Bambi talk, 11 June 1992, BCI

Density dependence and population regulation in tropical forest trees

I. Introduction

A. Tropical forest trees occur at very low densities, even the more abundant ones. If we believe that species composition of these communities are tightly regulated, then we must believe that there are factors that can regulate individual species abundance at very low density. One such factor would be density-reacting herbivores or pathogens, which maintain their prey (individual tree species) at low densities. Janzen and Connell, in 1970 and 1971, explained one way that herbivores in tropical forests could respond to tree density and regulate populations: by selectively destroying seedlings and juveniles close to adults. This hypothesis is a special case of a more general hypothesis about density-dependent population regulation in plants -- that individuals perform worse when they have more neighbors, leading to reduced population growth at high density.

B. I have sought to evaluate the extent of density-dependence in the 50 ha plot as thoroughly as the available data allow. Previous studies have generally only examined seedling survival as a function of distance from a single conspecific adult. By using the large sample size I have sought to be much more precise in defining the distance over which plants can inhibit conspecifics, the sizes that can affect, the sizes effected, and also consider more than the first nearest neighbor. My limitation with the plot data is that I can't work with plants below 1 cm dbh, although I can examine recruitment into the 1 cm class. When I'm done, I will reveal the results of modeling studies aimed at assessing the effect of density-dependence on population growth and population regulation.

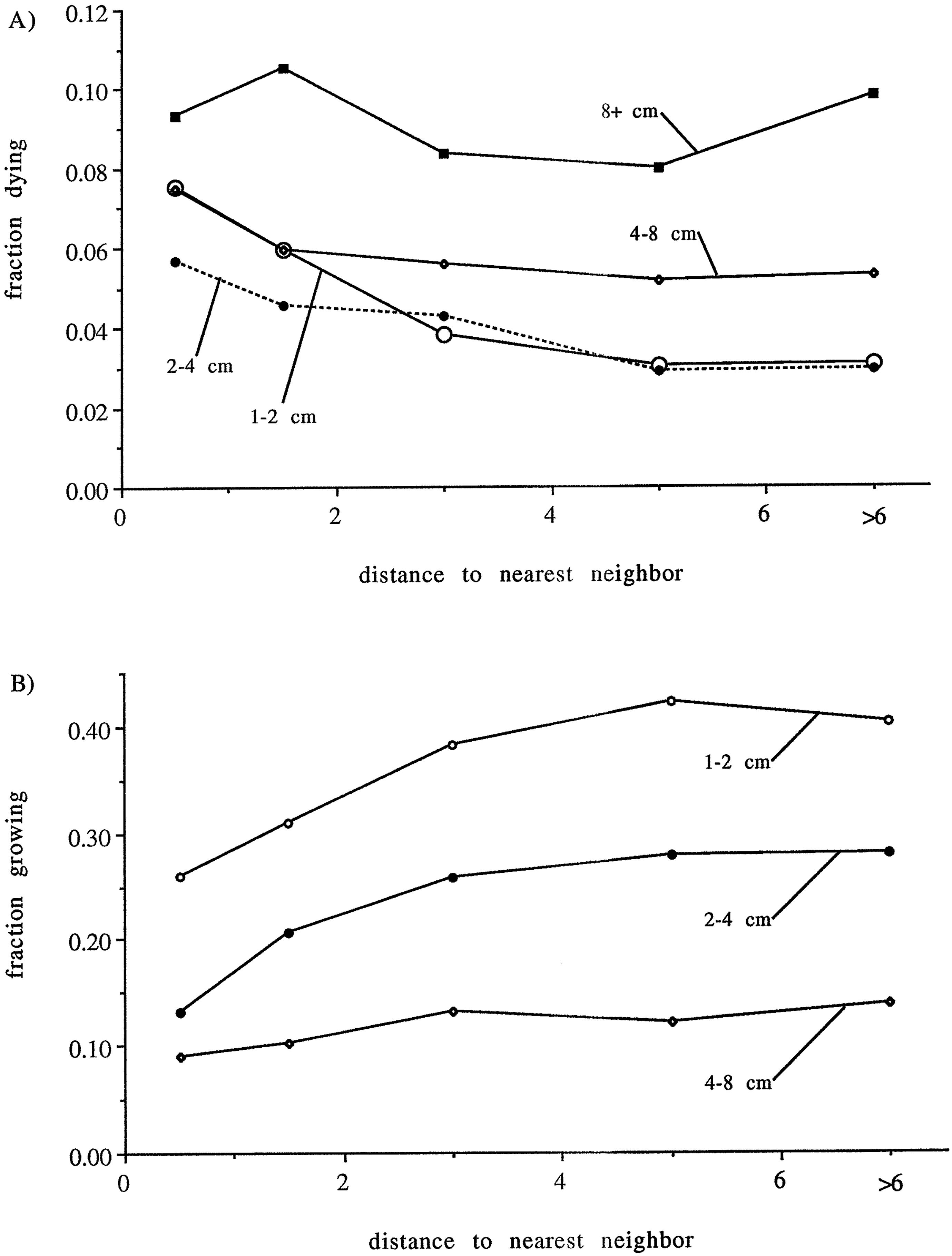
II. Data

A. I will explain the analyses in some detail, giving you the chance to understand the results clearly, including the pitfalls and shortcomings, and perhaps offer suggestions. To do so, I will provide data from one abundant species, where problems with sample sizes are unimportant, then show data from several other species more quickly

