Facilitative Effects of a Sand Dune Shrub on Species Growing beneath the Shrub Canopy
Author(s): Scott W. Shumway
Source: *Oecologia*, Vol. 124, No. 1 (2000), pp. 138-148
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4222675
Accessed: 17-11-2015 18:10 UTC

Oecologia (2000) 124:138–148

Scott W. Shumway

Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy

Received: 21 July 1999 / Accepted: 18 January 2000

Abstract Only recently has the importance of positive interactions among plant species in structuring natural communities been supported by experimental evidence. Most studies have focused on interactions between a pair of species at a single life-history stage. In this study positive interactions between a woody nitrogen-fixing shrub (*Myrica pensylvanica*) and two herbaceous sand dune species (*Solidago sempervirens*, *Ammophila breviligulata*) which frequently grow beneath shrub canopies are examined throughout the life cycles of the herbaceous species. Comparisons of *S. sempervirens* and *A. breviligulata* growing beneath and outside *M. pensylvanica* shrubs show that plants growing in association with shrubs are larger, are more likely to flower, produce greater numbers of flowers and seeds, have higher midday xylem water potentials, have higher tissue nitrogen concentrations, and have higher photosynthetic efficiencies. Measurements of environmental conditions show that areas beneath shrubs are more shaded, have lower soil temperatures, and have higher soil nitrogen levels. The results from experimental manipulations designed to test the effects of *Myrica* shrubs on understory species suggest that the observed differences in plant performance are strongly influenced by canopy shading and soil nutrient enrichment associated with the shrubs. The results demonstrate that *M. pensylvanica* facilitates growth, reproduction, and recruitment of *S. sempervirens* and *A. breviligulata* growing beneath it. This study, one of the few to examine positive interactions at different life-history stages, supports previous predictions that positive interactions may be particularly important in plant communities characterized by physiologically stressful conditions.

Key words *Ammophila breviligulata* · Facilitation · *Myrica pensylvanica* · Sand dune ecology · *Solidago sempervirens*

Introduction

Recent studies reveal that positive (facilitative) species interactions are not only important in shaping plant community processes, but may be common where environmental conditions are physiologically stressful (reviewed by Bertness and Callaway 1994; Callaway 1995). Positive interactions among plant species have been demonstrated in a variety of communities, often within the context of community succession. To date most studies have focused on interactions during a particular stage of the beneficiary (*sensu* Callaway 1995) plant's life history. Seedling recruitment may be facilitated by close proximity to adult nurse plants that protect seedlings from adverse physical conditions (Niering et al. 1963; Franco and Nobel 1989). During succession initial colonizers may pave the way for vegetative expansion, as well as seedling recruitment, by ameliorating stressful environmental conditions (Connell and Slatyer 1977; Bertness and Shumway 1993; Bertness and Hacker 1994). Nitrogen-fixing plants have been shown to enhance growth of other plants, enhance rates of colonization, and to alter species compositions by enriching otherwise nutrient poor soil (Walker and Chapin 1986; Morris and Wood 1989; Vitousek and Walker 1989; Chapin et al. 1994). Few studies have examined the effects of a benefactor on more than one species. Few studies have tested for facilitative effects at different stages in the life history of a plant (Chapin et al. 1994) or conducted measurements on multiple components of plant fitness. The present study examines the effects of a nitrogen-fixing shrub on two herbaceous perennials living beneath the shrub canopy. The effects of shrubs on seedlings and adults of the herbaceous species will be tested by measuring survival, growth, physiology, and reproduction. Examination of multiple parameters and different life-history stages is

---

S.W. Shumway
Department of Biology, Wheaton College, Norton,
MA 02766, USA
e-mail: scott_shumway@wheatonma.edu
Fax: +1-508-2858278

necessary for a more complete understanding of plant interactions in natural communities.

Sand dunes have long been cited as classic examples of plant community development with vegetation change mediated by constantly shifting sands, high temperatures, and a scarcity of accessible water and nutrients (Cowles 1899; Ranwell 1972). In the 100 years since H.C. Cowles' classic studies of vegetation change on Lake Michigan dunes, there has been relatively little experimental study of the nature of species interactions on sand dunes (Ehrenfeld 1990; see Keddy 1981; Silander and Antonovics 1982 for notable exceptions). In a study of nitrogen fixation in root nodules of the dune shrub *Myrica pensylvanica*, Morris et al. (1974) declared *Myrica* "to be a key successional plant on nitrogen impoverished coastal soils and dunes." However, the potential positive effects of this species on other plants have not been examined (purported negative effects are addressed in the discussion). Initial observations of sand dunes at Cape Cod National Seashore suggested that interspecific facilitative interactions may be taking place between *Myrica* shrubs and the herbaceous species growing beneath them (S.W. Shumway, unpublished work). Rather than being adversely affected by growth beneath the shrub canopy, *Solidago sempervirens* and *Ammophila breviligulata* growing beneath *Myrica* were taller and more robust than individuals growing in open sand outside shrubs.

I hypothesize that *Myrica* facilitates survival, growth, and reproductive output of *Solidago* and *Ammophila*. Possible mechanisms for the proposed facilitation may include decreased physiological stress due to shading by shrub canopies and increased nutrient availability beneath shrubs. In this study I quantify the observed pattern by comparing plant growth and physiology, population density, and reproductive output of plants growing in these two areas. I then use manipulative field and greenhouse experiments to explicitly test the facilitation hypothesis and identify a mechanistic explanation for the observed facilitation.

Materials and methods

Study site and species descriptions

All field work was performed at the Marconi Station of the Cape Cod National Seashore, South Wellfleet, Massacusetts, United States between 1992 and 1998. Before being designated as a National Seashore 30 years ago the site was heavily disturbed by military vehicles. Today it is covered by vegetation typical of coastal sand dune and dry heathland (Godfrey et al. 1991). The study site occupies a 1000 m long by 50 m wide area just above the scarp dropping off to the Atlantic Ocean. The area is inhabited primarily by *A. breviligulata*, *S. sempervirens*, and *M. pensylvanica*. *A. breviligulata* (Poaceae), American beachgrass, is a spreading rhizomatous perennial with widely spaced ramets and is the dominant sand dune species along the Western Atlantic coast from the Canadian Maritime Provinces to North Carolina. *S. sempervirens* (Asteraceae), seaside goldenrod, is a rosette-forming perennial. *M. pensylvanica* (Myricaceae), northern bayberry, is a woody shrub which produces root nodules that house a symbiotic nitrogen-fixing actinomycete bacteria (*Frankia*). At the Marconi site *Myrica* shrubs are typically 0.5–2 m tall and 1–3 m in diameter. *Ammophila*, *Solidago*, *Chrysopsis falcata*, *Hudsonia ericoides*, *Rosa rugosa*, and *Toxicodendron radicans* often grow beneath the shrub canopy.

