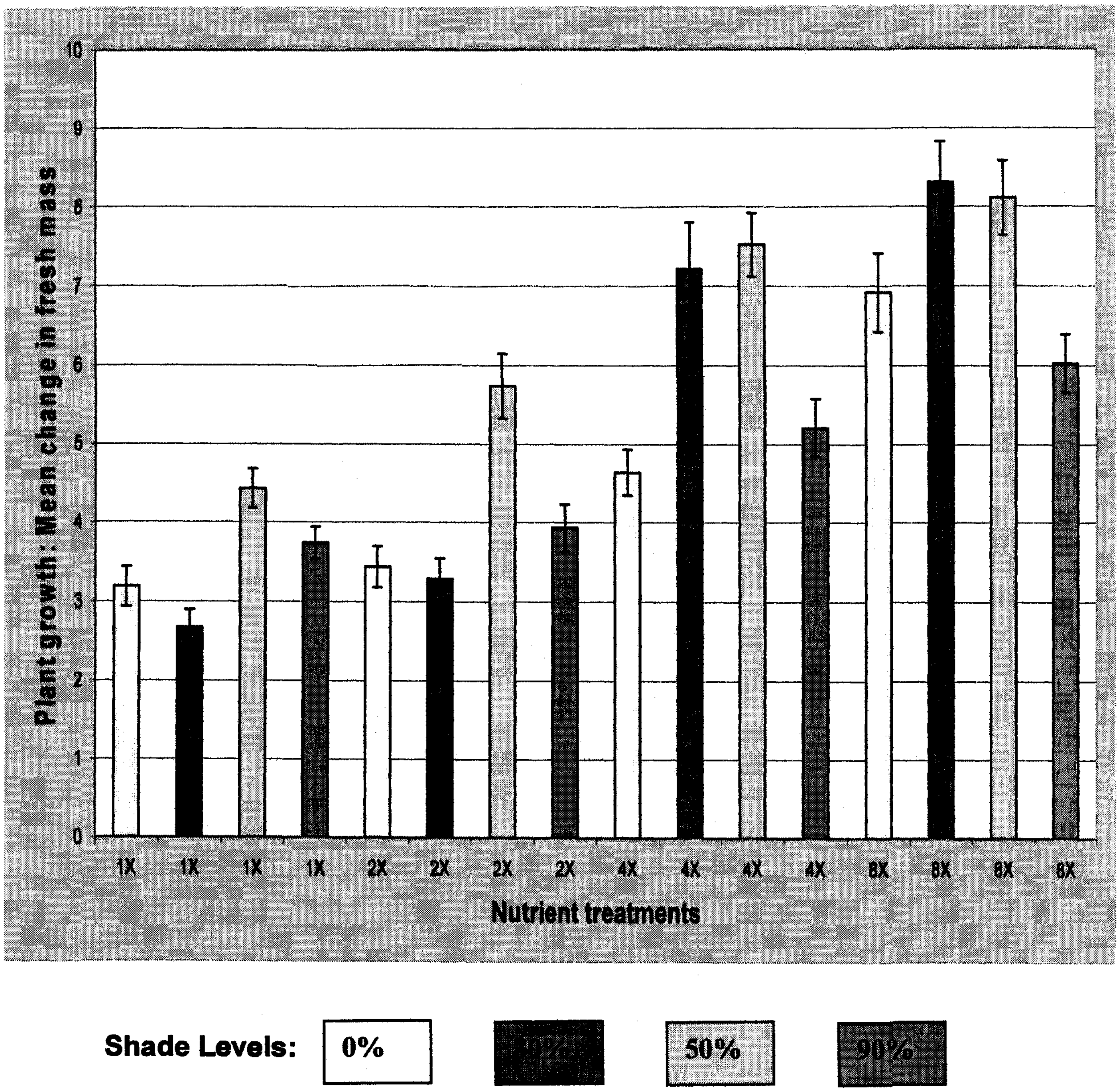

Figure 3.1 - Interactive effects of light x nutrient addition on mean (± SE) plant fresh mass change measured under four nutrient treatments and four shade levels.

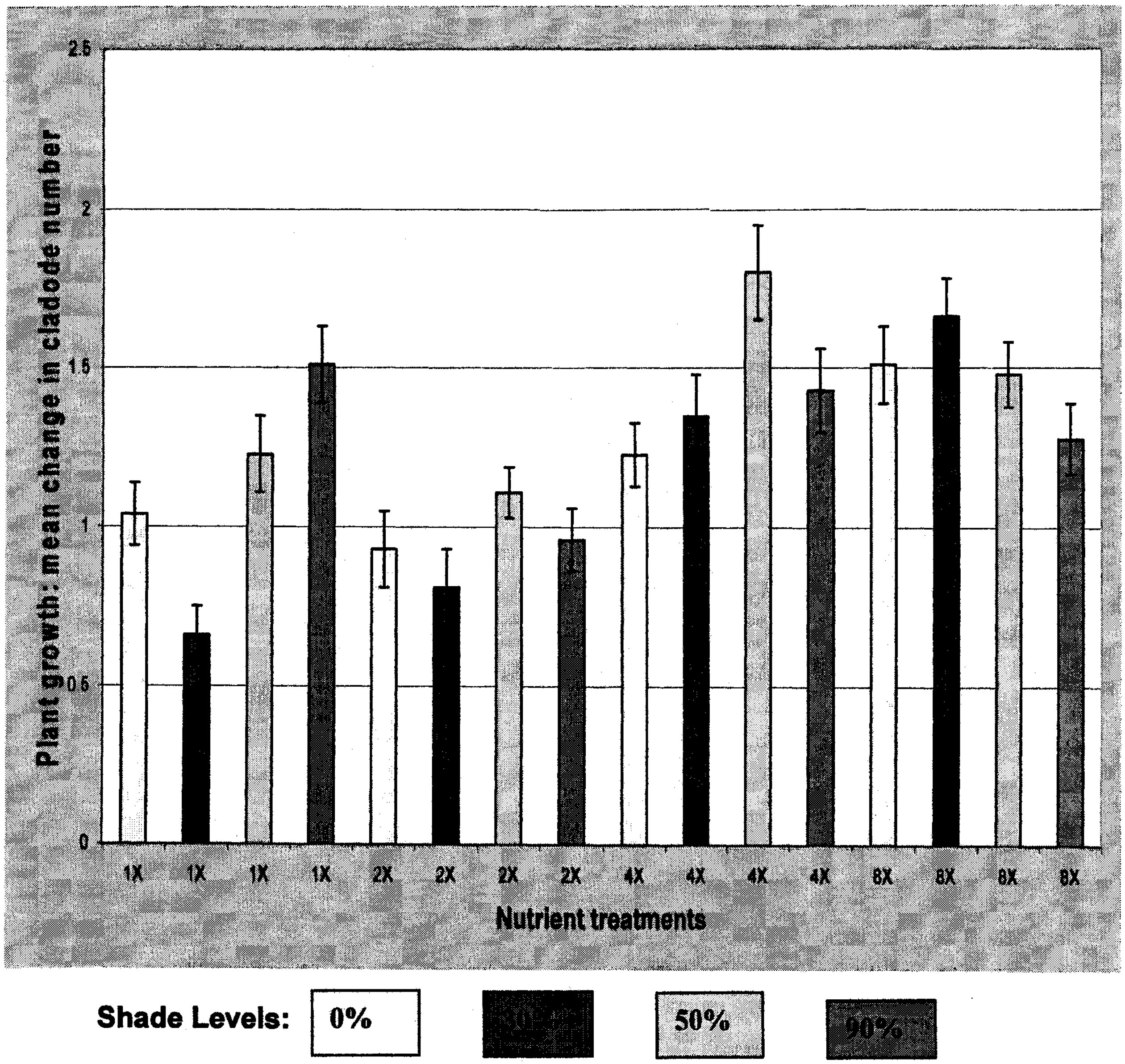

Figure 3.2 - Interactive effects of light x nutrient addition on mean (± SE) cladode number change measured under four nutrient treatments and four shade levels.