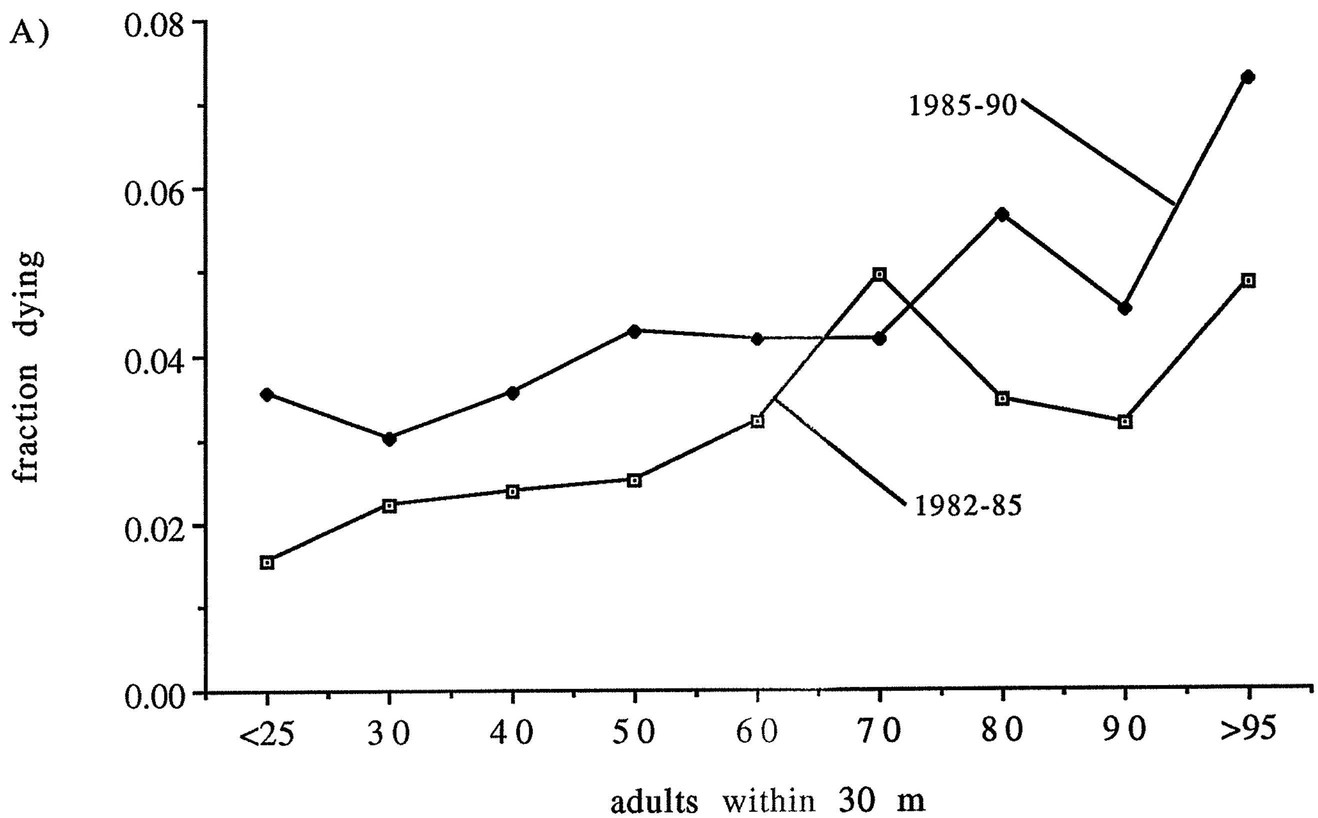
B. Explain methods at blackboard
C. Faramea data, growth, survival, and recruitment, including regional effects; discussing assumption that closer and larger plants have stronger effects
D. Data from other species, discussing small samples and short distances
E. Show summary table

III. Simulations
A. Explain briefly how the population model works, how I ignore spatial patterns
B. Trichilia results, explaining how carrying capacity is affected by density-dependent and density-independent parameters, but how I draw conclusion
C. Summary slide of carrying capacities
D. Summary slides from ESA talk