This paper compares plants (*Ammophila* and *Solidago*) growing in two areas. The area beneath the canopy of *Myrica* shrubs will be referred to as "beneath shrubs." The second area is dominated by *Ammophila* and represents the predominant vegetation type at the site. These areas have sparse canopy development and cast minimal shade upon the soil. The *Ammophila*-dominated areas studied in this paper are located 2–5 m away from the nearest *Myrica* shrub and will be referred to as "outside shrubs."

Individual, seedling, and flower density

Densities of adult stems, flowering stems, and seedlings of *Solidago* and *Ammophila* were compared beneath and outside *Myrica* shrubs located along a 500-m-long transect parallel to the coast. Stem densities were counted within a 0.25-m^2 quadrat randomly placed beneath the canopies of 20 different *Myrica* shrubs and 2–5 m outside shrubs in October 1998. Many of the *Solidago* rosettes growing in open sand do not produce flowers annually, whereas plants beneath shrubs flower profusely. In order to quantify the frequency of flowering of *Solidago* and *Ammophila* growing in the different areas the number of stems in flower was recorded for each quadrat. Seedling densities were quantified in May 1993 within a 0.25-m^2 quadrat randomly placed beneath and outside 25 different *Myrica* shrubs.

Reproductive output

Reproductive output was compared for *Solidago* and *Ammophila* growing in each area. Flowering individuals of each species growing beneath and outside ten different *Myrica* shrubs were randomly harvested in October 1998 by cutting stems at ground level. Plant height, leaf number, flower number, and dry biomass were determined for each individual. *Solidago* flower number was determined by counting the total number of capitula (composite flower heads) on an inflorescence. Three capitula were randomly selected from each inflorescence and the number of florets with maturing ovaries were counted. These three values were used to calculate the average number of flowers per capitula which was then multiplied by the number of capitula to estimate the total number of flowers per inflorescence. *Solidago* flowers were harvested prior to seed maturation, however most ovaries appeared to be ripening into viable achenes and, therefore, flower number will be used as a measure of future seed production. The presence of insect larvae feeding in some capitula was also recorded. The number of individual spikelets (flowers) and mature caryopses (seeds) was counted on each *Ammophila* inflorescence. Biomass was determined by weighing plants after they had been dried in a 70°C oven.

Seedling survivorship

Survival rates of *Solidago* and *Ammophila* seedlings emerging beneath *Myrica* shrubs and outside shrubs were compared by marking them with color-coded plastic toothpicks in May and examining them for survival in August. Approximately 100 seedlings of each species were marked beneath each of four *Myrica* shrubs. An identical number of seedlings were marked in nearby areas outside shrubs. Survival through the first growing season was assayed with a single census at the end of August.

Physiological comparisons beneath and outside *Myrica* shrubs

Chlorophyll fluorescence, photosynthetic rate, pre-dawn water potential, and midday water potential were measured on plants (n=8 to 10) growing beneath eight to ten different *Myrica* shrub canopies and outside shrubs in July 1997. Chlorophyll fluorescence was measured using a portable CF-1000 chlorophyll fluorescence measurement system (P.K. Morgan Instruments) between 0800 and 1000 hours. Healthy leaves were dark-adapted for 20 min after which fluorescence was measured during a 10-s period at a light intensity of 500 μmol m^{-2} s^{-1}. The ratio of fluorescence parameters F_v/F_m is an indication of the photochemical efficiency of photosystem II and is commonly interpreted as a measure of overall plant stress and photosynthetic efficiency (Greaves et al. 1991). This is the only fluorescence parameter that will be reported. Photosynthetic rate and transpiration rate were measured using a portable LCA-2 infrared gas analysis system (Analytical Development Company). Measurements were made between 1100 and 1500 hours when light levels were consistently above 2000 μmol m^{-2} s^{-1}. Water use efficiency was calculated as the ratio of photosynthesis/transpiration. Xylem water potential was determined in the field using a pressure chamber (PMS Instruments model 1002). Single leaves were severed from the plants and immediately sealed in the pressure chamber. Predawn water potentials were measured between 0400 and 0600 hours. Midday water potential measurements were conducted on sunny days between 1100 and 1400 hours.

The plant nutrient status of *Solidago* and *Ammophila* growing beneath *Myrica* shrubs (*n*=5 per species from 5 different shrubs) and outside shrubs (*n*=5 per species) was compared by collecting plants from the two areas and measuring tissue nitrogen content (all nutrient analyses were performed by the University of Massachusetts soil testing laboratory).

Physical parameters beneath and outside *Myrica* shrubs

Physical parameters that might influence plant growth (solar irradiance, soil temperature, soil water content, soil nutrients) were measured beneath and outside *Myrica* shrubs. Solar irradiance was measured using a LI-COR LI-190SA quantum sensor and LI-189 meter. Measurements were taken above the vegetation canopy and 10 cm away from the ground and used to calculate the percentage of ambient light reaching the ground. This was repeated beneath and outside 12 different *Myrica* shrubs. Measurements beneath the *Myrica* canopy were made approximately 0.5 m in from the edge of the canopy. For each location four subsamples were taken and then averaged prior to analysis to compensate for within shrub heterogeneity in canopy shading. Soil and air temperatures (*n*=10 separate shrubs) were measured in each area on a relatively mild day in September using a YSI tele-thermistor. Soil temperatures were measured by inserting the probe into the top 1 cm of the sand and waiting until the temperature stabilized. Soil water content was determined gravimetrically by collecting a 1-l beaker full of sand from 30 cm below the surface. Samples were collected beneath and outside ten separate *Myrica* shrubs. Soil samples were weighed immediately in the field with a portable balance, dried in an oven for 2 weeks, and reweighed. Percentage soil water content was calculated using the formula (Wet weight–dry weight)×100/wet weight. Soil collected similarly to that used for water content was analyzed for total (Kjehldahl) nitrogen content (*n*=5).

Solidago seedling greenhouse experiment

The influence of soil type on seedling growth was examined by raising *Solidago* seedlings in soil collected beneath and outside *Myrica* shrubs. Soil was collected from the top 15–30 cm in each area and placed in 7.5-cm (3-inch) pots (*n*=18/treatment) which were sown with *Solidago* seeds purchased from the New England Wildflower Society (Framingham, Mass., USA). Multiple seeds were sown in each pot and the first seedling to emerge was used for the experiment while all others were thinned. Seedlings were grown under natural light in the Wheaton College greenhouse from June-September. Plants were then harvested and measured for leaf number, plant height, and above- and belowground dry biomass.

Solidago transplant experiment

To test the hypothesis that plants grow better beneath *Myrica* shrubs than outside shrubs, *Solidago* adults were transplanted to each of these locations and monitored for growth. In early June 1992 *Solidago* individuals of similar height and leaf number (4–6) growing in open sand were excavated, being careful to obtain as much of the root mass as possible. Eight individuals were transplanted 0.5 m inside the leaf canopy of a *Myrica* shrub. An equal number of controls were replanted 2 m away from the shrub. All plants were carefully removed from the soil in September and measured for leaf number, total height, and above- and belowground dry biomass.