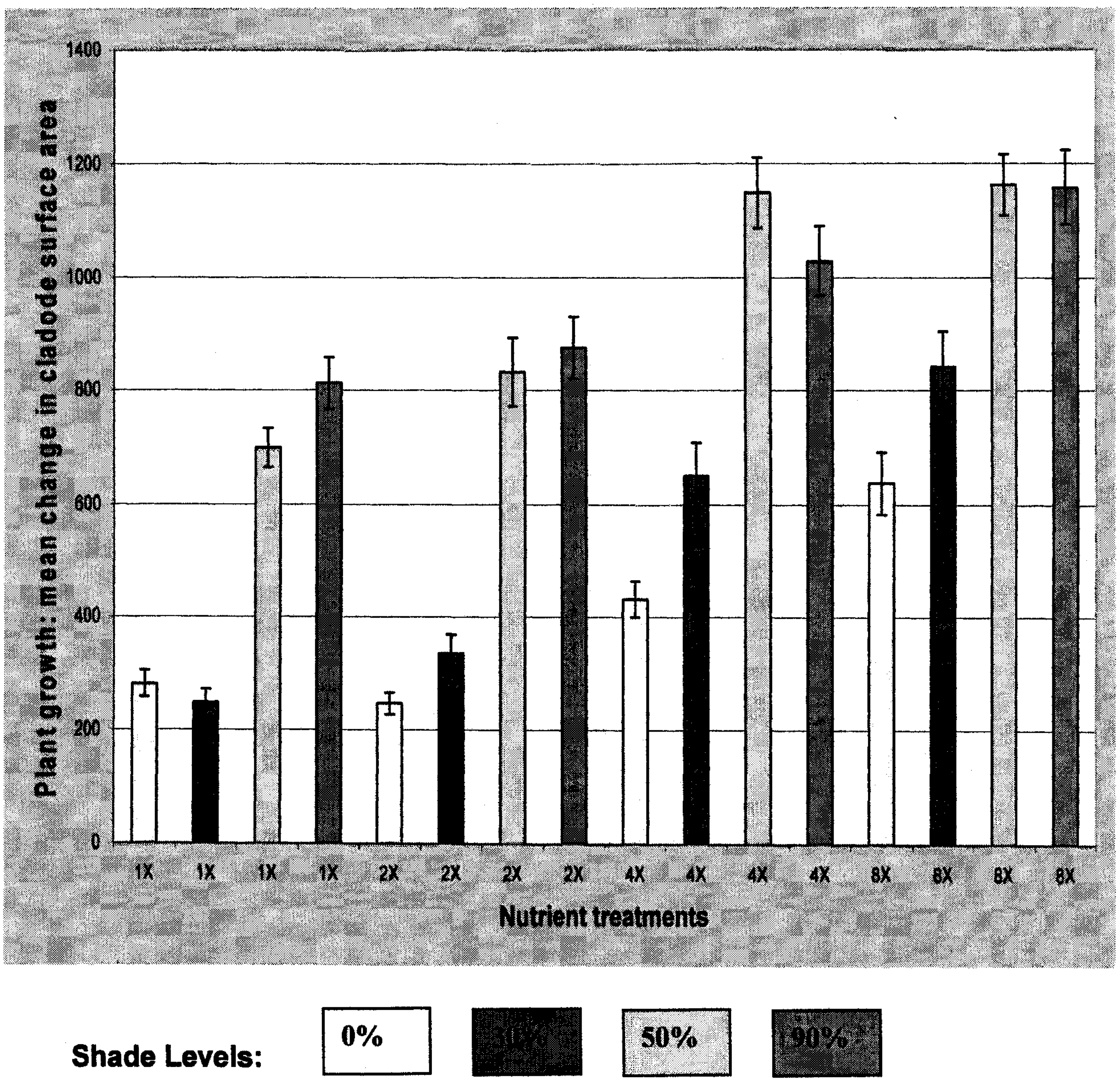

Figure 3.3 - Interactive effects of light x nutrient addition on mean (± SE) cladode surface area chang measured under four nutrient treatments and four shade levels.

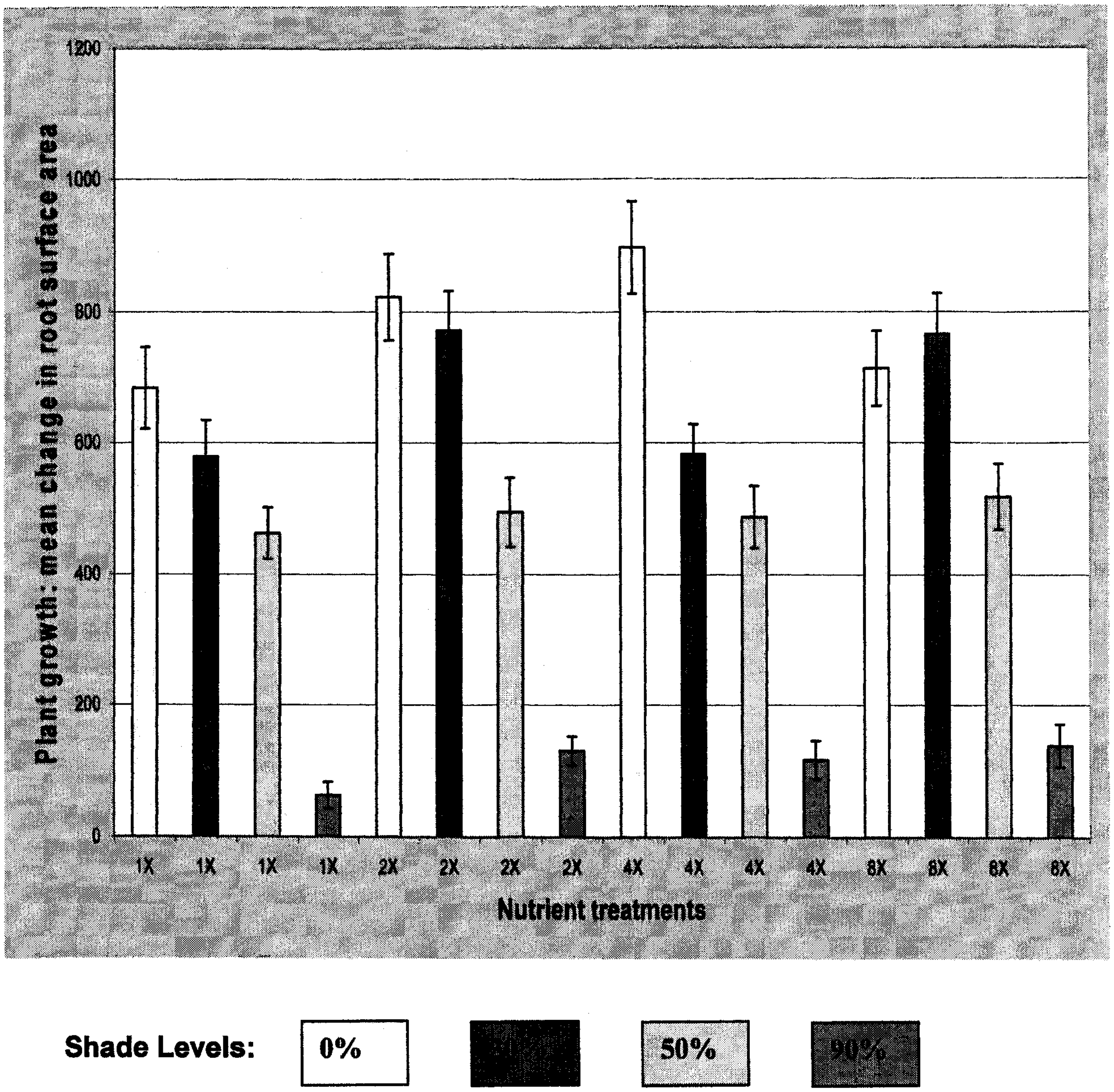

Figure 3.4 Interactive effects of light x nutrient addition on mean (± SE) root surface area change measured under four nutrient treatments and four shade levels.

Table 3.5 Plant growth as indicated by mean change in root-to-shoot surface area ratio under different nutrient x shade treatments (mean values displayed with standard errors ±). 1x = Extra low nutrient (159 mg/kg), 2x = Low nutrient (318 mg/kg), 4x = Medium nutrient (636 mg/kg), 8x = High nutrient (1272 mg/kg)..

		Root-to-shoot surface area ratio			
Nutrients	Shade (%)	Planting	Harvest	Change	Relative change
1x	0	0.38 ± 0.03	1.19 ± 0.07	0.81 ± 0.08	3.80 ± 0.62
	30	0.36 ± 0.03	0.94 ± 0.05	0.58 ± 0.06	2.90 ± 0.45
	50	0.34 ± 0.02	0.53 ± 0.03	0.19 ± 0.04	1.04 ± 0.18
	90	0.34 ± 0.02	0.18 ± 0.01	-0.16 ± 0.03	-0.30 ± 0.07
	Total	0.36 ± 0.01	0.71 ± 0.03	0.36 ± 0.03	1.86 ± 0.22
2x	0	0.32 ± 0.02	1.33 ± 0.08	1.00 ± 0.08	4.02 ± 0.36
	30	0.37 ± 0.03	1.22 ± 0.07	0.85 ± 0.07	3.61 ± 0.40
	50	0.30 ± 0.02	0.54 ± 0.04	0.24 ± 0.04	1.46 ± 0.30
	90	0.38 ± 0.03	0.22 ± 0.01	-0.16 ± 0.03	0.13 ± 0.29
	Total	0.34 ± 0.01	0.83 ± 0.04	0.48 ± 0.04	2.31 ± 0.19
4x	0	0.40 ± 0.05	1.17 ± 0.05	0.77 ± 0.07	3.63 ± 0.41
	30	0.32 ± 0.03	0.69 ± 0.04	0.36 ± 0.05	2.35 ± 0.35
	50	0.33 ± 0.03	0.40 ± 0.03	0.07 ± 0.04	1.26 ± 0.42
	90	0.35 ± 0.02	0.18 ± 0.02	-0.17 ± 0.02	-0.34 ± 0.07
	Total	0.35 ± 0.02	0.61 ± 0.03	0.26 ± 0.03	1.72 ± 0.19
8x	0	0.30 ± 0.02	0.76 ± 0.04	0.45 ± 0.04	2.54 ± 0.33
	30	0.30 ± 0.02	0.65 ± 0.03	0.35 ± 0.04	1.92 ± 0.29
	50	0.34 ± 0.02	0.40 ± 0.03	0.06 ± 0.04	0.64 ± 0.16
	90	0.37 ± 0.03	0.18 ± 0.02	-0.19 ± 0.03	-0.33 ± 0.07
	Total	0.33 ± 0.01	0.50 ± 0.02	0.17 ± 0.02	1.19 ± 0.13
Total	0	0.35 ± 0.02	1.11 ± 0.03	0.76 ± 0.04	3.50 ± 0.22
	30	0.34 ± 0.01	0.87 ± 0.03	0.53 ± 0.03	2.70 ± 0.19
	50	0.33 ± 0.01	0.47 ± 0.02	0.14 ± 0.02	1.10 ± 0.14
	90	0.36 ± 0.01	0.19 ± 0.01	-0.17 ± 0.01	-0.21 ± 0.08
	Total	0.34 ± 0.01	0.66 ± 0.02	0.32 ± 0.02	1.77 ± 0.09

Table 3.6 Plant growth as indicated by mean change in perimeter-area ratio of cladode under different nutrient x shade treatments (mean values displayed with standard errors ±). 1x = Extra low nutrient (159 mg/kg), 2x = Low nutrient (318 mg/kg), 4x = Medium nutrient (636 mg/kg), 8x = High nutrient (1272 mg/kg).