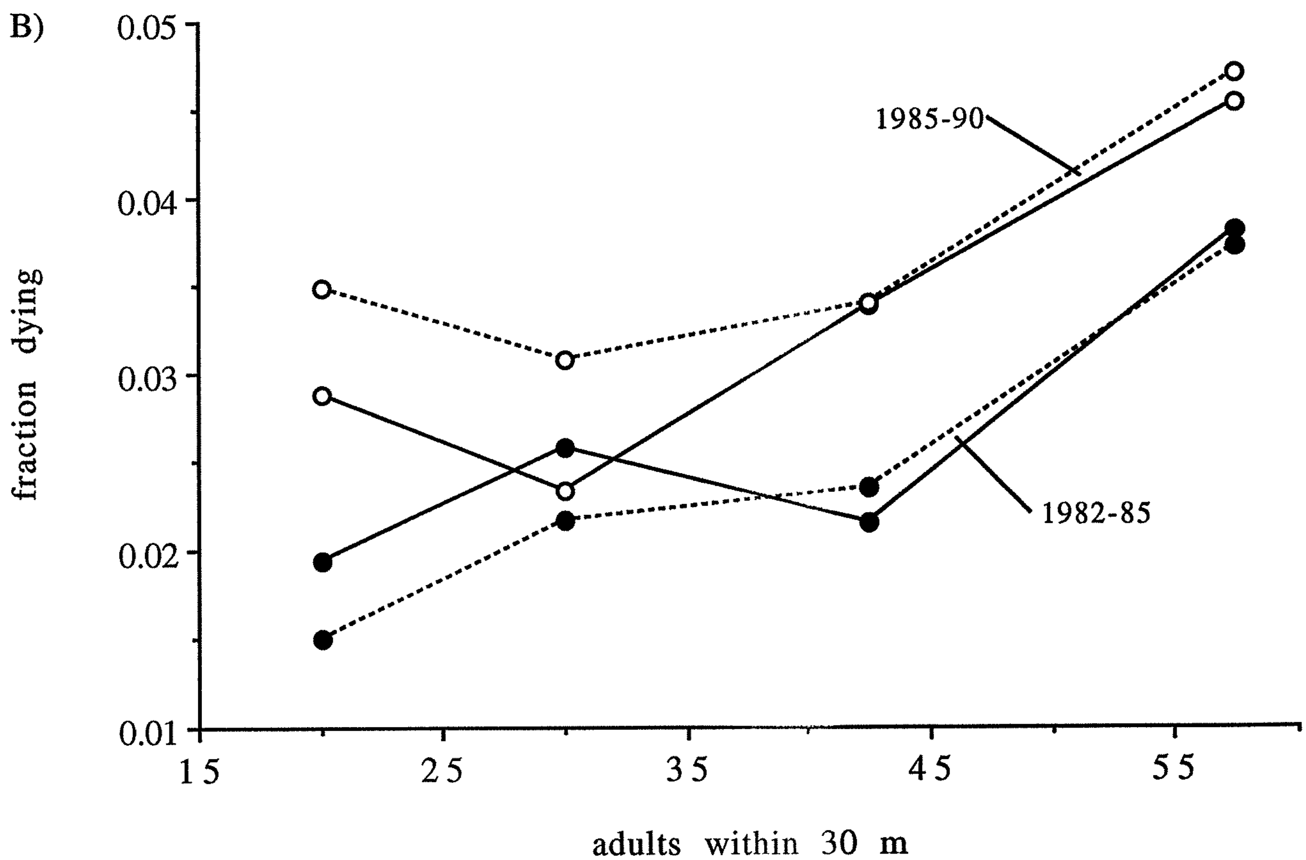
IV. Conclusions
A. I can precisely show the limits of density-dependence at scales below about 1 ha, which was my main purpose
B. We lack data on seedlings and scales above 1 ha
C. It seems likely that the most abundant species have populations strictly limited by herbivores; although only a minority of species, this can play a role in maintaining species diversity (by preventing the Trichilia's from ascending to dominance)
D. Most populations are far below carrying capacity and drifting about in the space of species abundance; maintenance of all these species requires other hypotheses


A)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
fraction dying
8+ cm
4-8 cm
2-4 cm
1-2 cm
0
2
4
6
>6
distance to nearest neighbor
B)
0.40
0.30
0.20
0.10
0.00
fraction growing
1-2 cm
2-4 cm
4-8 cm
0
2
4
6
>6
distance to nearest neighbor

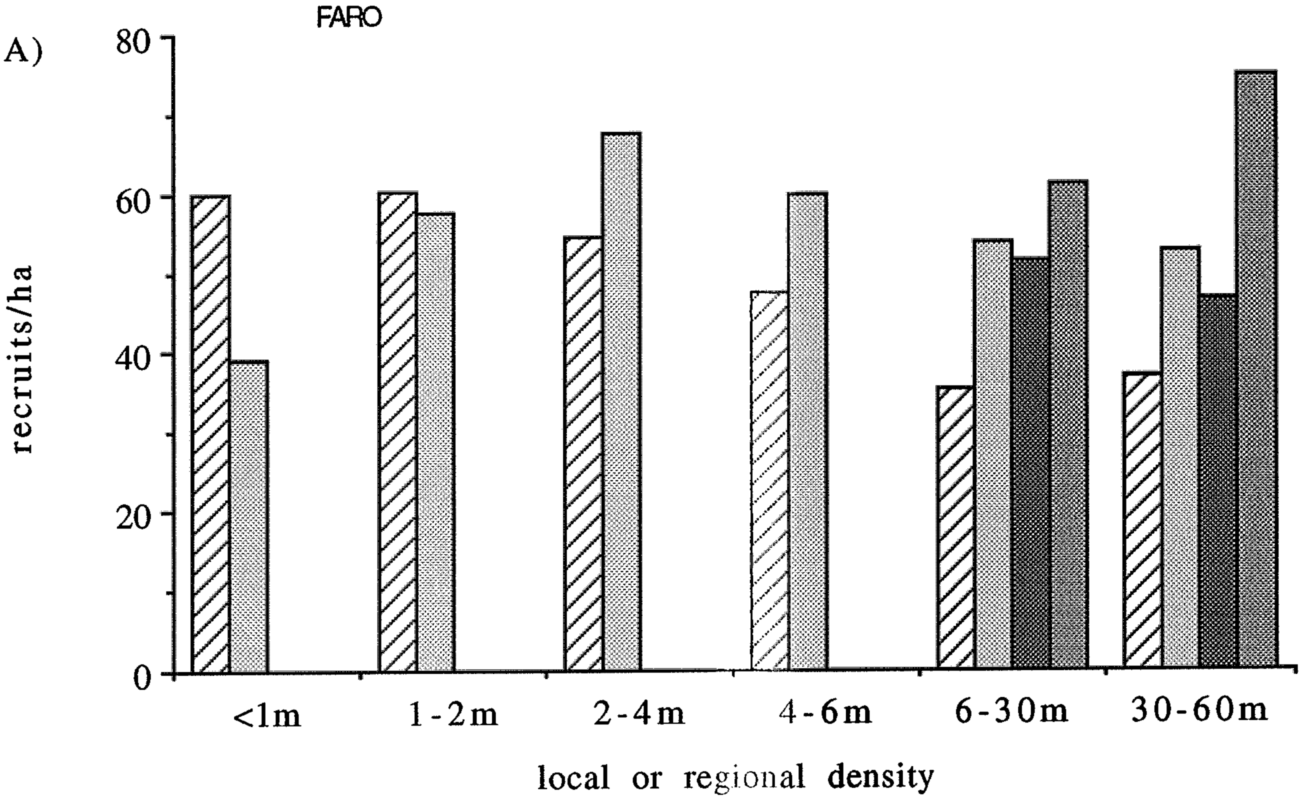
A)