Shade-fertilizer experiment

To test the hypothesis that the facilitative effects of living beneath *Myrica* shrubs result from shading by the canopy and soil nutrient enrichment, I performed a two-factor field experiment in which plants were provided with artificial shade and fertilizer. Five sets of experimental plots were established randomly within *Ammophila* dominated dune in May 1993. Each set consisted of four 1 m× 2 m plots which received the full combination of shade, fertilizer addition, and control treatments: Shade-Fertilizer, Shade-Control (no fertilizer), Control (no shading)-Fertilizer, Control (no shading)-Control (no fertilizer). Shade treatments were covered by a neutral shade consisting of a double layer of 0.6-mm (0.25-inch) mesh black plastic screening (Vexar) supported by a 50-cm-high wooden frame. The screen covered the top and sides of the frame. Shading reduced light levels by 72%. Fertilizer treatments received a mix of 10 g urea: 10 g ammonium sulphate per 2-m^2 plot at monthly intervals from May to September.

To determine plant physiological responses to the experimental treatments, photosynthetic rate, chlorophyll fluorescence, and midday water potential (*Ammophila* only) were measured on random individuals (*n*=8) of *Solidago* and *Ammophila* in each plot during the growing season using the same methods.

In September stem densities and the number of flowering stems of *Solidago* and *Ammophila* were counted in each plot. To determine the effects of shade and fertilizer on flower production, flowering individuals (up to 8 per plot) were randomly harvested from each plot and the numbers of flowers were counted on each inflorescence. Plant height, leaf number, and biomass were also determined for eight randomly chosen non-flowering *Ammophila* and *Solidago* individuals from each plot.

Seedling survival was monitored by marking all naturally occurring seedlings in each plot at the beginning of the experiment. In late August the markers were recovered and seedlings scored as dead or alive. Because of the low number of natural seedlings present, treatment replicates were lumped together for data analysis.

Survival was also monitored for seedlings that were transplanted into each treatment. Ten seedlings of *Solidago* and *Ammophila* were transplanted into each plot in May. Many seedlings did not survive the transplant process (73% *Solidago* and 45% *Ammophila* transplant mortality after 2 weeks) and were excluded from further analysis. The remaining seedlings were censused again for survival in late August.

Analysis

Comparisons of plant density, growth, reproductive output, physiological parameters, and physical parameters beneath and outside shrubs were made using unpaired *t*-tests. The results of the *Solidago* seedling greenhouse and *Solidago* field transplant experiments were also analyzed using unpaired *t*-tests. All percentage data were arcsin-square-root-transformed prior to analysis. Survival of marked seedlings was compared using *G*-tests of independence between seedling survival and treatment. The results of the shade-fertilizer experiment were analyzed using two-way analysis of

Table 1 Comparisons of densities of adult stems, flowering stems, and seedlings ($\bar{x}$±SE per 0.25 m^2) of *Solidago* and *Ammophila* growing beneath the canopy of *Myrica* shrubs and outside shrubs

	Adult stems	Flowering stems	Percentage in flower	Seedlings
Solidago				
Beneath shrubs	2.00±0.38	1.25±0.28	63.7±10.3	22.10±6.35
Outside shrubs	2.35±0.25	0.25±0.12	9.2±4.6	0.16±0.09
df	38	38	34	48
t	–0.76	3.18	4.96	3.45
P	0.45	0.002	0.0001	0.001
Ammophila				
Beneath shrubs	15.80±0.88	1.55±0.33	10.8±2.5	9.24±5.61
Outside shrubs	12.85±1.1	0.20±0.11	2.2±1.5	12.68±5.82
df	38	38	38	48
t	1.98	3.79	3.67	0.42
P	0.05	0.0005	0.0007	0.67

Table 2 Comparison of growth performance and reproductive output ($\bar{x}$±SE) of randomly harvested flowering *Solidago* and *Ammophila* growing beneath *Myrica* shrubs and outside shrubs (n=10 individuals per location; *df*=18 for each test)

	Height (cm)	Leaf number	Biomass (g)	Flower heads (capitula)	Flowers (florets) per head	Total flowers
Solidago						
Beneath shrubs	70.5±4.1	35.2±1.4	22.07±4.10	222.4±48.8	33.5±1.0	7250.32±1418.65
Outside shrubs	33.3±1.8	24.1±2.4	5.65±0.60	79.4±11.8	29.2±1.1	2340.50±369.29
t	8.17	3.88	3.95	2.84	2.83	3.34
P	0.0001	0.001	0.0009	0.01	0.01	0.003

	Height (cm)	Leaf number	Biomass (g)	Flowers (spikelets)	Seeds	Percent seed set
Ammophila						
Beneath shrubs	84.8±4.2	5.3±0.2	4.34±0.58	431.7±21.0	77.2±13.3	17.9±3.1%
Outside shrubs	61.7±2.6	4.8±0.3	2.00±0.26	209.2±26.0	39.6±6.7	19.9±2.9%
t	4.61	1.12	3.62	6.63	2.50	–0.48
P	0.0002	0.27	0.001	0.0001	0.02	0.63

variance with shade and fertilizer as main effects. In the event of a significant two-way interaction term, least-square means were compared for all pairs of treatments.

Results

Plant density and the frequency of flowering by *Solidago* and *Ammophila*

Densities of *Solidago* adults were similar beneath and outside shrubs (Table 1). However, there were 5 times as many flowering individuals beneath *Myrica* shrubs than in the areas surrounding shrubs. *Ammophila* stem densities were 1.2 times higher beneath shrubs than outside shrubs and the number of flowering stems was more than 7 times higher beneath shrubs. These results indicate that *Solidago* and *Ammophila* growing beneath shrubs are more likely to flower than individuals growing outside shrubs. *Solidago* seedling densities were over two orders of magnitude higher beneath *Myrica* shrubs than outside shrubs (Table 1). In comparison, *Ammophila* seedling densities did not differ significantly between the two areas.

Comparisons of flowering *Solidago* and *Ammophila*

Flowering individuals of *Solidago* growing beneath *Myrica* shrubs not only produced significantly more flowers than individuals growing outside shrubs, they were much larger in size (Table 2). *Solidago* growing beneath *Myrica* shrubs grew twice as tall, had more leaves, and attained nearly 4 times the biomass compared with plants outside shrubs. They also produced 2.8 times as many flower heads, averaged more flowers per capitula, and had 3 times the total number of flowers as those growing outside shrubs. Of the 30 capitula examined from each area 13% collected from beneath shrubs (30% of inflorescences) were occupied by insect larvae (mostly Coleoptera) while 40% from outside shrubs contained larvae (60% of inflorescences). *Ammophila* plants growing in association with *Myrica* shrubs were taller and their biomass twice as great as plants growing outside *Myrica* shrubs. There were no differences between the number of leaves produced by *Ammophila* in the two locations. *Ammophila* plants beneath shrubs produced twice as many flowers per inflorescence than plants outside shrubs. Percent seed set did not differ significantly between the two areas.