		Perimeter-area ratio of cladode			
Nutrients	Shade (%)	Planting	Harvest	Change	Relative change
1x	0	0.54 ± 0.04	0.48 ± 0.03	-0.06 ± 0.03	0.02 ± 0.05
	30	0.87 ± 0.05	0.53 ± 0.04	-0.34 ± 0.04	-0.35 ± 0.04
	50	0.72 ± 0.04	0.54 ± 0.03	-0.18 ± 0.04	-0.13 ± 0.06
	90	0.56 ± 0.04	0.58 ± 0.03	0.02 ± 0.04	0.44 ± 0.10
	Total	0.67 ± 0.02	0.53 ± 0.02	-0.14 ± 0.02	0.00 ± 0.04
2x	0	0.70 ± 0.05	0.52 ± 0.04	-0.18 ± 0.04	-0.18 ± 0.04
	30	0.56 ± 0.05	0.39 ± 0.02	-0.17 ± 0.04	-0.10 ± 0.06
	50	0.69 ± 0.05	0.54 ± 0.03	-0.15 ± 0.04	-0.02 ± 0.06
	90	0.75 ± 0.05	0.60 ± 0.02	-0.14 ± 0.04	0.09 ± 0.09
	Total	0.68 ± 0.02	0.52 ± 0.01	-0.16 ± 0.02	-0.05 ± 0.03
4x	0	0.91 ± 0.04	0.49 ± 0.03	-0.42 ± 0.04	-0.41 ± 0.05
	30	0.78 ± 0.04	0.56 ± 0.03	-0.21 ± 0.04	-0.19 ± 0.04
	50	0.68 ± 0.04	0.50 ± 0.02	-0.19 ± 0.04	-0.12 ± 0.05
	90	0.54 ± 0.05	0.63 ± 0.03	0.09 ± 0.04	0.51 ± 0.09
	Total	0.73 ± 0.02	0.54 ± 0.01	-0.18 ± 0.02	-0.05 ± 0.04
8x	0	0.52 ± 0.04	0.45 ± 0.03	-0.07 ± 0.03	0.02 ± 0.06
	30	0.61 ± 0.04	0.47 ± 0.03	-0.14 ± 0.04	-0.09 ± 0.06
	50	0.63 ± 0.04	0.48 ± 0.03	-0.15 ± 0.04	-0.05 ± 0.07
	90	0.81 ± 0.06	0.64 ± 0.03	-0.17 ± 0.05	0.02 ± 0.06
	Total	0.64 ± 0.02	0.51 ± 0.02	-0.13 ± 0.02	-0.02 ± 0.03
Total	0	0.67 ± 0.02	0.48 ± 0.02	-0.18 ± 0.02	-0.14 ± 0.03
	30	0.71 ± 0.02	0.49 ± 0.02	-0.22 ± 0.02	-0.18 ± 0.03
	50	0.68 ± 0.02	0.51 ± 0.01	-0.17 ± 0.02	-0.08 ± 0.03
	90	0.67 ± 0.02	0.61 ± 0.01	-0.05 ± 0.02	0.27 ± 0.05
	Total	0.68 ± 0.01	0.53 ± 0.01	-0.15 ± 0.01	-0.03 ± 0.02

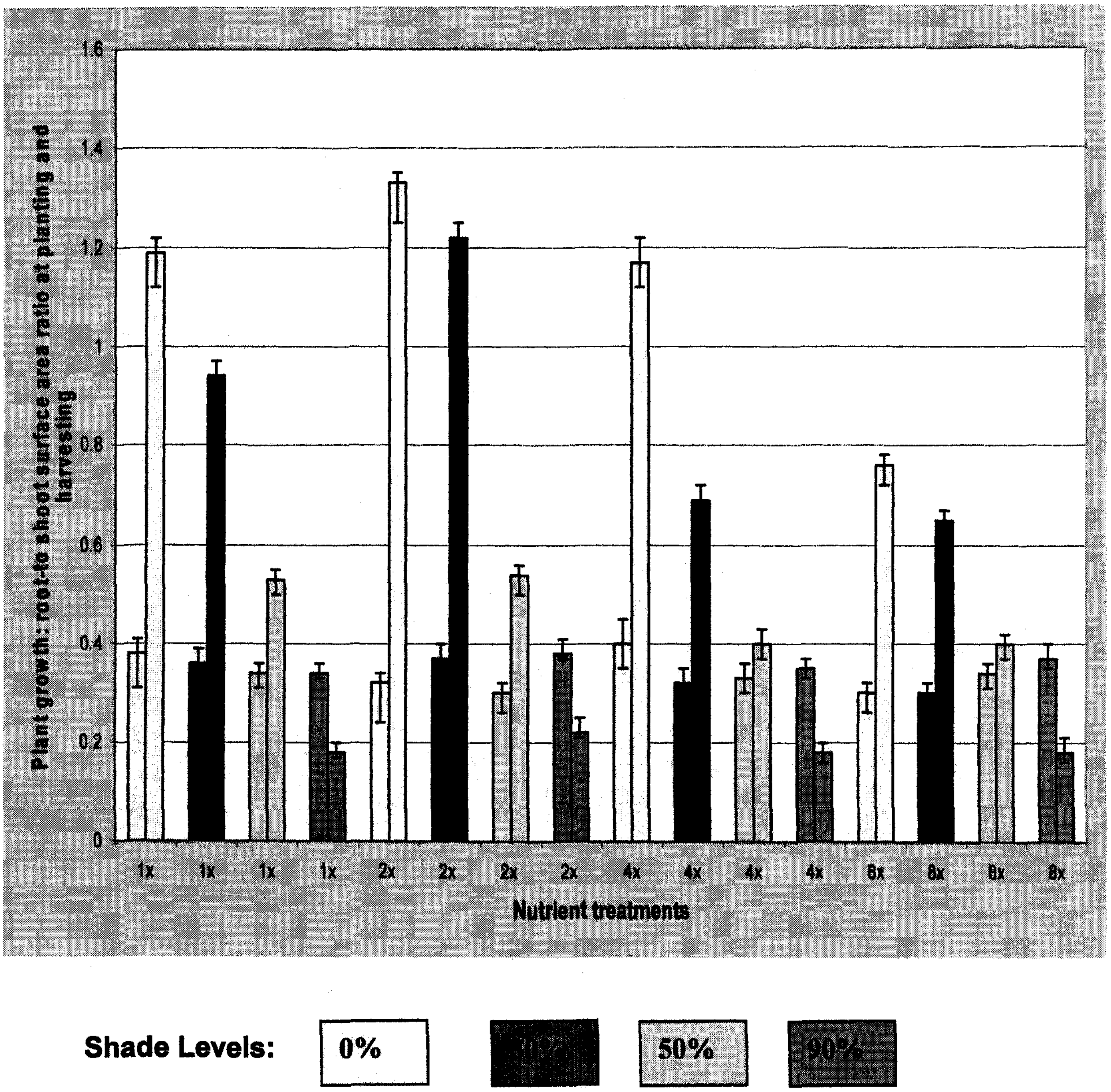

Figure 3.5 Interactive effects of light x nutrient addition on mean (± SE) root-to-shoot surface area ratio change measured under four nutrient treatments and four shade levels

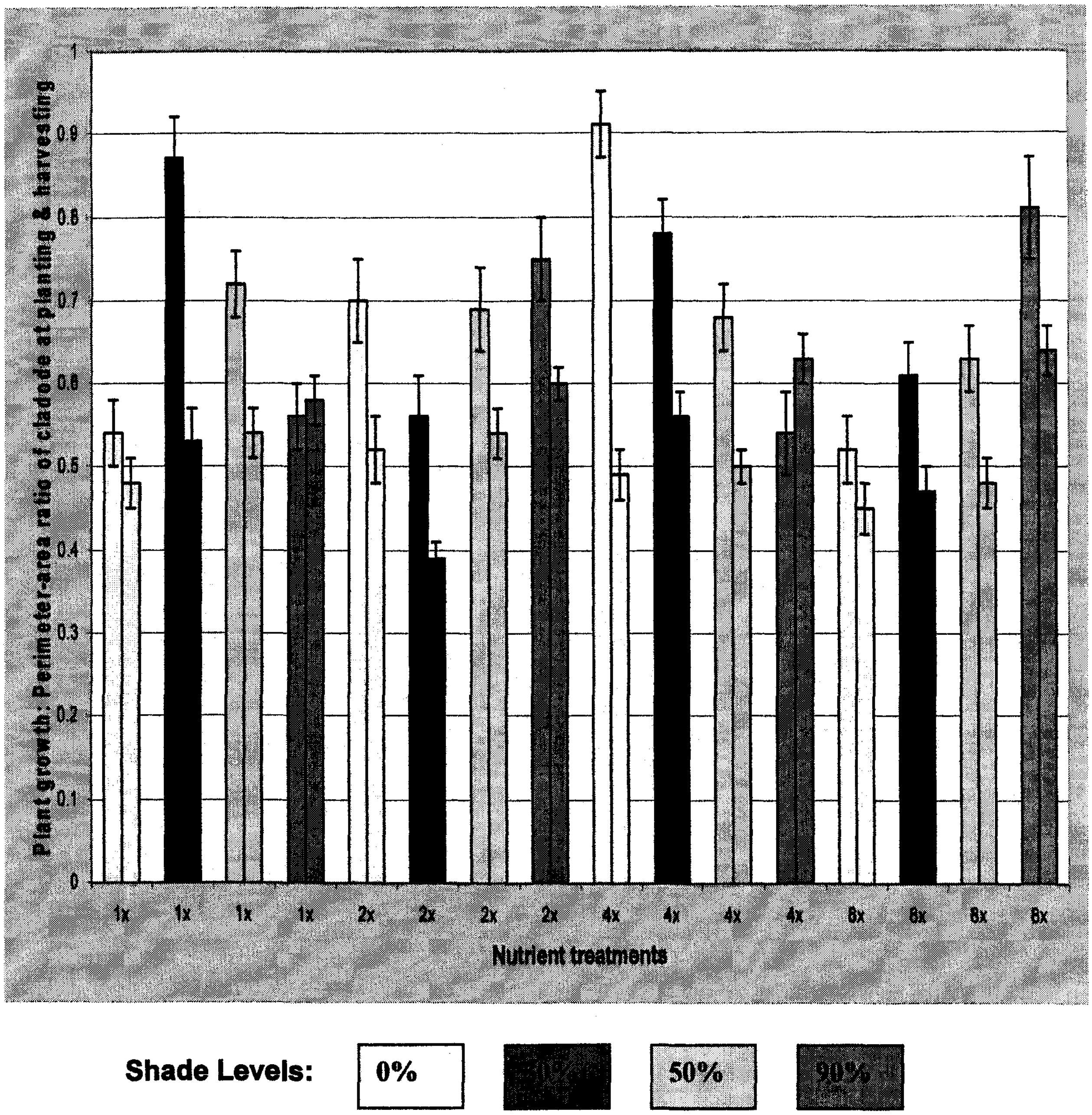

Figure 3.6 Interactive effects of light x nutrient addition on mean (± SE) perimeter area ratio of cladode change measured under four nutrient treatments and four shade levels.