0.08
0.06
0.04
0.02
0.00
fraction dying
1985-90
1982-85
<25
30
40
50
60
70
80
90
>95
adults within 30 m

B)

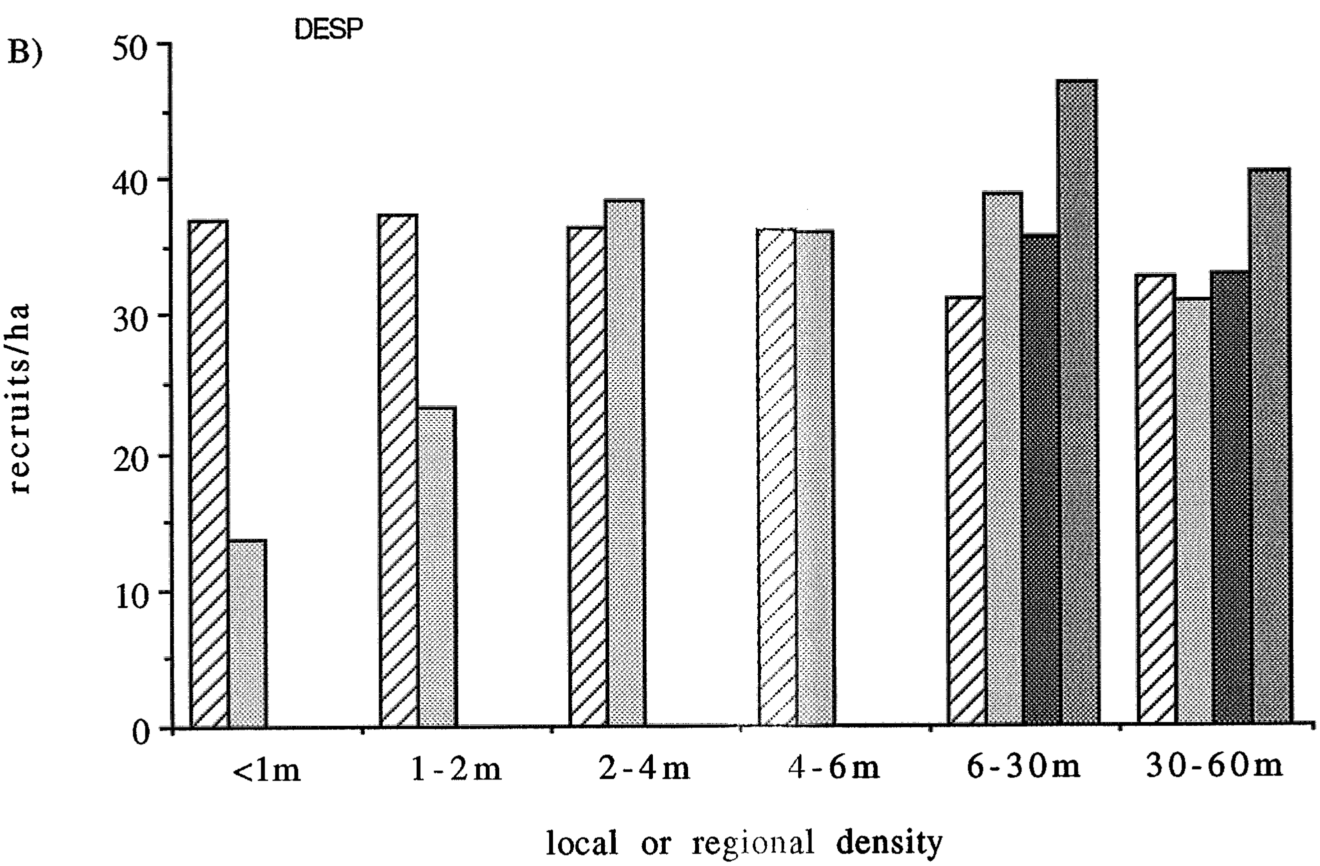

0.05
0.04
0.03
0.02
0.01
fraction dying
1985-90
1982-85
15
25
35
45
55
adults within 30 m

A)