Table 3 Comparisons of physiological parameters ($\bar{x}$±SE) for *Solidago* and *Ammophila* growing beneath the canopy of *Myrica* shrubs and outside shrubs

	Chlorophyll fluorescence (F_v/F_m)	Photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	Transpiration rate (μmol H_2O m^{-2} s^{-1})	Water use efficiency	Pre-dawn water potential (MPa)	Midday water potential (MPa)
Solidago						
Beneath shrubs	0.886±0.002	3.56±0.81	3.70±0.31	0.88±0.14	–0.375±0.03	-1.20±0.07
Outside shrubs	0.863±0.005	5.41±0.72	4.64±0.16	1.14±0.13	–0.412±0.02	-1.59±0.02
df	16	16	16	16	14	18
t	4.58	-1.69	-2.65	-1.33	–0.91	-5.11
P	0.0003	0.10	0.01	0.20	0.37	0.0001
Ammophila						
Beneath shrubs	0.891±0.002	3.71±0.59	9.14±0.35	0.40±0.06	–0.451±0.07	-1.80±0.09
Outside shrubs	0.874±0.003	4.76±0.86	10.8±0.67	0.45±0.08	–0.357±0.06	-2.11±0.07
df	16	16	16	16	12	18
t	4.49	-1.00	-2.16	–0.40	0.95	-2.40
P	0.0004	0.32	0.04	0.68	0.35	0.02

Seedling survival

Seedling survival was analyzed by lumping data from all areas to calculate the overall percentage of individuals that survived. *Solidago* seedling survival did not differ beneath (21.5%) and outside (20.8%) shrubs. Similarly, *Ammophila* seedling survival, was not different for seedlings emerging beneath shrubs (7.9%) and outside shrubs (11.5%). Survival of marked seedlings was variable between shrubs and the averaged results mask the fact that seedling survival was much higher beneath some shrubs than others.

Physiological comparisons beneath and outside shrubs

Most of the measured physiological parameters differed for plants growing beneath and outside *Myrica* shrubs (Table 3). The chlorophyll fluorescence ratio of F_v/F_m was significantly higher for plants growing inside shrubs compared to plants growing outside shrubs for both *Solidago* and *Ammophila*. Transpiration rates of *Solidago* and *Ammophila* growing beneath shrubs were 20% and 16% lower than for plants growing outside shrubs while there were no differences in photosynthetic rates or water use efficiencies between the two areas. Predawn xylem water potentials were not significantly different between plants growing beneath and outside shrubs for either species. In sharp contrast, midday xylem water potentials were 0.3 Mpa higher for *Solidago* and *Ammophila* growing beneath shrubs compared to plants growing outside shrubs (Table 3). Plant nitrogen levels were only slightly higher for *Solidago* growing beneath shrubs (1.79±0.16% vs. 1.34±0.13% outside; df=8, t=2.14, P=0.06), but were 1.6 times higher for *Ammophila* collected inside shrubs (1.18±0.07% vs. 0.70±0.27%, df=8, t=6.27, P=0.0002).

Physical comparisons beneath and outside shrubs

In July, 97.8±1.3% of ambient sunlight reached the soil surface in the open *Ammophila*-dune outside shrubs compared to the 6.7±1.5% of ambient sunlight that reached the soil surface beneath *Myrica* shrubs (df=22, t=44.56, P=0.0001). Soil temperature was 1.4 times higher outside shrubs than beneath *Myrica* shrubs (df=28, t=16.07, P=0.0001). Outside shrubs the soil temperature was significantly hotter than the air temperature (32.5±0.5°C vs. 27.6±0.2°C; df=28, t=8.50, P=0.0001). In sharp contrast the soil temperature beneath *Myrica* shrubs was cooler than the corresponding air temperature (22.7±0.3°C vs. 26.8±0.3°C; df=28, t=9.97, P=0.0001). Soil water content beneath *Myrica* shrubs (1.5%) was not significantly different from soil water content outside shrubs (2.3%; df=10, t=1.56, P=0.14). Soil nitrogen content was highly variable ranging from 33 to 130 μg g^{-1} beneath shrubs and 30 to 92 μg g^{-1} outside shrubs. The highest value and lowest two values from each location were considered to be outliers and were excluded from further analysis aimed at comparing general patterns in soil nitrogen availability. Soil nitrogen was significantly greater beneath shrubs compared to outside shrubs (64.2±2.3 vs. 52.6±3.6 μg g^{-1}; df=5, t=2.7, P=0.02)

Solidago seedling greenhouse experiment

Solidago seedlings grown in sand collected beneath *Myrica* were significantly larger than seedlings grown in sand collected from the open dune (Table 4). Seedlings grown in sand from beneath shrubs were more than 2.5 times taller, averaged 1 more leaf, and had nearly 10 times the biomass of seedlings grown in sand from the open dune.

Solidago transplant experiment

Solidago transplants grew better beneath *Myrica* shrubs. Transplants growing in association with *Myrica* were significantly taller in height (21.0±1.0 cm vs. 17.8±0.8 cm, df=14, t=2.90, P=0.02) and had a heavier total bio-

Table 4 Results from greenhouse experiment in which *Solidago* seedlings ($n=18$) were grown in soil collected from beneath *Myrica* shrubs and outside shrubs in *Ammophila*-dominated open dune ($df=35$)

Soil source	Height (cm)	Leaf number	Aboveground biomass (g)	Belowground biomass (g)	Total biomass (g)
Beneath shrubs	14.48±0.83	5.47±0.22	0.133±0.018	0.150±0.029	0.290±0.046
Outside shrubs	5.57±0.31	4.61±0.27	0.013±0.002	0.021±0.003	0.034±0.004
t	9.78	2.48	6.55	4.31	5.42
P	0.0001	0.01	0.0001	0.0001	0.0001

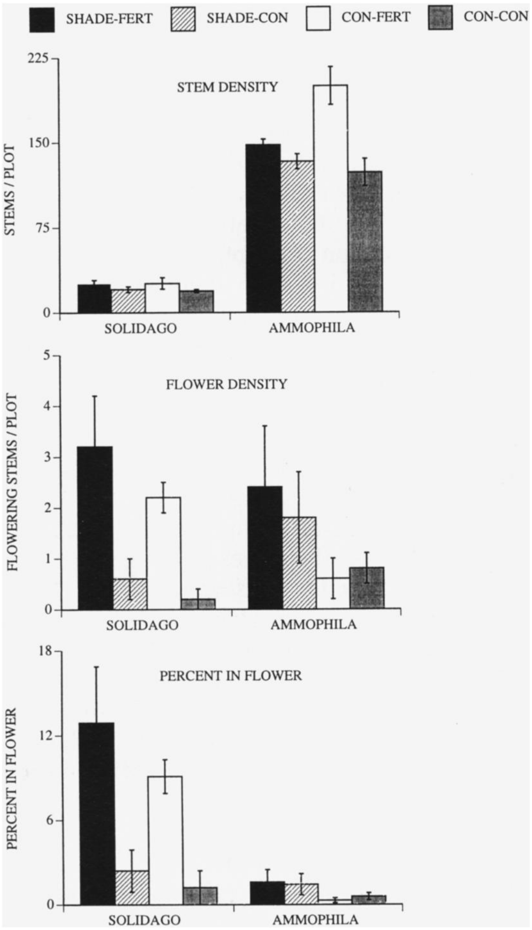

Fig. 1 Final census of the shade-fertilizer experiment showing stem density, flowering stem density, and the percentage of stems in flower ($\bar{x}\pm$SE per 2-m^2 plot) for *Solidago* and *Ammophila* growing in each treatment (*dark fill* Shade-Fertilizer, *shading* Shade-Control, *open* Control-Fertilizer, *light fill* Control-Control)