3.6 General Conclusions

The most important findings of the present study are:

1. Full light is not best for the optimal growth of *Opuntia humifusa* as soil becomes dry easily.
2. Light levels under 30% - 50% shade are optimal for growth.
3. More nutrients are beneficial only if light levels are sufficiently higher.

Results of the present greenhouse study highlight the role of habitat-specific factors on *O. humifusa*, and revealed the impacts of various light and nutrient treatments on survival and growth of this imperiled Canadian cactus. A species' tolerance range in a greenhouse environment reflects its fundamental niche; our findings suggest that *O. humifusa* would be able to inhabit a wide range of habitats and microhabitats within PPNP, considering only the light and nutrient regime, and ignore other factors such as competition and predation. Under controlled conditions, *O. humifusa* plants responded to an array of resource quality in a manner that supports other assorts of the suitability of the present habitats within PPNP, from optimal habitat (savanna), through sub-optimal (back beach) to unsuitable (forest). Although light is a critical resource, clearly, maximum light levels are not necessarily optimal. Photosynthetic rates of plants have been found to be affectected by the interaction of light and nutrient addition (Gulman and Chu 1981) that influences plant performance (Mariono *et al.* 1997). Indeed, 70% of full sunlight, along with high nutrient availability (8x) gave the greatest increase in biomass and cladode numbers. Nutrient levels in the savanna habitats correspond to the 1x treatments (primary successional savanna i.e., West Beach) and 1x – 2x for the secondary successional savanna (DeLaurier). Clearly nutrient supplementation would enhance the vigour of *O. humifusa*, which in turn might enhance reproduction and substanability, but it would also enhance the vigour of competitors, so nutrient supplementation is not recommended at this point.

Rajaniemi *et al.* (2003) studies pellets of fertilizers creating resource patches that could be pre-empted by plants with extensive root systems; and increased root competition may result in reduced diversity. On the other hand, existing *O.humifusa* microsites may be at an advantage as uptake of soil resources is expected to be size symmetric, with uptake directly proportional to plant size as suggested by Newman (1973), Schwinning and Fox (1995), and Zobel (1992). This suggests that a small plant should still be able to benefit from increased nutrient supply even under intense competition.

Sites currently occupied by *O. humifusa* at PPNP will change during succession. The inland areas of PPNP, i.e., secondary successional savanna sites require close monitoring to detect the point where cactus is experiencing 80-90% shade (10-20% of full sunlight) where growth will suffer. Nothing that stress from competition will be added to effects of low light and nutrient, managers should probably become concerned if light levels reach 30% of full sunlight. At that point either thinning of the surrounding canopy or restoration plantings at other more open locations would be advisable. Moreover, it is advisable that even sites in the vicinity of park that have moderate levels of light intensity may not be overlooked as they may serve as the suitable habitat for *O. humifusa* provided they are nutrient rich.

Clearly survival, vigour, and reproduction in *Opuntia humifusa* depend on sites where its particular niche requirements are best met (Higashi 1993, Brown *et al.* 1995, Anthony and Connolly 2004). This work supports the notion that plant species segregate along one or more environmental niche axes (see Silvertown 2004), in this case axes correspond to light and soil nutrient availability.

In defining habitat requirements for an endangered species, it is useful to determine its edaphic and climatic tolerances, such as nitrogen supply, soil pH, tolerance to drought, and shade (see Ellenberg and Mueller-Dombois 1974), and to track floristic changes in the surrounding plant communities (see Grime 2001).

This study was aimed to identify optimal light and nutrient conditions for the survival and growth of *O. humifusa,* but the same niche-based methodological framework could readily be applied to other species. Processes causing extinction at a local scale may be very complex; therefore, even within a single species the particular causes of extinction are not always the same at all sites (see Grime 2001).

It will therefore be important for the protective management of this species to continue the demographic surveys initiated by our laboratory, in order to detect (and anticipate) symptoms of declining vigour in different parts of the park.

Chapter 4 - Integration and reconciliation of field and greenhouse studies: general discussion and conclusions

Opuntia humifusa, grown in a controlled and competition free environment not only survived at all light levels and nutrient treatments but also was capable of acclimating to different light conditions through plasticity in cladode morphology. Based on these results, it can be inferred that the fundamental niche of this cactus is wide enough, such that restoration planting and management of *O. humifusa* could be justified across a widen range of light and nutrient conditions than it presently occupies at Point Pelee National Park as suggested by Levi (2001). However, results also clearly indicated that not all of the nutrient and light conditions provided for these plants in the greenhouse were optimal for their growth during this greenhouse study. Irradiance levels at 70% of full sunlight, along with high nutrient availability, were found to enhance growth of *O. humifusa* cactus, but that treatment provided nutrients at 8x the level presently found in savanna, forest and back beach (see Table 2.1)

O. humifusa often grows as a prostrate perennial. In the beginning of the study it was therefore speculated that plants grown in full sunlight conditions (o% shade) would develop more biomass. However, growth was better in partial shade (70% of full sunlight) in terms of plant biomass and number of cladode change (Table 3.4). An important factor may be the rapid desiccation of surface soils in full sun (Lichter 1998). Direct solar radiation had also been found to decrease the growth of several cacti such as *Neobuxbaumia tetetzo*, *Opuntia rastrea*, *Pachycereus hollianus*, *P. pringlei*, and *Stenocereus thurberi* seedlings (see Godinez-Alvarez *et al.* 2000). The reduction in growth in full sunlight has been attributed to partial stomatal closure response to high vapour pressure deficits under high light conditions (Schmidt and Zotz 2001). Similarly a decline in water availability may affect photosynthesis and nutrient uptake, depending upon the mobility of the ions (Nye and Tinker 1977). Several other studies suggest that when nutrient availability declines due to the lower mobility of ions, an increase in rooting density may result in order to maintain nutrient uptake rates (Nye and Tinker 1977). This may require increased biomass allocation to roots (McConnaughay and Coleman 1999). This is in agreement with the observed increase in root surface area with increasing light intensity in the present study (see Tables 3.3 & 3.4), and also in field studies (see Appendix A).

Reduced rates of CO_2 exchange, decreased vegetative growth and low fecundity are usually assumed to be due to water stress, nutrient deficiencies, or low or excessive light intensities (Zotz and Hietz 2001), e.g., the cause of slow growth in vascular epiphytes is evident by short and irregular availability of water and nutrients (Benzing 1990, Zotz and Heitz 2001). In dry sites, shade increases seedling survival by reducing water stress, and under dry conditions photosynthesis would be higher in the shade than in full sun; however, in wet sites shade tend to inhibit seedlings as it represents increased competition for light (Holmgren *et al.* 1997).

Field observations and experiments indicated high growth performance of *O. humifusa* transplants in both primary and secondary savanna. A more developed A horizon in the soil, with significant organic matter accumulation (providing some extra nutrients and superior water holding capacity) may have been responsible for greater growth in secondary savanna as compared to primary savanna despite the competition in the herb layer which was greater in the secondary savanna (see Chapter 2).

In the greenhouse study, the best growth was seen in plants at 8x (high nutrients) x 50-70% sunlight, rather at 1x (nutrient) x 50-70% sunlight (conditions more or less comparable to those in savanna sites). This indicates that the currently occupied habitats (primary and secondary savanna) seem to be macro-nutrient limited. So growth and vigour of *O. humifusa* in the primary and secondary savvana at PPNP could be enhanced through NPK supplementation. Indeed using nitrogen alone may be enough as Phosphorus and Potassium levels are quite good in the field (see Chapter 2, Table 2.1).

A recent study, though, suggests that fertilization of mid-elevation *Trachypogon* savanna in Venezuela, an African habitat, with NPK greatly increased seedling biomass of *Melinis minutiflora* (an African grass) and this effect was greatly enhanced when competition was reduced through clipping of competing vegetation (Barger *et al.* 2003). Soil nutrients and presence of native savanna species are important factors in the ability of native savanna to resist *Melinis* invasion and establishment. The implications of this for conservation of *O. humifusa* in the Lake Erie sandspit savanna are that nutrient supplementation may favour invasive species to detriment of the endemic vegetation.

As mentioned earlier (see Chapter 3), numerous studies have pointed out that cacti are slow-growing species, and several abiotic factors, such as water and nutrient availability, may affect their growth (see Godinez—Alvarez *et al.* 2000). A high concentration of nutrients can significantly increase growth in some cacti like *Mammillaria magnimamma*, *Pachycereus hollianus*, and *P. pringlei* (Godinez-Alvarez and Valiente-Banuet 1998, Carrillo-Garcia *et al.* 2000, Ruedas *et al.* 2000).

At the back beach, in addition to the low level of Nitrogen, coastal winds and storms, and the resulting disturbances and seedling burial are significant physical constraints (Figure 2.2). Disturbance results into poor performance and/or failure of establishment despite the good light intensity level, well drained soils, and reduced competition thanks to sparse vegetation. Moreover, as observed in the present greenhouse experiment where sand was used as the substrate, since surface soils of exposed non-forested dunes dry extremely rapidly (Lichter 1998), the rate of juvenile survival may become so low that may lead to mortality. Supplying NPK fertilizer supplements to the back beach, therefore, is likely to be of little benefit.

Levi (2001) indicated that there was no seed bank for *O. humifusa* in the back beach at PPNP. The absence of *O. humifusa* from that habitat may reflect dispersal limitation, since the site seemed otherwise suitable in terms of light intensity, presence of free-draining soils and low competition because of sparse vegetation (Benson, 1982; Table 2.1). The field experiment was designed to explore the possibility that the back beach might serve as a suitable habitat for *O. humifusa* transplants. In the greenhouse study, conditions otherwise comparable to those at back beach habitat (full sunlight and low nutrient treatment), allowed plant survival and growth, so the physical environment is sufficient to support *O. humifusa* but the results from our field studies suggest the back beach, is too unstable; plants are frequently buried by moving sand, and unless fencing is set up to reduce sand movements the back beach remains unsuitable for restoration plantings.