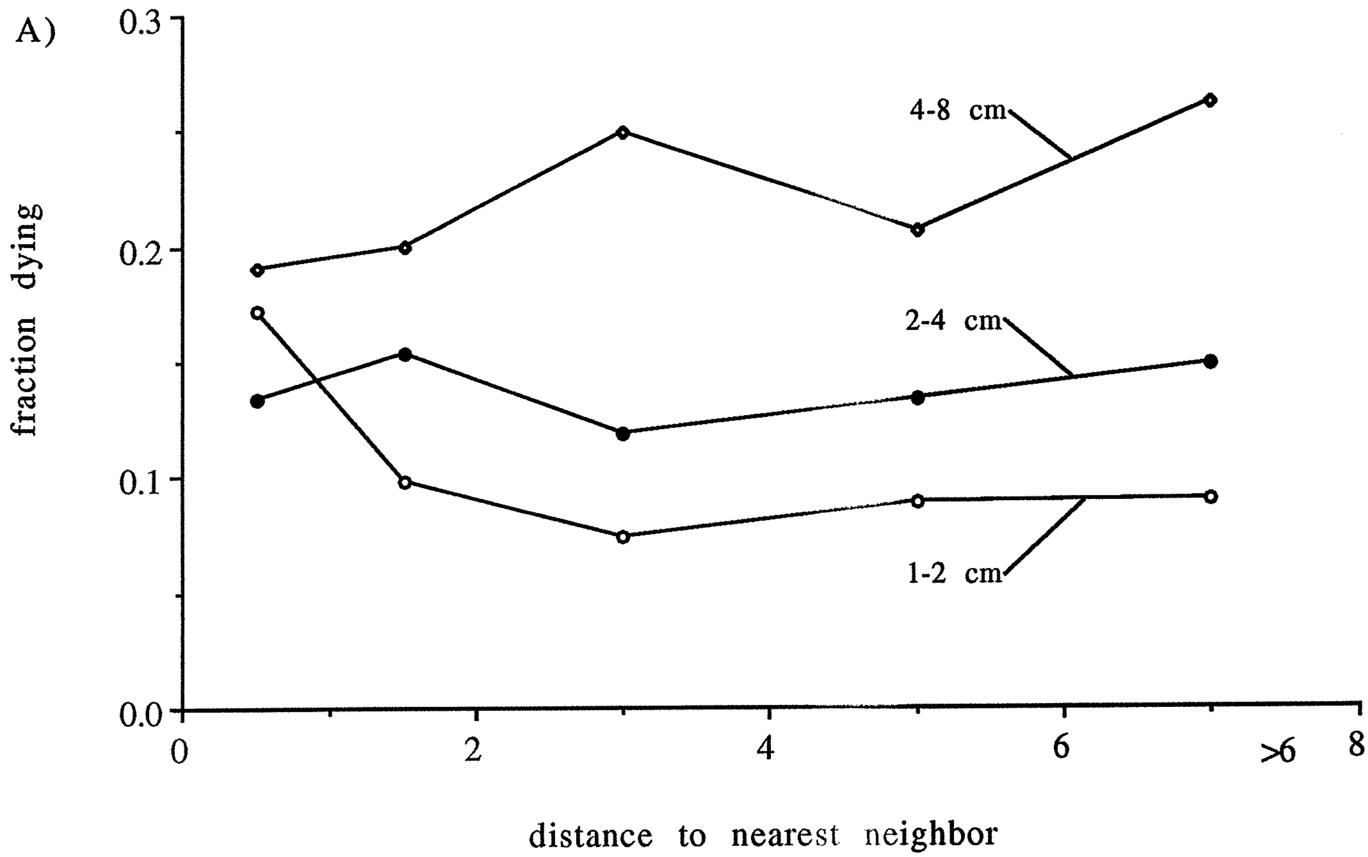
FARO
80
60
40
20
0
recruits/ha
<1m
1-2m
2-4m
4-6m
6-30m
30-60m
local or regional density

B)