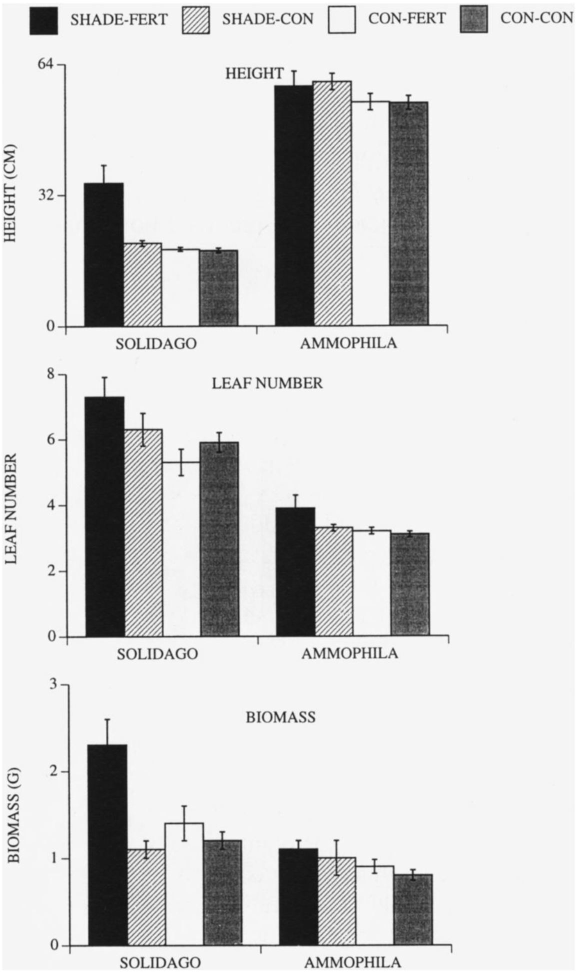

Fig. 2 Comparisons of height, leaf number, and biomass ($\bar{x}\pm$SE) for randomly harvested *Solidago* and *Ammophila* ($n=8$ per plot) growing in each treatment of the shade-fertilizer experiment

mass (3.6±0.3 g vs. 2.5±0.2 g, $df=14$, $t=3.04$, $P=0.01$) than transplants growing 2 m away from the shrubs. Total leaf number, however, did not differ between treatments. Although the total biomass differed significantly between treatments, this result should be viewed with caution. Aboveground biomass did not differ significantly between treatments, although aboveground biomass was slightly higher for transplants located beneath *Myrica* shrubs. Belowground biomass did, however, differ between treatments ($df=14$, $t=2.88$, $P=0.01$) and is largely responsible for the reported difference in total biomass. None of the transplants produced flowers.

Shade-fertilizer experiment

Final census

Fertilizer addition increased both the final density of *Solidago* stems in flower ($F_{1,16}=14.29$, $P=0.001$) and the total percentage of plants that produced flowers sixfold ($F_{1,16}=15.46$, $P=0.001$; Fig. 1). Shading had no effect on either the density of flowering individuals or on the percentage of individuals that produced flowers. *Solidago* stem density did not change in response to either shading or fertilizer addition relative to controls. *Ammophila* stem density, however, increased by 37% in response to fertilizer addition ($F_{1,16}$=16.83, P=0.0008). The greatest response was found in the Control-Fertilizer treatment (LSM, P=0.05). There was no difference in the density of flowering stems in response to either treatment. Even though *Ammophila* stems in shade treatments were three times more likely to flower than non-shaded individuals, the difference was not statistically significant ($F_{1,16}$=3.15, P=0.09).

Final harvest

Both shade ($F_{1,134}$=17.90, P=0.0001) and fertilizer ($F_{1,134}$=12.39, P=0.0006) treatments resulted in significant increases in *Solidago* height (Fig. 2). This response was greatest in replicates that received both shading and fertilizer addition (LSM, P=0.001). Shading significantly increased *Solidago* leaf number ($F_{1,134}$=5.67, P=0.01), while fertilization had no effect on leaf number. Fertilization resulted in a 38% increase in *Solidago* biomass relative to controls ($F_{1,134}$=12.02, P=0.0007). Shading alone did not result in a significant increase in biomass. The greatest biomass was found in replicates receiving both shade and fertilizer (LSM, P=0.005). *Ammophila* leaf number increased significantly in response to shading ($F_{1,145}$=4.52, P=0.03), but not in response to fertilizer addition. Neither treatment resulted in significant changes in plant height or dry biomass. Due to the low number of flowering individuals available for harvest (n=1 or 0 in several cases due to low frequency of flowering combined with predation by rodents that removed entire inflorescences), the flower production results are reported graphically (Fig. 3) without statistical comparisons. *Solidago* flower production was greatest in the two fertilizer treatments. No flowering individuals were available for harvest from the control treatment receiving neither shading nor fertilizer addition. *Ammophila* flower production was 2–3 times greater in the shaded treatments than in controls and highest in the treatment receiving both shade and fertilizer.

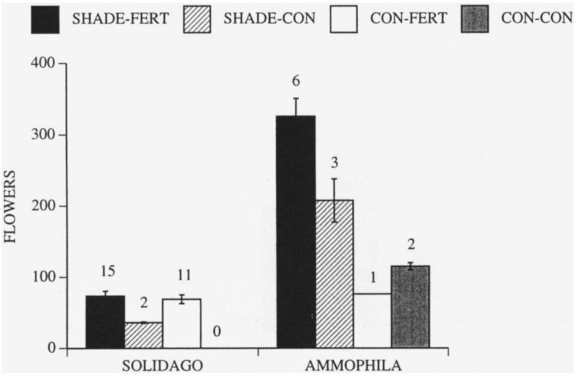

Fig. 3 Average flower production ($\bar{x}\pm$SE) by *Ammophila* and *Solidago* in the shade-fertilizer experiment. The *numbers* of plants measured are indicated *above each bar*

Physiology

Solidago photosynthetic rates in fertilizer treatments were 23% lower than in control treatments ($F_{1,96}$=9.22, P=0.003), while there were no reductions in photosynthesis in response to shade treatments (Fig. 4). Transpiration rate, however, was lowered by 22% by both shade ($F_{1,96}$=4.09, P=0.04) and fertilizer ($F_{1,96}$=13.30, P=0.0004) treatments. There were no differences in wa-