Optimal habitat for *O. humifusa* is very much in transition conditions. It is not only vulnerable to shade resulting from encroachment of woody vegetation into secondary savanna due to successional process, and the slower process of primary succession at West B, but nutrient scarcity and disturbance of the substrate also limit its distribution and growth. In general, savanna species exhibit greater plasticity than the forest species (Meekins and McCarthy 2000); this has been interpreted as a strategy to improve resource uptake; however, it is also important to note that as savanna is characterized by heterogenous light levels and hot drier conditions in places, therefore water can be a limiting factor in the field. It is evident from some field and greenhouse experiments with different nutrient and water regimes that photosynthetic capacity as well as leaf N was controlled by water rather than by nutrient addition (Schmidt 2000, Laube and Zotz 2003). Since water uptake is lower in the drier places, the possibility of the nutrient uptake is also lowered (Schmidt 2000). In the greenhouse plants were watered on a regular schedule and grown in a uniform light in weather constraint-free greenhouse environment. These may have allowed the survival of plants under conditions evaluateing the back beach in terms of light and nutrient alone.

In the climax – forest at PPNP light is a limiting factor, as it is less than 1/10 the light level in the other three habitats (i.e., back beach, West Beach, and DeLaurier, see Chapter 2, Table 2.1). This corresponds to the 90% shade treatment in the greenhouse experiment. However, forest soils have the higher concentration of nutrients (Nitrogen concentration is 3 times more than in the rest of other habitats at PPNP) and almost 5x the moisture level at the back beach. As *Opuntia* cladodes remain green throughout the year, it was speculated initially that this might allow them to take advantage of more light for their growth as compared to grasses and other understorey herbs early in the season before the forest canopy. However, cladodes were clearly stressed in both the forest site and the 90% shade treatment; a strong etiolation response and low growth eventually lead to plant mortality in the field, and poor growth in the greenhouse study. Thus the absence or elimination of *O. humifusa* from forest sites can be explained not only by the reduction in incident light but also additional factors such as competition in the ground layer, litter accumulation and litter burial.

Many studies have suggested that litter burial frequently becomes an important recruitment constraint for open-dune species during old-field succession (see Lichter 2000). In *O. humifusa* vulnerability of the juvenile to light limitation in deciduous forest may be increased by burial in litter falling over the year. Higher level of humidity and tree litter production in more humid forests limits the rate of decomposition, which eventually reduces the availability of nitrogen to plants. Since water uptake is lower in drier forests, nutrient uptake is automatically reduced (Schmidt 2000).

It is often suggested that tolerance based competitive strategies are best expressed in habitats with more litter accumulation and less disturbance (MacDougall and Turkington 2004). In contrast, the finding of Fynn *et al.* (2005) suggested that *Themeda triandra*, a litter- as well as shade-intolerant small herb shows a 'suppression-based' competitive strategy, requiring regular disturbances to reduce shading and remove litter.

Results from both field and greenhouse studies indicated that *O. humifusa* is a light-demanding species. *Opuntia humifusa* is susceptible to competition for light and likely to be out shaded as the productivity of the savanna grasses and presence of perennial herbs and shrubs increases. The present study suggests that *O. humifusa* can grow for short time in the forest habitat when the greater moisture and nutrient levels are advantageous but it does not persist for long (50% mortality after 4 months, in the field transplant experiment). Periodic high intensity disturbances, therefore, may be needed for *O. humifusa* to survive in savanna habitat that is subject to encroachment by woody plants during succession.

In the greenhouse study, plants (transplanted cladodes) grew under heavy shading (under all nutrient treatments: 1x, 2x, 4x, and 8x) but gradually lost their vigour by the end of the experiment despite the fact that mortality had occurred. However, plants grown under medium shade (at all nutrient levels: 1x, 2x, 4x, and 8x) showed superior plant growth performance (see Table 3.4 for mean values) and showed better vigour (comparatively) than those grown either in full light, or under heavy shading. This provides some indirect support to those studies which suggest that in arid environments, "nurse plants" generally provide safe site for seed germination (Harper 1977, Fowler 1988, Chambers 2001, Ibanez and Schupp 2001) and have positive effects on early stages. Genetic studies in our laboratory (VanDerWal *et al.* 2003) indicate that microsites are in first made up of one large and several small genetic individuals. So there is supporting evidence that this is occurring for *O. humifusa* at PPNP.

Studies of the family Cactaceae (reviewed by Godinez-Alvarez *et al.* 2000) suggest that species shaded by nurse plants, particularly during early life phases and in low herbivory conditions, experience reduced transpiration, and buffered temperatures that enhance cactus germination and establishment (as in *Opuntia rastrera* [Mandujano *et al.* 1998]). This suggests that the niche of the plant may change during its life stages, e.g., juvenile versus adult changes (Pianka 1983). This is comparable to some recent findings which suggest that seedling establishment can be enhanced by nurse plants, though long-term survival may not be (see Maschinski *et al.* 2004), as seedling recruits grow in size, and competition becomes more intense (Keyes *et al.* 2001).

It is well documented from the literature that niche features necessary for regeneration and survival through juvenile life stages are perhaps different and may be more restricted than the niche features necessary for survival as an adult (see Bazzaz 1979, Pianka 1983, Parrish and Bazzaz 1985, Akcakaya *et al.* 1999). The present study also supports the view that the niche of a species may vary in time and space because the physiological or behavioural properties of individuals in the population may differ at different times and in different sites (Parrish and Bazzaz 1985).

Initially, it was suggested that traits such as low stature (see Connor 1991), and poor competitive ability with taller vegetation (Lloyd *et al.* 2003) as found in *O. humifusa*, an early colonizer, should restrict the species to the resource-poor portions of their fundamental niche (i.e., to habitats in which strong competitors are physiologically less able to succeed). Resource competation models based on the Liebig's Law of Minimum assume that the species that has the minimum requirement for the most limiting resource win the competition at equilibrium (see Anten 2005). Tilman (1980) however argued, if *n* different resources limit growth through temporal and spatial heterogeneity of these resources, a maximum of *n* different species could coexist provided that growth of each species is limited by a different resource (reviewed by Anten 2005). It is now evident from several studies that coexistence requires some form of niche differentiation (Amarasekare 2003). The persistence of *O. humifusa* with relatively good vigour and growth, as revealed by field results, in secondary successional savanna at PPNP, in the presence of shrubs and tall prairie grasses, therefore also suggest that species do segregate along one or more niche axes and that species-specific niche requirement among plants are likely to facilitate coexistence (Silvertown 2004).

O. hunifusa grows in savanna at PPNP, a habitat undergoing successional changes. Coastal sand dunes represent complex environmental gradients, along which sand movements during early succession, and competition as primary succession proceeds; are the major environmental stresses (Lichter 2000) hampering colonization, establishment, reproduction, and successful seedling recruitment.

O. humifusa, an early colonizer of disturbed or open areas, is highly susceptible to subsequent invasion by mid- and late-successional species (Reznicek 1983, Jock 1984, Chiarot 1992), for example, *Rhus aromatica* (Fragrant Sumac), *Rhus typhina* (Staghorn Sumac), *Cornus* spp. (Dogwood), *Vitis riparia* (Frost Grape), *Poa compressa* (Canada Blue Grass), *Ptelea trifoliata* (Hop Tree), *Parhtenocissus vitacea* (Virgina Creeper), *Juniperus virginiana* (Eastern Red Cedar), and *Celtis occidentalis* (Hackberry)(for detailed list, see Jock 1984). The earlier dominant colonizer species are thought to be out-competed, in later successional stages, by the larger species for the amount of available light and soil nutrients (Tilman 1985, 1988). It is evident that succession is the primary threat to the survival of *O. humifusa* at PPNP (see Kraus 1991). However, competitors are important in as much as they impacts an environmental requirements, such as light or nutrients. Some neighbouring effects ameliorate the environment especially by providing partial shade or active as nurse plants, see above so) The concept of environmental requirements and environmental impacts, therefore, should not be confused and should be used cautiously when considering niche-based relationships between species (Leibold 1995).

Since *O. humifusa* is an early colonizer and can be out-competed in the later stages of succession by trees and even perhaps grasses or other vegetation, it is interesting to consider how *O. humifusa* is able to persist in the transitional habitats at PPNP. It is subject to several threats and environmental constraints including disturbance, herbivory, collecting, trampling, and instability of the sandspit etc (Lovett-Doust 2003). *Opuntia humifusa* grows at PPNP in a dynamic environment (dune influenced habitat) along the coast of Lake Erie, on sandspits that shift in space and time. Based on our field and greenhouse studies it seems that *O. humifusa* may need recurrent disturbance events, like strong winds, and sandspit erosion that periodically reset the successional sequence to earlier stages (Martinez 2003). On one hand, this supports the belief expressed by Kraus (1991) that the back beach which is naturally maintained in a disturbed condition by waves, winds, and storm action may be suitable for the colonization of *O. humifusa*; and on the other hand, reduces the chance of success for the Fish Point population of this cactus (on Pelee Island) given that it was nearly eliminated by such disturbances alone (NHIC 2003) and has been severely impacted by collecting and human disturbance.

Dune colonizers often require disturbances that eliminate plant cover and create sites with high substrate mobility that may be re-colonized later (see Martinez 2003). There is also evidence that habitat disturbance is generally associated with increased genetic diversity (Eriksson, 1993), and though this still needs to be examined for *O. humifusa*.

Not only is *O. humifusa* capable of benefiting from a level of disturbance, but also some populations are capable of surviving harsh environmental fluctuations such as freezing and drought (Benson 1982). *Opuntia humifusa* has been reported to survive winter freeze by producing its own anti-freeze solutes in the cytoplasm (see Kraus 1991). The ability of *O. humifusa* to survive in the wide range of environmental conditions occurring over its entire geographical range, plus its ability to reproduce both by seed and clonal propagation have likely helped this species to persist despite a reduction in available suitable habitat, to persist in the dynamic system at PPNP (Oakwood *et al.* 1993, Edwards and Westoby 1996), and may explain its ability to acclimate and adapt at the northern edge of its range.

Some authors have predicted that, within the next 45 years, early successional grassland and/or savanna plant communities, once prominent on the Pelee sandpits (Maycock 1969-1972, Battin and Nelson 1978) will be replaced by mature forest (Sharpe *et al.* 1987, Maycock 1969-1972, Schwartz and Heim 1996). Since the system is dynamic in space and time, the present study emphasizes the conservation of suitable successional savanna conditions; these conditions need not necessarily remain at the same geographical locations over time. Also the environmental variables that define the niche of a species are not fixed, but may themselves change in time and space (Parrish and Bazzaz 1985).