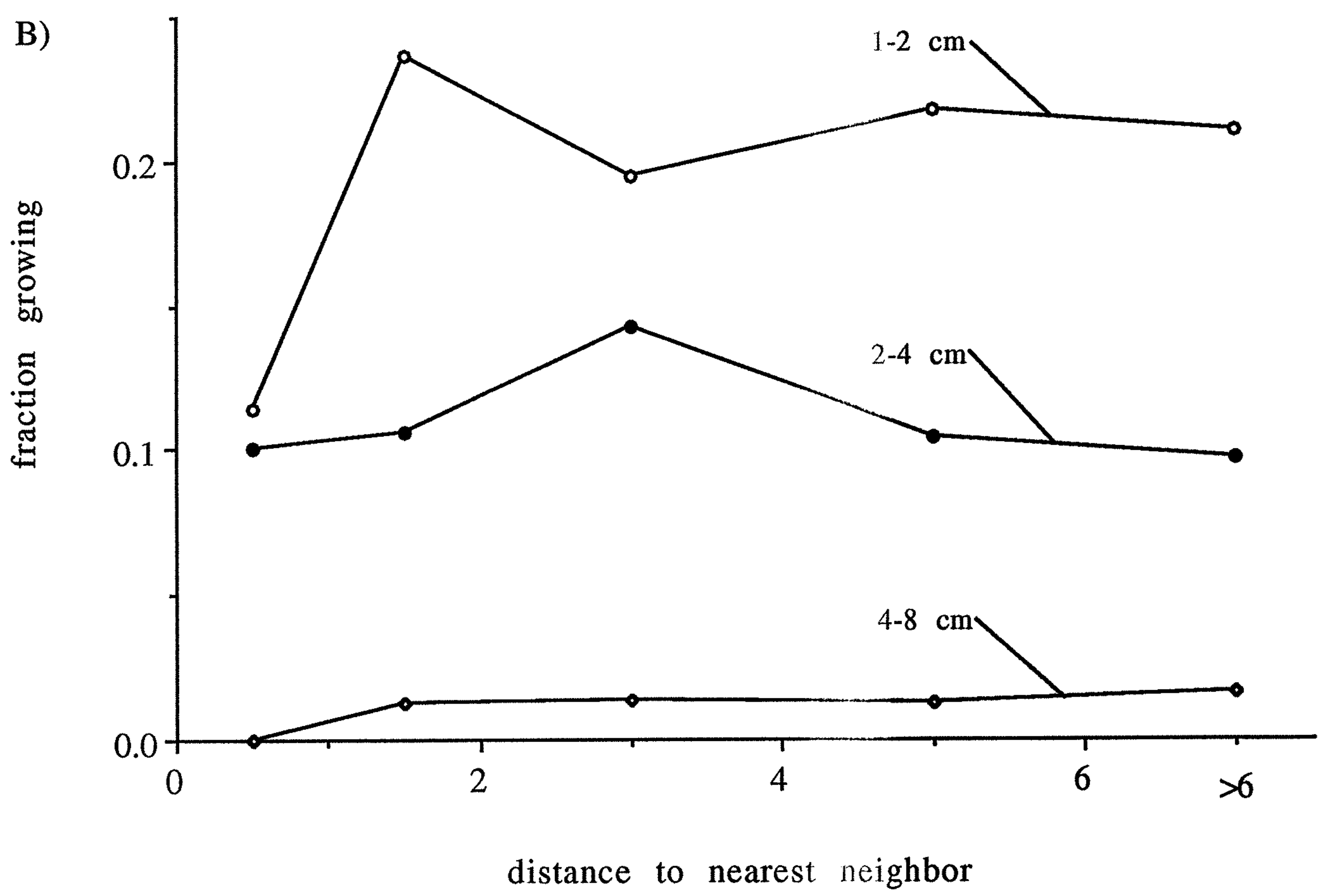


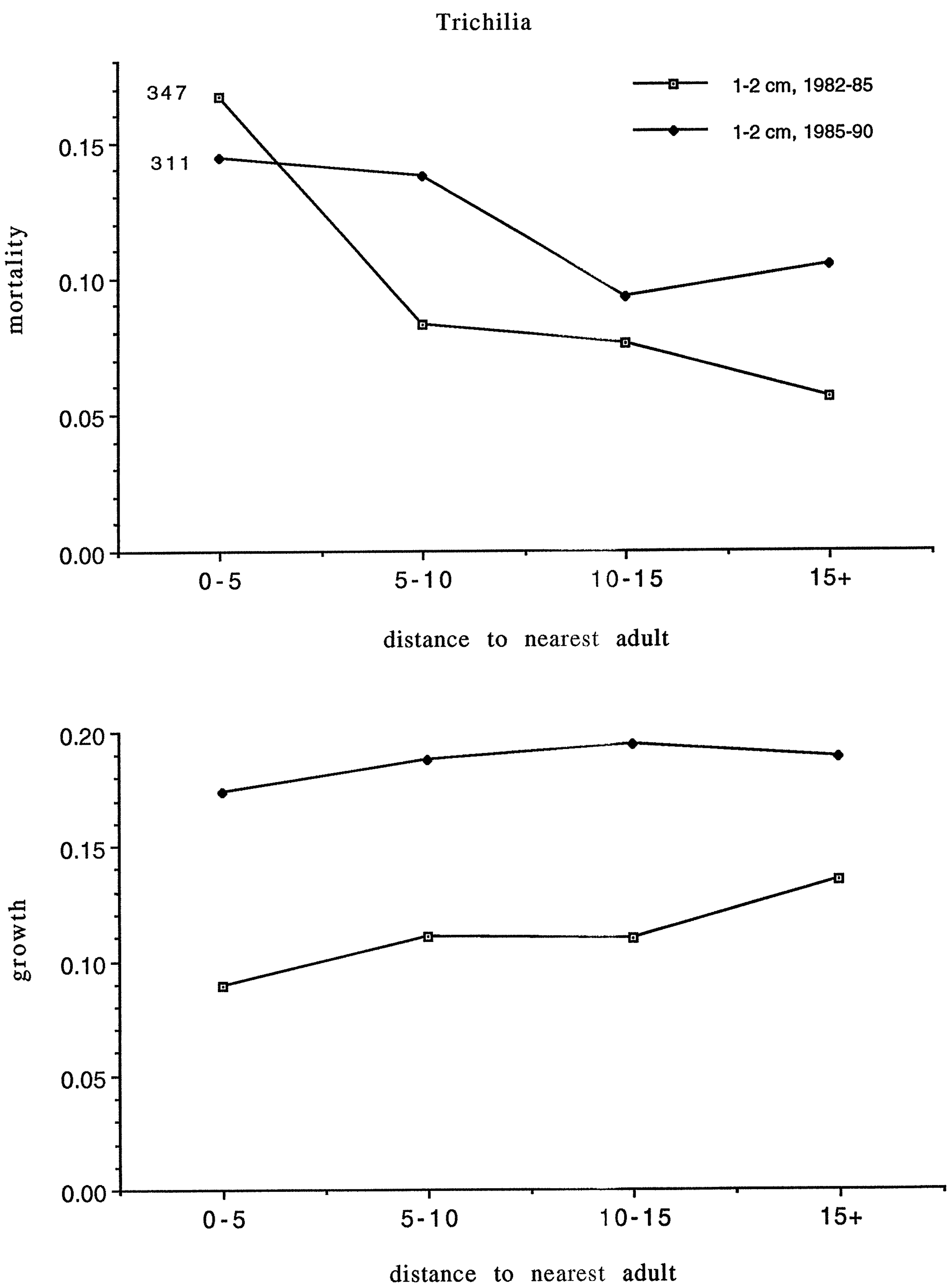
DESP
50
40
30
20
10
0
recruits/ha
<1m
1-2m
2-4m
4-6m
6-30m
30-60m
local or regional density

A)