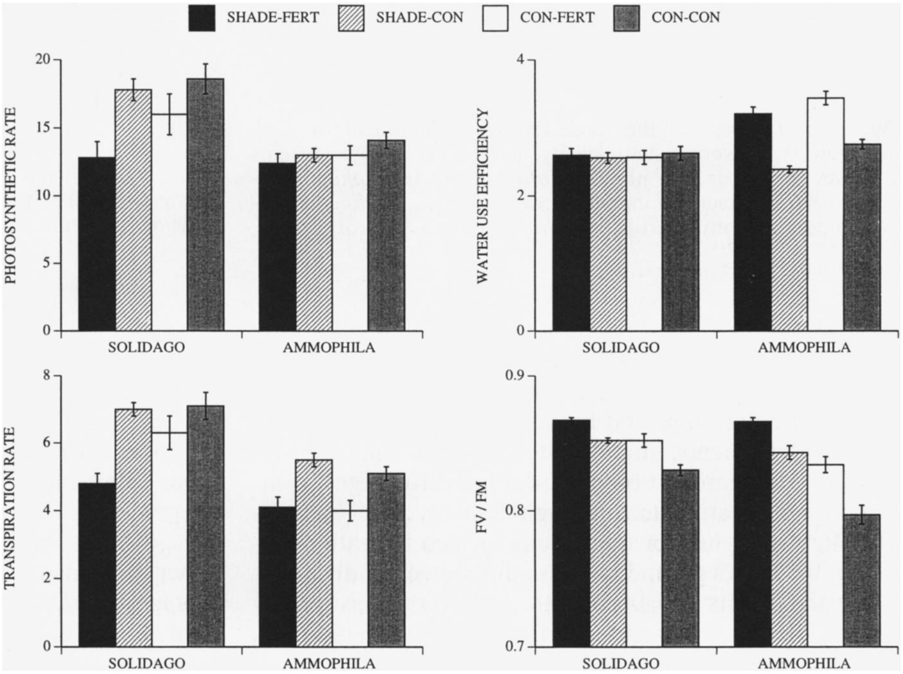

Fig. 4 Average ($\bar{x}\pm$SE) photosynthetic rate (μmol CO_2 m^{-2} s^{-1}), transpiration rate (μmol H_2O m^{-2} s^{-1}), water use efficiency (photosynthesis/transpiration), and photosystem efficiency (F_v/F_m) for *Solidago* and *Ammophila* in the shade-fertilizer experiment

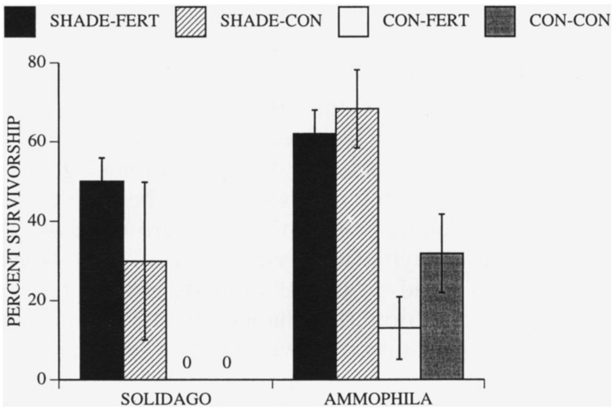

Fig. 5 Survivorship of *Solidago* and *Ammophila* seedlings ($\bar{x}$±SE) transplanted to each treatment of the shade-fertilizer experiment

ter use efficiency for *Solidago* in response to any of the treatments. Photosynthetic efficiency, as measured by F_v/F_m ratios, increased markedly in response to both the shade and fertilizer treatment ($F_{1,156}$=26.60, P=0.0001 each effect). There was no effect of shade or fertilizer treatments on photosynthetic rate in *Ammophila* (Fig. 4). Transpiration rate for *Ammophila* was 15% lower in fertilizer treatments than in controls ($F_{1,95}$=20.39, P=0.0001). Shading had no detectable effect on transpiration rate. Water use efficiency increased significantly in response to both shading ($F_{1,95}$=5.12, P=0.02) and fertilizer addition ($F_{1,95}$=32.15, P=0.0001). F_v/F_m for *Ammophila* was significantly higher in both the shade ($F_{1,156}$=50.37, P=0.0001) and fertilizer treatments relative to controls ($F_{1,156}$=28.29, P=0.0001 each effect). *Ammophila* midday xylem water potentials were higher (less negative) by 12% in the shade ($F_{1,158}$=46.49, P=0.0001) and by 5% in the fertilizer ($F_{1,158}$=7.10, P=0.008) treatments relative to controls.

Seedling survival

Survival of marked natural *Solidago* seedlings was highest in Shade-Fertilizer (55%, n=9) treatments followed by Control-Control (44%, n=9), Shade-Control (25%, n=4), and Control-Fertilizer (0%, n=2) treatments. However, there were no significant differences in seedling survival in shade or fertilizer treatments compared to controls (P>0.05, G-tests). *Ammophila* seedlings survived best in shade treatments with the highest survival rates in Shade-Control (64%, n=48) and Shade-Fertilizer (46%, n=28) replicates and lower survival rates in Control-Control (15%, n=45) and Control-Fertilizer (0, n=30) replicates. Shade and fertilizer treatments were each responsible for increased *Ammophila* seedling survival (P<0.05, G-test). The different treatment responses by the two species may be due to the low sample sizes for *Solidago* seedlings. The survival of transplanted *Solidago* and *Ammophila* seedlings was greatly increased by the shade treatments (P<0.05; Fig. 5), but was not effected by fertilizer addition. *Solidago* seedlings in shade treatments had a 40% survival rate, while no unshaded seedlings survived. Similarly, beachgrass seedlings in shade treatments had a 3 times higher survival rate than controls.

Discussion

The results support the hypothesis that *Myrica* shrubs facilitate growth, reproductive output, and seedling recruitment in *Solidago* and *Ammophila* living beneath shrub canopies. Comparisons between individuals growing beneath shrubs and outside shrubs indicate that growth, likelihood of flowering, flower production, and seed production are consistently higher beneath shrubs. Plants growing in association with shrubs exhibit significantly higher photosystem efficiencies (F_v/F_m), higher midday xylem water potentials, and lower transpiration rates.

The experimental results indicate that shading by *Myrica* canopies and higher nutrient availability beneath shrubs may be responsible for the observed facilitation. Plants growing outside shrubs in the open dune are subjected to potentially lethal soil temperatures, intense solar- and wind-driven water loss by transpiration and evaporative water loss of soil water, wind-driven sand movement, and low nutrient availability. Shading by shrubs maintains low soil temperatures and buffers plants against midday water stress. These factors combined with the greater availability of nutrients beneath shrubs enables plants to grow larger and to allocate energy to reproduction. Although this study was not designed to examine herbivory, the lower incidence of herbivorous insect larvae in the flower heads of *Solidago* growing beneath shrubs suggests associational defenses (Atsatt and O'Dowd 1976) as another benefit to growing beneath shrubs. These factors and other shrub-generated influences may have different effects on each species and may vary in importance at different stages in their life cycles.