Ecological succession is a powerful agent of change. Thus a site that was a suitable habitat in one year may not be suitable 5 or 10 years later, if conditions change. Clearly in this case the niche of the species is not changing, but rather the habitat. The abundance of a species in a particular site thus depends on how the site-specific factors meet the specific niche requirements of the particular species.

Species associated with disturbance events may have a particularly transient presence in some areas. The progress of successional processes may result in the loss of habitat types from individual areas for long periods or perhaps indefinitely. Broadly speaking, the greater the size of individual areas, the greater will be the probability of larger population size tending to have smaller risks of extinctions (e.g., Berger 1990, Pimm 1991, Gaston 1994).The distribution of naturally-occuring *O. humifusa* at PPNP is focussed in two thin parallel strips and there is little evidence of gene flow between them (VanDerWal *et al.* 2003); as a result, these thin ribbons of suitable habitat may be particularly threatened.

Generally population sizes need to be large to increase the probability of persistence following catastrophes (Mangel and Tier 1994). The existing populations of *O. humifusa* show relatively good vigour and reproduction on the currently available suitable sites, but that do not guarantee that these sites will have long-term viability (Wolf *et al.* 1999, Hedge and Ellstrand 1999). It is therefore necessary to be pro-active in efforts to protect this species. Given the limited resources available for conservation measures, and what we now know about the plants' response to light and nutrients, it seems reasonable to maintain the cactus populations by sustaining the two savanna habitats rather than by introducing populations to the unsuitable forest habitat or the marginal (unstable) back beach.

Potential management tools for maintaining savannas generally include fire, and vegetation thinning thus setting back, or slowing down the process of secondary succession. The role of fire recently studied by Foxcroft *et al.* (2004) has suggested that *Opuntia stricta* (Haworth) is extremely fire-sensitive. Several other studies have also suggested that species of *Opuntia* including *O. humifusa* often retain high moisture levels which increases the temperature required for combustion (Wright and Baily 1982, Whelan 1995, Bond and van Wilgen 1996). Bunting *et al.* (1980) found that fire in Texas prairie environments was very detrimental to *O. humifusa*, causing 20% mortality initially, followed by 70% mortality through the secondary effects of bacterial and fungal infection of fire-scarred tissues. From such studies it may be inferred that fire cannot be used as a restoration technique to benefit *O. humifusa*. It could be argued, based on the results of Bunting *et al.* (1980), that at least, 30% of the population of *O. humifusa* could survive versus the inevitable loss of the whole site if succession is allowed to proceed ('something is better than nothing'), but fire is clearly a crude tool that has the potential to decimate the gene pools of the two "Element Occurrences" or EO's of cactus at PPNP The significant role of fire as a disturbance mechanism maintaining the environmental conditions required for pioneer plant species and promoting habitat renewal in grasslands is well documented from several studies (Daubenmire 1968, Connell and Slatyer 1977, Vogl 1977, Bazzaz 1983, Grime 1987, Abbadie et al. 1992, Sinclair *et al.* 1995). Following a fire, there is often a flush of growth (Ehrenreich and Aikman 1963). Increased nutrient result, available from the burning of living and decaying biomass and when these are added to the soil surface then become available due to mineralization, or because of increase in soil pH (Ehrenreich and Aikman 1963, Stock and Lewis 1986, Whelan 1995). As post-burning effects include increased incident light conditions, higher temperature, higher water availability due to reduced transpiration, and reduced competition, these factors can aid in the rejuvenation (Ehrenreich and Aikman 1963). The fact that fire can alter the outcome of plant competition, invasion and succession (Vogl 1977, Rowe 1983, Foxcroft *et al.* 2004), suggests that fire frequency could potentially be manipulated as part of an integrated restoration program; however, it seems apparent that *O. humifusa* is adapted to substrate disturbance rather than fire, and the best opinion may simply be removal of competitors. If fire is applied, thorough wetting or watering of cactus microsites may protect them from extreme damage.

Early successional species, for example, *Plantago* have been assumed to be more palatable than later successional species such as *Atriplex* (White 1984, Coley 1987). Dormann *et al.* (2000) reviewed some studies (Reader and Southwood 1981, White 1984, Davidson 1993) which argued that higher concentrations of stress proteins in plants produced as a result of higher disturbance effects in early successional stages make early successional plants attractive to herbivores. Based on the present field study it was inferred that the fencing treatment used in the experimental savanna plots not only protected *O. humifusa* from deer browsing but also significantly reduced the rate of plant mortality. The low abundance of *O. humifusa* in savannas at PPNP is not attributed to herbivory alone, but field observations and experiments do indicate that young seedlings are especially vulnerable to herbivory (the organs for defense (spines) are not fully developed at that stage). As Meekins and McCarthy (2000) observed in their case study of *Alliaria petiolata*, winter grazing by rabbits and deer may be even more important when other species are not available to herbivores, whereas the evergreen and palatable cladodes of *Opuntia humifusa* can be found year-round.

For dominant species growing in transitional habitats following disturbance, it is suggested that the ability to dominate space and resources below-ground may allow species to set up dominance before light becomes limiting (Rajaniemi *et al.* 2003). *Opuntia humifusa* is assumed to be a weak competitor (Jock 1984) and a few authors have also noted that seed germination is at best very slow in the species (Thornber 1911, Baskin and Baskin 1977, 1998). However, in our laboratory, Levi (2001) found that acid scarfication greatly increased the rate and frequency of seed germination in this species. It is therefore suggested that seedling transplantation should be preferred over seed-broadcasting to avoid the problem of overcoming dormancy, and the high risk period of seedling establishment if any restoration effort is undertaken. As seen in our field experiments, planting well-established seedlings with healthy root systems will enhance survival. Fencing could also minimize the effects of herbivory, and substrate instability, weather constraints and, thus making the restoration efforts successful.

The causes of low recruitment at PPNP may include absence of some co-evolved herbivore that released dormancy of seeds, low genetic diversity compared to the centre of the species' range, or limitations due to self-incompatibility. A follow-up study comparing PPNP with populations from other parts of the species' range to determine overall genetic diversity, will be very helpful in this context. Additional threats to the species at PPNP (e.g., poaching, trampling, exotic introduction, and other human activities) should be considered in designing an effective conservation management strategy.

Finally, monitoring of change in the species composition of plant communities is a critical tool for the detection of long-term effects of succession, climate change, land fragmentation, habitat isolation, habitat loss, and the impacts of vegetation management. The best way to protect the critical habitat of a species at risk is to protect the entire ecological community of which it is a part (Miller and Douglas 1999). To achieve this goal, conservation has to be carried out at a landscape level, where managers put effort into saving habitats and communities while being well informed about the niche of particular species at risk.

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Appendix A. The mean values of plant growth and performance parameters for plants transplanted to experimental plots in each of four successional habitats. Means in the same row with the same superscript letter do not differ significantly; those with distinct superscript letters are significantly different at $p<0.05$. The significance of the F-ratio from the ANOVA comparing means between sites is indicated as follows: *** = $p< 0.001$, ** = $p< 0.01$, * = $p< 0.05$, NS = not significant.

Growth parameters	Back Beach	Primary Successional Savanna	Secondary Successional Savanna	Forest	Significance
Volume	4.13^{b}	12.69^{a}	16.79^{a}	3.50^{b}	***
Shoot fresh mass	4.17^{b}	12.64^{a}	16.97^{a}	3.43^{b}	***
Root fresh mass	0.18^{bc}	0.73^{a}	0.47^{b}	0.11^{c}	***
Number of cladodes	1.97^{b}	2.59^{ab}	3.09^{a}	2.29$^{a b}$	***
Mean cladode area	245.58^{b}	722.42^{a}	722.15^{a}	167.37$^{a b}$	***
Total cladode surface area	451.46^{c}	2091.18^{b}	2294.92^{a}	405.98^{c}	***
Perimeter area ratio of cladode	0.57^{ab}	0.56^{ab}	0.45^{b}	0.80^{a}	***
Cladode length to width ratio	1.70^{b}	1.71^{b}	1.62^{b}	3.92^{a}	***
Total height	41.72^{c}	86.09^{b}	106.86^{a}	67.49^{bc}	***
Chlorotic cladode surface area	189.17^{a}	144.07^{b}	172.46^{a}	81.41^{c}	**
Root surface area	955.70^{b}	1886.18^{a}	805.19^{c}	454.25^{d}	***
Total surface area	1592.48^{c}	4121.43^{a}	3272.57^{b}	941.64^{d}	***

Total plant mass	4.32	c	13.37	b	17.45	a	3.54	c	***
Shoot to root surface area ratio	1.16		1.58		3.59		1.70		NS
Root to shoot surface area ratio	1.63	a	1.20	ab	0.41	c	1.02	b	***
% of surface area that is shoot	43.37	c	49.80	bc	72.55	a	55.41	b	***
% of surface area that is cladode	29.72	c	44.97	b	65.70	a	46.84	b	***
% of surface area chlorotic cladode	13.64	a	4.83	c	6.85	bc	8.57	b	***
% of surface area that is root	56.63	a	50.20	ab	27.45	c	44.59	b	***
% of mass that is shoots	95.86	ab	94.40	b	96.79	a	96.78	a	***
% of mass that is root	4.14	ab	5.60	a	3.21	b	3.22	b	***
Root to shoot mass ratio	0.04	ab	0.06	a	0.03	b	0.03	b	***
Area to mass ratio for shoots	170.46		260.31		156.11		136.56		NS
Mass to area ratio for shoots	0.007	b	0.008	a	0.007	b	0.007	b	***

Appendix B. A comparison of fenced (f) and open (n) plots in terms of the mean values of plant growth and performance parameters for plants transplanted to experimental plots in each of four successional habitats. The significance of the difference between means for the two treatments within site is indicated in the right hand column for each habitat as follows: *** = p< 0.001, ** = p< 0.01, * = p< 0.05, NS = not significant.