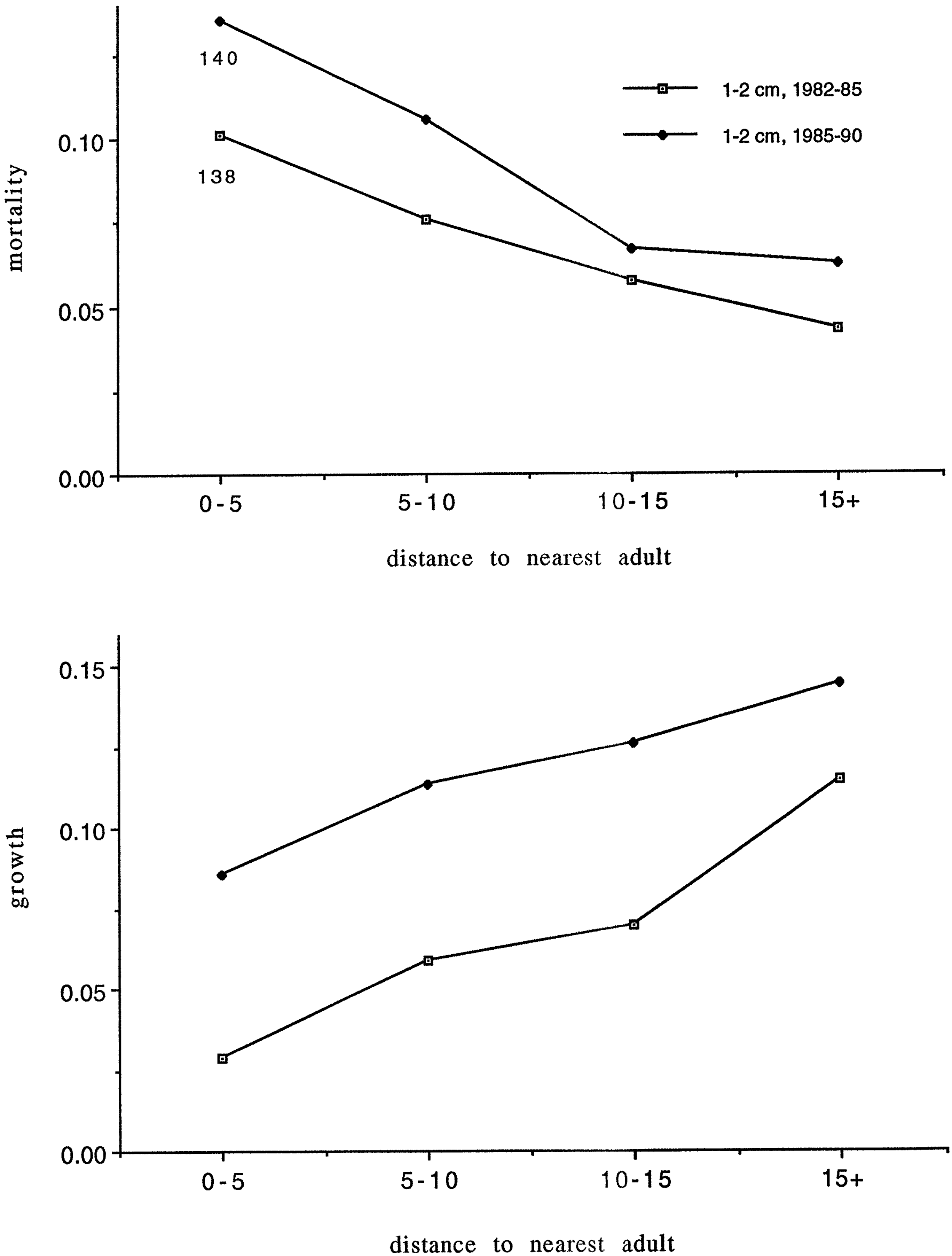

0.3
0.2
0.1
0.0
fraction dying
4-8 cm
2-4 cm
1-2 cm
0
2
4
6
>6
8
distance to nearest neighbor

B)