Implications for seedlings

Differences in seedling survival beneath and outside shrubs were not detected for naturally occurring seedlings of either *Ammophila* or *Solidago*. Seed germination on Cape Cod dunes may begin in early spring, so it is possible that the experiment was initiated after much of the selection on seedling survival had taken place, especially if the mortality risk is highest in the first few days or weeks of life (Brewer 1998). The large variation in seedling survival between shrubs could be attributed to differences in leaf litter between areas. However, the survival of transplanted seedlings of both species increased significantly in response to artificial shading and the survival of naturally occurring *Ammophila* seedlings increased in response to both shading and nutrient enrichment. The density of *Solidago* seedlings was over 100 times greater beneath shrubs and may be due to shrubs acting as seed traps, high seed production and short distance dispersal by plants living beneath shrubs, relaxed selection pressures beneath shrubs, or a combination of these. Even if there is not a survival advantage to being located beneath a shrub canopy, the vast difference in numbers of *Solidago* seedlings will likely result in greater recruitment beneath shrubs. High soil temperatures have been shown to exert a strong selective force on seedling recruitment on sand dunes by inhibiting seed germination (Seneca and Cooper 1971), inducing thermal stress in seedlings, and accelerating evaporative water loss from soil and plants (Maun 1994). Soil surface temperatures were significantly lower beneath shrubs. Together these results indicate that positive interactions with *Myrica* shrubs may have a great influence on seedling recruitment of *Ammophila* and *Solidago*. If seedling recruitment on the majority of the sand dune is restricted by unfavorable environmental conditions, then areas beneath *Myrica* "nurse" shrubs may represent one of the few safe sites for recruitment of new individuals into the community.

Implications for long-lived perennials

Most of the measurements in this study were conducted on mature plants of long-lived perennial species. *Solidago* has slowly spreading storage rhizomes while *Ammophila* has extensive rhizomes capable of spreading over several meters (Krajnyk and Maun 1981; Maun 1985). Due to their growth habits and longevity, the positive interactions with *Myrica* may have long-term implications for the perennial plants involved. Differences in belowground biomass exhibited by *Solidago* transplants suggests that plants may respond to increased availability of nutrients by sequestering them in the rhizome until a critical amount is available for flowering. Perennial plants are able to store nutrients and energy for one or more growing seasons for future allocation to reproductive structures (Harper 1977). That this occurs in *Solidago* is supported by the fact that the majority of plants at the study site do not flower in any given year and those that do are considerably larger than their non-flowering counterparts. Similarly, *Solidago* grown from seed and raised in the greenhouse under nutrient-poor conditions failed to flower for 3 years and remained as low lying rosettes, but when given fertilizer the plants grew to be over 1 m tall and flowered within 3 months (author, personal observation). For both *Solidago* and *Ammophila*, individuals growing beneath shrub canopies produce many more flowers than plants outside shrubs and, as a result, are likely to be making disproportionate contributions to future generations. This effect may be accentuated if their seeds also land beneath the shrubs. The benefits to *Ammophila* may extend beyond the ramets growing beneath shrubs. Presumably many of the ramets studied were connected by rhizomes to ramets growing outside shrubs. Many studies of clonal plants have demonstrated physiological integration of ramets and the ability to share carbon, nutrients, and water across resource gradients (Pitelka and Ashmun 1985). Therefore, the more robust and nitrogen-rich ramets of *Ammophila* may be able to translocate resources to sister ramets growing outside shrubs. The perennials may also be able to outlive the shrub under which they are growing. At the study site the decaying woody remains of dead *Myrica* shrubs can be found as well as mounds of sand that appear to have been formerly inhabited by *Myrica* (7 years of personal observation by the author). In both instances lush growth of *Ammophila* and *Solidago* form a stark contrast with the surrounding sparsely vegetated dune.

Nitrogen enrichment

Soil nitrogen levels are higher beneath shrubs compared to surrounding areas outside shrubs and plants beneath shrubs have higher tissue nitrogen levels. The greenhouse experiment demonstrated that *Solidago* seedlings raised in soil collected from beneath shrubs grew to be 10 times larger than seedlings raised in soil from outside shrubs. Fertilizer addition in the field greatly increased the likelihood that *Solidago* would flower. Increased nitrogen availability associated with *Myrica* shrubs is the result of nitrogen fixation by symbiotic bacteria residing in root nodules. High rates of nitrogen fixation have been documented for *M. pensylvanica* (Morris et al. 1974) and a related species, *M. gale* (Schwintzer 1979). Morris et al. (1974) postulated that nitrogen enrichment by *Myrica* was important for its success during sand dune community succession, but did not examine the effects of soil nitrogen enrichment on other species. The present study indicates that nitrogen enrichment by *Myrica* is also important for successful establishment and growth of two other species in the hostile dune environment. In addition to the interactions described in this paper, wild and cultivated cranberry vines (*Vaccinium macrocarpon*) growing beneath *M. pensylvanica* shrubs exhibit increased height, increased production of upright stems, and decreased fruit production which are symptoms of high soil nitrogen levels (Frank Caruso, U. Massachusetts Cranberry Experimental Station, personal communication). Vitousek et al. (1987) have determined that an introduced species, *M. faya*, increases nitrogen availability in the volcanic soil of Hawaii and may alter subsequent patterns of ecosystem development by excluding native species and accelerating invasion by other exotics (Vitousek and Walker 1989; Walker and Vitousek 1991). Similarly, nitrogen-fixing legumes have been shown to increase soil nitrogen levels and to facilitate seedling growth in other early successional communities (Boring and Swank 1984; Morris and Wood 1989). In general nitrogen-fixing plants have beneficial effects on neighbors in nutrient-poor environments, but these may be offset by competition for other resources such as light and water (Walker and Chapin 1986; Morris and Wood 1989; Chapin et al. 1994).

Negative effects of *Myrica*

In sharp contrast to the present study, several investigators have reported that *M. pensylvanica* and *M. cerifera* have allelopathic properties (Dunevitz and Ewel 1981; Collins and Quinn 1982; Tolliver et al. 1995). They found that growth and germination of other plants were inhibited beneath the shrub canopy or in the leaf litter of *Myrica*. The reasons for such conflicting results between these studies and the present one are unclear, and raise the questions of whether *Myrica* may have positive influences (facilitation) on neighbors under one set of conditions and negative influences (allelopathy, competition) under a different set of conditions. Similarly, is it possible for the *Myrica*-generated environmental modifications to be beneficial to one suite of species and detrimental to other species? Such questions have received inadequate consideration from ecologists. Despite demonstrating allelopathic inhibition by *M. cerifera*, Tolliver et al. (1995) did note that under high-light conditions the growth of pine seedlings increased in *Myrica* soils and leaf litter. Similarly Walker and Vitousek (1991) reported a mix of positive and negative effects of *M. faya* on a native tree species. They also suggest that *M. faya* may facilitate invasion by other exotic species that require nitrogen rich soil for establishment. Callaway and Walker (1997) have reviewed similar examples of co-occurring facilitative and competitive effects and note that "the factors that determine the balance between positive and negative are poorly understood." Taken together, the results of these studies indicate that *Myrica* leaf litter may, at least in some ecosystems, represent a double-edged sword capable of beneficial nutrient enrichment and detrimental allelopathic inhibition. The results of the marked seedling experiment were highly variable between shrubs and may be related to differences in leaf litter depth as well as canopy cover between shrubs. Differences in leaf litter accumulation could also explain the variation in soil nitrogen levels between shrubs and may be associated with potential allelopathic ability or potential shading (mulching) of seedlings. Previous measurements on physiology and growth of *Solidago* and *Ammophila* adults did not reveal differences between shrubs (author, unpublished work). Therefore between shrub differences in leaf litter accumulation and the effects of leaf litter on seedlings should be addressed in future studies.