Locations	Back Beach			Secondary Successional Savanna			Primary Successional Savanna			Forest		
Treatment fenced or open	f	n		f	n		f	n		f	n	
Volume	4.21	4.03	NS	12.10	13.34	NS	18.30	14.81	**	2.80	5.25	NS
Shoot fresh mass	4.18	4.08	NS	12.17	13.15	NS	18.23	15.32	**	2.67	5.32	NS
Root fresh mass	0.18	0.19	NS	0.65	0.82	*	0.50	0.43	*	0.09	0.16	NS
Number of cladodes	1.743	2.183	***	2.54	2.64	NS	3.04	3.15	NS	2.00	3.00	NS
Mean cladode area	258.70	228.71	NS	878.39	547.91	NS	704.34	745.62	NS	134.59	249.33	NS
Total cladode surface area	429.30	479.93	NS	2619.95	1499.56	NS	2216.29	2398.54	NS	269.17	748.10	NS
Perimeter area ratio of cladode	0.56	0.58	NS	0.59	0.53	NS	0.42	0.48	NS	0.77	0.87	***
Cladode length to width ratio	1.61	1.81	*	1.79	1.62	*	1.60	1.64	NS	2.79	6.73	*
Total height	37.85	46.67	***	89.85	81.88	NS	107.20	106.42	NS	39.61	137.22	**
Chlorotic cladode surface area	175.21	207.08	**	158.95	127.43	NS	175.11	168.96	NS	81.92	80.13	NS
Root surface area	796.09	1159.22	***	2244.56	1485.19	NS	822.79	781.99	NS	529.02	267.32	NS
Total surface area	1394.92	1846.23	***	5023.46	3112.17	NS	3214.20	3349.50	NS	880.11	1095.45	NS
Total plant mass	4.36	4.27	NS	12.82	13.97	NS	18.73	15.76	**	2.76	5.49	NS
Shoot to root surface area ratio	1.18	1.14	NS	1.80	1.34	NS	3.38	3.85	NS	0.98	3.50	**

Root to shoot surface area ratio	1.58	1.70	NS	1.22	1.17	NS	0.42	0.40	NS	1.31	0.30	NS
Percent of surface area that is shoot	44.22	42.27	NS	49.38	50.26	NS	72.08	73.18	NS	46.69	77.23	*
Percent of surface area that is cladode	30.42	28.83	NS	44.29	45.72	NS	65.05	66.57	NS	37.87	69.27	*
Percent of surface area that is chlorotic cladode	13.80	13.45	NS	5.09	4.54	NS	7.03	6.62	NS	8.81	7.96	NS
Percent of surface area that is root	55.78	57.73	NS	50.62	49.74	NS	27.92	26.82	NS	53.31	22.77	*
Percent of mass that is shoots	95.90	95.81	NS	94.77	93.98	NS	96.6	97.04	**	96.56	97.33	NS
Percent of mass that is root	4.10	4.20	NS	5.23	6.0	NS	3.40	2.96	**	3.44	2.67	NS
Root to shoot mass ratio	0.04	0.05	NS	0.06	0.07	NS	0.04	0.03	**	0.04	0.03	NS
Area to mass ratio for shoots	152.62	192.94	***	376.34	131.21	NS	141.76	175.23	NS	131.21	149.93	NS
Mass to area ratio for shoots	0.007	0.006	***	0.008	0.008	NS	0.008	0.007	NS	0.008	0.007	NS

Appendix C. Main effects and interactions. Results of greenhouse experiment using ANOVA. SS = Sum of Square, df = degree of freedom, MS = Mean Square, *F* = F-ratio, P = Significance of effect.

Change in:	Source	SS	df	MS	F	Sig.
	Corrected Model	4423.71	31	142.70	12.95	0.000
Fresh Mass	Intercept	35595.70	1	35595.70	3229.11	0.000
	Nutrient_Cat	3044.48	3	1014.83	92.06	0.000
	Shade_Cat	711.02	3	237.01	21.50	0.000
	Site	60.50	1	60.50	5.49	0.019
	Nutrient_Cat * Shade_Cat	496.42	9	55.16	5.00	0.000
	Nutrient_Cat * Site	9.02	3	3.01	0.27	0.845
	Shade_Cat * Site	28.93	3	9.64	0.87	0.454
	Nutrient_Cat * Shade_Cat * Site	73.34	9	8.15	0.74	0.673
	Error	13757.20	1248	11.02		
	Total	53776.61	1280			
	Corrected Total	18180.91	1279			
	R Squared = .243 (Adjusted R Squared = .225)					

Number of Cladodes	Source	SS	df	MS	F	Sig.
	Corrected Model	145.09	31	4.68	4.53	0.000
	Intercept	1903.69	1	1903.69	1844.25	0.000
	Nutrient_Cat	77.94	3	25.98	25.17	0.000
	Shade_Cat	11.82	3	3.94	3.82	0.010
	Site	0.96	1	0.96	0.93	0.336
	Nutrient_Cat * Shade_Cat	24.94	9	2.77	2.68	0.004
	Nutrient_Cat * Site	6.02	3	2.01	1.94	0.121
	Shade_Cat * Site	5.66	3	1.89	1.83	0.140
	Nutrient_Cat * Shade_Cat * Site	17.74	9	1.97	1.91	0.047
	Error	1288.23	1248	1.03		
	Total	3337.00	1280			
	Corrected Total	1433.31	1279			
	R Squared = .101 (Adjusted R Squared = .079)					

Cladode area	Source	SS	df	MS	F	Sig.
	Corrected Model	131801638.65	31	4251665.76	22.07	0.000

Intercept	649506860.01	1	649506860.01	3371.47	0.000
Nutrient_Cat	40876217.85	3	13625405.95	70.73	0.000
Shade_Cat	84330273.98	3	28110091.33	145.91	0.000
Site	385790.28	1	385790.28	2.00	0.157
Nutrient_Cat * Shade_Cat	3804292.73	9	422699.19	2.19	0.020
Nutrient_Cat * Site	165360.93	3	55120.31	0.29	0.835
Shade_Cat * Site	1700579.14	3	566859.71	2.94	0.032
Nutrient_Cat * Shade_Cat * Site	539123.74	9	59902.64	0.31	0.972
Error	240424371.01	1248	192647.73		
Total	1021732869.66	1280			
Corrected Total	372226009.65	1279			

R Squared = .354 (Adjusted R Squared = .338)

Root area

Source	SS	df	MS	F	Sig.
Corrected Model	91665944.95	31	2956965.97	14.54	0.000
Intercept	338141472.11	1	338141472.11	1662.88	0.000
Nutrient_Cat	2106862.28	3	702287.43	3.45	0.016
Shade_Cat	82752812.13	3	27584270.71	135.65	0.000
Site	12623.77	1	12623.77	0.06	0.803
Nutrient_Cat * Shade_Cat	3483369.39	9	387041.04	1.90	0.048
Nutrient_Cat * Site	487632.72	3	162544.24	0.80	0.494
Shade_Cat * Site	720328.86	3	240109.62	1.18	0.316
Nutrient_Cat * Shade_Cat * Site	2102315.79	9	233590.64	1.15	0.325
Error	253776302.50	1248	203346.40		
Total	683583719.55	1280			
Corrected Total	345442247.44	1279			

R Squared = .265 (Adjusted R Squared= .247)

Root:Shoot ratio

Source	SS	df	MS	F	Sig.
Corrected Model	195.73	31	6.31	31.02	0.000
Intercept	128.03	1	128.03	629.06	0.000
Nutrient_Cat	17.22	3	5.74	28.20	0.000
Shade_Cat	164.08	3	54.69	268.74	0.000
Site	0.41	1	0.41	2.02	0.156
Nutrient_Cat * Shade_Cat	10.31	9	1.15	5.63	0.000
Nutrient_Cat * Site	0.52	3	0.17	0.85	0.465
Shade_Cat * Site	0.19	3	0.06	0.30	0.822
Nutrient_Cat * Shade_Cat * Site	3.00	9	0.33	1.64	0.100
Error	253.99	1248	0.20		
Total	577.75	1280			
Corrected Total	449.72	1279			

R Squared = .435 (Adjusted R Squared = .421)

Perimeter:Area ratio

Source	SS	df	MS	F	Sig.
Corrected Model	18.24	31	0.59	4.63	0.000
Intercept	30.69	1	30.69	241.46	0.000
Nutrient_Cat	0.45	3	0.15	1.18	0.315
Shade_Cat	4.79	3	1.60	12.56	0.000
Site	0.06	1	0.06	0.51	0.477
Nutrient_Cat * Shade_Cat	11.91	9	1.32	10.42	0.000
Nutrient_Cat * Site	0.28	3	0.09	0.74	0.528
Shade_Cat * Site	0.37	3	0.12	0.98	0.402
Nutrient_Cat * Shade_Cat * Site	0.36	9	0.04	0.32	0.969
Error	158.62	1248	0.13		
Total	207.54	1280			
Corrected Total	176.85	1279			

R Squared = .103 (Adjusted R Squared = .081)

Relative change in : Fresh Mass	Source	SS	df	MS	F	Sig.
	Corrected Model	474.23	31	15.30	10.13	0.000
	Intercept	3062.56	1	3062.56	2027.37	0.000
	Nutrient_Cat	298.63	3	99.54	65.90	0.000
	Shade_Cat	62.73	3	20.91	13.84	0.000
	Site	3.57	1	3.57	2.36	0.125
	Nutrient_Cat * Shade_Cat	77.87	9	8.65	5.73	0.000
	Nutrient_Cat * Site	5.37	3	1.79	1.19	0.314
	Shade_Cat * Site	5.02	3	1.67	1.11	0.345
	Nutrient_Cat * Shade_Cat * Site	21.04	9	2.34	1.55	0.126
	Error	1885.23	1248	1.51		
	Total	5422.02	1280			
	Corrected Total	2359.47	1279			

R Squared = .201 (Adjusted R Squared = .181)

Number of Cladodes	Source	SS	df	MS	F	Sig.
	Corrected Model	104.37	31	3.37	4.11	0.000
	Intercept	1042.18	1	1042.18	1271.05	0.000
	Nutrient_Cat	38.57	3	12.86	15.68	0.000
	Shade_Cat	19.77	3	6.59	8.04	0.000
	Site	0.45	1	0.45	0.55	0.459
	Nutrient_Cat * Shade_Cat	19.39	9	2.15	2.63	0.005
	Nutrient_Cat * Site	7.04	3	2.35	2.86	0.036
	Shade_Cat * Site	3.26	3	1.09	1.33	0.264
	Nutrient_Cat * Shade_Cat * Site	15.89	9	1.77	2.15	0.023
	Error	1023.27	1248	0.82		
	Total	2169.82	1280			
	Corrected Total	1127.64	1279			

R Squared = .093 (Adjusted R Squared = .070)

Cladode area

Source	SS	df	MS	F	Sig.
Corrected Model	899.89	31	29.03	8.91	0.000
Intercept	4053.01	1	4053.01	1243.80	0.000
Nutrient_Cat	303.38	3	101.13	31.03	0.000
Shade_Cat	498.03	3	166.01	50.95	0.000
Site	2.50	1	2.50	0.77	0.381
Nutrient_Cat * Shade_Cat	62.45	9	6.94	2.13	0.025
Nutrient_Cat * Site	9.40	3	3.13	0.96	0.410
Shade_Cat * Site	5.79	3	1.93	0.59	0.620
Nutrient_Cat * Shade_Cat * Site	18.35	9	2.04	0.63	0.776
Error	4066.70	1248	3.26		
Total	9019.60	1280			
Corrected Total	4966.59	1279			

R Squared = .181 (Adjusted R Squared = .161)

Root area

Source	SS	df	MS	F	Sig.
Corrected Model	18.24	31	0.59	4.63	0.000
Intercept	30.69	1	30.69	241.46	0.000
Nutrient_Cat	0.45	3	0.15	1.18	0.315
Shade_Cat	4.79	3	1.60	12.56	0.000
Site	0.06	1	0.06	0.51	0.477
Nutrient_Cat * Shade_Cat	11.91	9	1.32	10.42	0.000
Nutrient_Cat * Site	0.28	3	0.09	0.74	0.528
Shade_Cat * Site	0.37	3	0.12	0.98	0.402
Nutrient_Cat * Shade_Cat * Site	0.36	9	0.04	0.32	0.969
Error	158.62	1248	0.13		
Total	207.54	1280			
Corrected Total	176.85	1279			

R Squared = .103 (Adjusted R Squared = .081)

Root:Shoot ratio

Source	SS	df	MS	F	Sig.
Corrected Model	3124.82	31	100.80	11.36	0.000
Intercept	4013.46	1	4013.46	452.42	0.000
Nutrient_Cat	201.75	3	67.25	7.58	0.000
Shade_Cat	2623.94	3	874.65	98.59	0.000
Site	67.48	1	67.48	7.61	0.006
Nutrient_Cat * Shade_Cat	72.10	9	8.01	0.90	0.522
Nutrient_Cat * Site	33.93	3	11.31	1.27	0.282
Shade_Cat * Site	25.21	3	8.40	0.95	0.417
Nutrient_Cat * Shade_Cat * Site	100.42	9	11.16	1.26	0.256
Error	11071.19	1248	8.87		
Total	18209.47	1280			
Corrected Total	14196.01	1279			

R Squared = .220 (Adjusted R Squared = .201)

Perimeter:Area ratio

Source	SS	df	MS	F	Sig.
Corrected Model	73.02	31	2.36	7.30	0.000
Intercept	1.36	1	1.36	4.22	0.040
Nutrient_Cat	0.50	3	0.17	0.52	0.671
Shade_Cat	39.85	3	13.28	41.16	0.000
Site	0.65	1	0.65	2.01	0.157
Nutrient_Cat * Shade_Cat	27.75	9	3.08	9.55	0.000
Nutrient_Cat * Site	0.81	3	0.27	0.83	0.475
Shade_Cat * Site	1.52	3	0.51	1.57	0.195
Nutrient_Cat * Shade_Cat * Site	1.94	9	0.22	0.67	0.738
Error	402.85	1248	0.32		
Total	477.23	1280			
Corrected Total	475.87	1279			

R Squared = .153 (Adjusted R Squared = .132)

Glossary

Abiotic: Nonbiological

Acclimation: A reversible change in morphology or physiology of an organism in response to environmental change (the modification of an organism's phenotypic traits by the environment)

Adaptation: the evolutionary process by which organisms become better able to exist under prevailing environmental conditions. The specific genetically determined trait that renders an organism more capable existence.

Assimilation: Incorporation of any material into the tissues, cells, and fluids of an organism (the movement of energy and nutrients from the digestive tract into an organism; often taken to be equivalent to gross productivity if it is a rate function).

Biomass: Weight of living material, usually expressed as a dry weight, in all or part of an organism, population, or community. Commonly presented as weight per unit area, a biomass density.

Biotic: Pertaining to living things.

Clay: A fine-grained component of soil, formed by the weathering of granitic rock, composed primarily of hydrous aluminum silicates.

Climax: The end point of a successional sequence, or sere; a community that has reached a steady state under a particular set of environmental conditions.

Coexistence: Occurrence of two or more species in the same habitat; usually applied to potentially competing species, (often to imply a stable situation).

Colonization: Initial stage of succession during which a vacant habitat becomes occupied by organisms.

Community: An association of interacting populations, usually defined by the nature of their interaction or in the place in which they live.

Competition Exclusive Principle: The hypothesis that two or more species cannot coexist on a single resource that is scarce relative to demand for it.

Competition: The negative biological interaction between two or more individuals whether of the same species (intraspecific competition) or other species (interspecific competition) that occurs when (a) a necessary resource is in limited supply relative to organism demands or (b) resource quality varies and demand is greater for higher quality resources.

Demography: Study of population of characteristics such as growth rate, sex ratio, and age structure and the underlying processes responsible for the set of characteristics.

Dispersal: Movement of organisms away from the place of birth of from centers of population density.

Diversity: The number of species in a local area (alpha diversity) or region (gamma diversity). Also, a measure of the variety of species in a community that takes into accounts the relative abundance of each species.

Dominant: An individual that is able to appropriate resources to the detriment of other subordinate individuals; also a species that is numerically superior in a community.

Ecological isolation: Avoidance of competition between two species by differences in food, habitat, activity period, or geographical range.

Ecological release: Expansion of habitat and resource utilization by populations in regions of low species diversity, resulting from interspecific competition.

Ecotype: A genetically differentiated subpopulation that is restricted to a specific habitat.(genetically distinct populations within the same species adapted to different environments).

Environment: All of the external physical and biological factors that directly influence the survival, growth, development, and reproductions of organisms.

Extinction: Disappearance of a species or other taxon from a region or biota.

Extrinsic factor: Environmental agent independent of an ecosystem that influences organisms and their environments without itself being modified.

Facilitation: Enhancement of a population of one species by the activities of another, particularly during early succession.

Fecundity: Rate at which an individual produces an offspring.

Fitness: The relative ability of a genotype to contribute genes to the next generation. "Inclusive fitness" is the total fitness of an individual and the fitnesses of its relatives, the latter weighted according to degree of relationship; usually applied to the consequences of social interaction between relatives.

Floristic: Referring to the species composition of plant communities.

Fundamental niche: The full range of environmental conditions within which a species can successfully survive and reproduce in the absence of deleterious interactions including competition, predation, and parasitism

Gene flow: The exchange of genes among population.Genetic drift: Change in allele frequency due to random variations in fecundity and mortality rate.

Genotype: All the genetic characteristics that determine the structure and functioning of an organism; often applied to a single gene locus to distinguish one allele, or combination of alleles from another.

Habitat: Place where an animal or plant normally lives, often characterized by a dominant plant form or physical characteristic (that is the stream habitat, the forest habitat); those areas that are actually occupied and meet the requirements for a species' growth, survival, and successful reproduction

Herbivore: An organism that consumes living plants or their parts.

Interspecific competition: Competition between individuals of different species.

Intraspecific competition: Competition between individuals of same species

Liebig's law of the minimum: The idea that the growth of an individual or population is limited by the essential nutrient present in the lowest amount relative to requirement.

Life history: The set of adaptations of and organism that more of less directly influence life table values of age–specific survival and fecundity; hence, reproductive rate, age at first reproduction, reproductive risk, and so on.

Limiting factor: Intrinsic or extrinsic factor limiting physiological or population processes; organisms will be limited by the factor or combination of the factors, with the value farthest from their requirements.

Limiting resource: A resource that is scarce relative to demand for it.

Limiting similarity: Minimum degree of ecological similarity compatible with the coexistence of two or more populations.

Litter: Organic matter that settles on the soil surface in terrestrial ecosystems.

Matrix: A rectangular array (rows and columns) of mathematical elements (such as the coefficients of simultaneous equations) that is subject to special mathematical manipulations.

Microhabitat: The particular parts of the habitat that an individual encounters in the course of its activities.

Natural selection: Change in the frequency of genetic traits in a population through differential survival and reproduction of individuals bearing those traits.

Niche breadth: The range of a single niche dimension occupied by a population. The variety of resource utilized and range of conditions tolerated by an individual, population, or species.

Niche overlap: The sharing of niche space by two or more species; similarity of resource requirement and tolerance of ecological conditions.

Niche preemption: A model in which species successively procure a proportion of the available resources, leaving less for the next.

Niche: The ecological role of a species in the community; the many ranges of conditions and resource qualities within which the organisms or species persists, often conceived as a multidimensional space (an abstract n-dimensional environmental space within which a population is capable of maintaining or increasing its size).

Nutrient: Any substance required by organisms for normal growth and maintenance.

Osmosis: Diffusion of substance in aqueous solution across the membrane of a cell.Perennial: Referring to an organism that lives for more than one year; lasting throughout the year.

pH: A scale of acidity or alkalinity; the logarithm of the concentration of hydrogen ions.

Phenotype: Physical expression in the organism of the interaction between the genotype and the environment; outward appearance and behavior of the organism (the observable characteristics of an organism).

Predation: An interaction in which one living organism serves as food source for another.

Predator: An organism that eats all or parts of other live organism.

Primary succession: Succession occurring on newly exposed sites devoid of life.

Quantitative trait: A trait having continuous variability within a population and revealing the expression of many gene loci.

Realized niche: The circumscribed physical space after exclusion by competitors, predators, and parasites.

Resource: Environmental factor that is directly utilized by organisms.

Secondary succession: Progression in communities in habitats where the climax community has been disturbed or removed entirely

Stochastic: Varying in nonsystematic, random fashion with time.

Succession: The directional change in community composition and associated biological and environmental properties in ecosystems.

Symbiosis: An interaction in which both species are positively influenced as a result of their co-occurrences (mutualism).

Tolerance limits: Range of conditions over which an organism can survive and reproduce.

Weathering: The process of physical and chemical decomposition of rocks and rock fragments.

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