Environmental stress and facilitative interactions

The results of this study demonstrate that *M. pensylvanica* facilitates the growth and reproduction of two of its immediate neighbors. This is contrary to the competitive dominance and suppression relationship between canopy and understory species that might be predicted from existing ecological theory. Such predictions have dominated ecological study for much of the past 30 years; however, recent reviews have pointed out the need to more fully understand the importance of facilitative interactions in shaping natural communities (Callaway 1995). Sand dune communities are highly stressful, characterized by dry nutrient-impoverished soils with patchy nutrient distributions, high summer temperatures, salt spray, and shifting soils (Barbour et al. 1984). *Myrica* shrubs influence their immediate environment by shading soils and enriching soil nutrients. They also aid in dune stabilization by trapping sand and creating airfoil-shaped mounds beneath the canopy (author, personal observation). The results from this study support recent proposals by Bertness and Shumway (1993), Bertness and Callaway (1994), and Bertness and Leonard (1997) that positive interactions between species may be particularly common in communities characterized by physiologically stressful environmental conditions.

Acknowledgements I would like to thank Tony Baptista, Betsy Dean, Dan Shumaker, and Lindsay Dudbridge for their help in the field and laboratory, David Crary, David Manski, and Brenda Boleyn for sharing their knowledge of CCNS, and Barbara Brennessel for housing. Comments by Mark Bertness, Steve Brewer, Aaron Ellison, and John Kricher greatly improved the manuscript. The research was supported by grants from the Nickerson Conservation Fellowship, the National Park Service, and Wheaton College. I would like to thank Mark Bertness for the use of the IRGA and chlorophyll fluorescence meters which were purchased through grants from the Ecology Program of the National Science Foundation.

References

Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. Science 193:24–29

Barbour MG, DeJong TD, Pavlik BM (1984) Marine beach and dune plant communities. In: Chabot B, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman and Hall, New York, pp 296–322

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol Biol 9:191–193

Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. Am Nat 144:363–372

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Bertness MD, Shumway SW (1993) Competition and facilitation in marsh plants. Am Nat 142:718–724

Boring LR, Swank WT (1984) The role of black locust (*Robinia pseudoacacia*) in forest succession. J Ecol 72:749–766

Brewer JS (1998) Effects of competition and litter on a carnivorous plant, *Drosera capillaris* (Droseraceae). Am J Bot 85:1592–1596

Callaway RM (1995) Positive interactions among plants. Bot Rev 61:306–349

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965

Chapin FS, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol Monogr 64:149–175

Collins BS, Quinn JA (1982) Displacement of *Andropogon scoparius* on the New Jersey piedmont by the successional shrub *Myrica pensylvanica*. Am J Bot 69:680–689

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Cowles HC (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part I: Geographical relations of the dune floras. Bot Gaz 27:95–117

Dunevitz VL, Ewel JJ (1981) Allelopathy of wax myrtle (*Myrica cerifera*) on *Schinus terebinthifolius*. Fla Sci 44:13–20

Ehrenfeld JG (1990) Dynamics and processes of barrier island vegetation. Rev Aquat Sci 2:437–480

Franco AC, Nobel PS (1989) Effect of nurse plants on the microhabitat and growth of cacti. J Ecol 77:870–886

Godfrey PJ,Fowler AM, Stack L (1991) Dune revegetation monitoring: Cape Cod National Seashore (Cooperative agreement CA1600–4-0005 amendment #25 between the University of Massachusetts and National Park Service). National Park Service North Atlantic Regional Office, Boston

Greaves JA, Blair BG, Russotti RM, Law EA, Cloud, NP (1991) Measurement of chlorophyll fluorescence kinetics in photosynthesis research with a new portable microprocessor and computer operated instrument. In: CF-1000 chlorophyll fluorescence measurement system instruction manual. P.K. Morgan Instruments, Andover, pp 21–39

Harper JL (1977) Population biology of plants. Academic Press,: London

Keddy PA (1981) Experimental demography of the sand dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. J Ecol 69:615–630

Krajnyk I, Maun MA (1981) Vegetative reproduction in the juvenile phase of *Ammophila breviligulata*. Can J Bot 59:883–892

Maun MA (1985) Population biology of *Ammophila breviligulata* and *Calamovilfia longifolia* on Lake Huron sand dunes. I. Habitat, growth form, reproduction, and establishment. Can J Bot 63:113–124

Maun MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111:59–70

Morris M, Eveleigh DE, Riggs SC, Tiffney WN (1974) Nitrogen fixation in the bayberry (*Myrica pensylvanica*) and its role in coastal succession. Am J Bot 61:867–870

Morris WF, Wood DM (1989) The role of lupine in succession on Mount St. Helens: facilitation or inhibition? Ecology 70:697–703

Niering WA, Whittaker, RH, Lowe CW (1963) The saguaro: a population in relation to environment. Science 142:15–23

Pitelka LF, Ashmun JW (1985) Physiology and integration of ramets in clonal plants. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale University Press, New Haven, pp 399–435

Ranwell DS (1972) Ecology of salt marshes and sand dunes. Chapman and Hall, London

Schwintzer CR (1979) Nitrogen fixation by *Myrica gale* root nodules in a Massachusetts wetland. Oecologia 43:283–294

Seneca ED, Cooper AW (1971) Germination and seedling response to temperature, daylength, and salinity by *Ammophila breviligulata* from Michigan and North Carolina. Bot Gaz 132:203–215

Silander JA, Antonovics J (1982) Analysis of interspecific interaction in a coastal plant community – a perturbation approach. Nature 298:557–560

Tolliver KS, Colley DM, Young DR (1995) Inhibitory effects of *Myrica cerifera* on *Pinus taeda*. Am Midl Nat 133:256–263

Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawai'i: Plant demography, nitrogen fixation, ecosystem effects. Ecol Monogr 59:247–265

Vitousek PM, Walker LR, Whiteaker LD (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804

Walker LR, Chapin FS (1986) Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508–1523

Walker LR, Vitousek PM (1991) An invader alters germination and growth of a native dominant tree in Hawai'i. Ecology 72:1449–1455