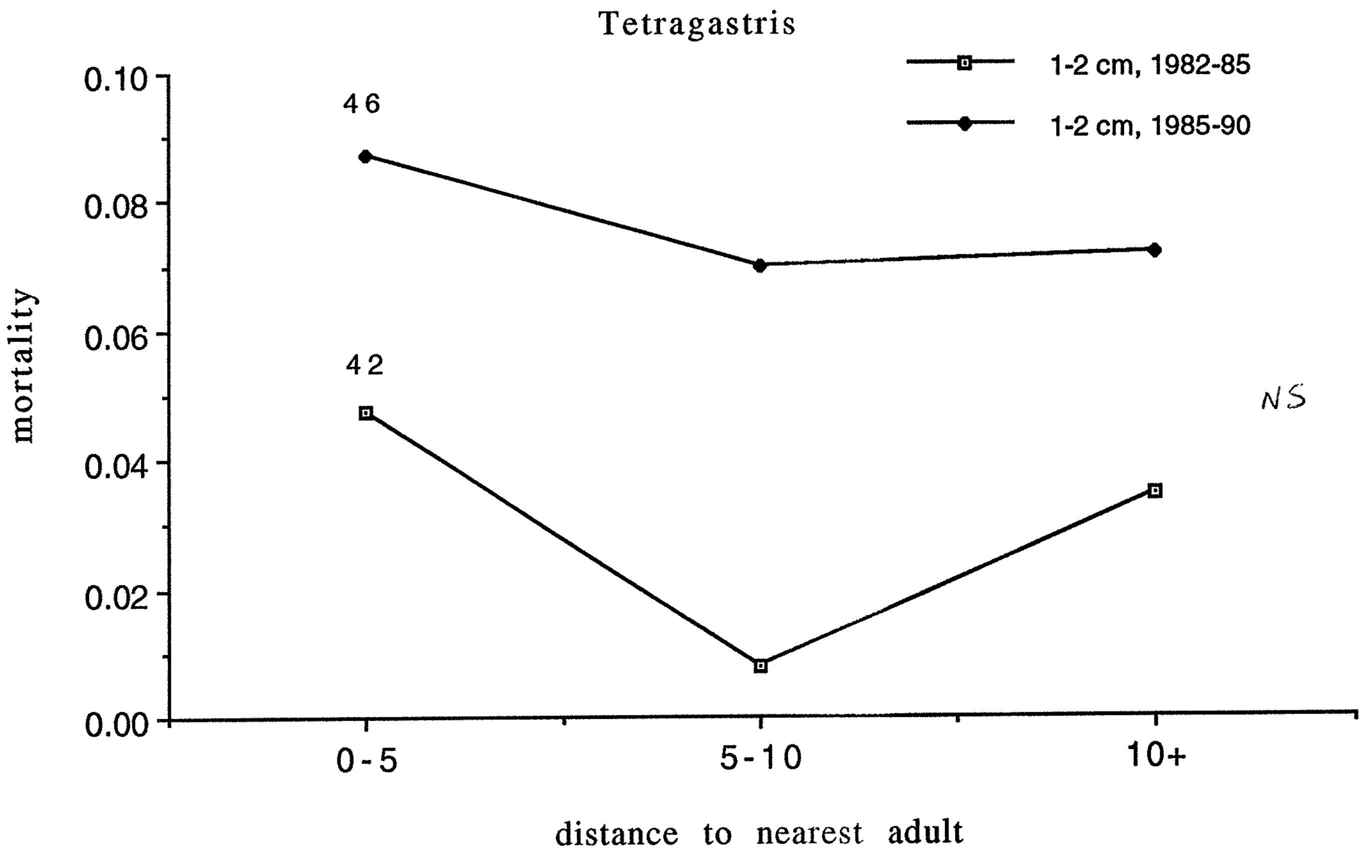

0.2
0.1
0.0
fraction growing
1-2 cm
2-4 cm
4-8 cm
0
2
4
6
>6
distance to nearest neighbor

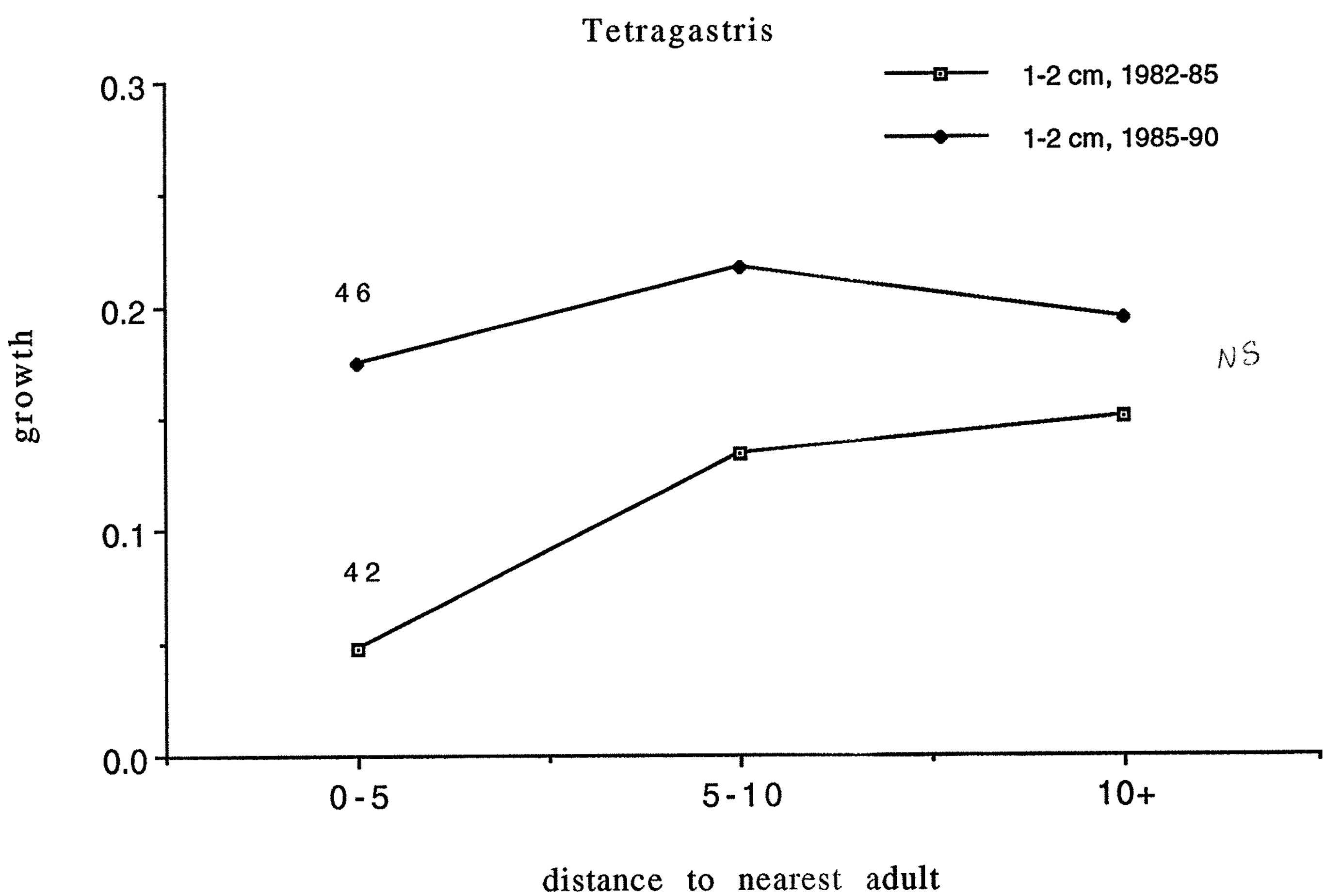

Trichilia
1-2 cm, 1982-85
1-2 cm, 1985-90
347
311
mortality
0.00
0.05
0.10
0.15
0-5
5-10
10-15
15+
distance to nearest adult
growth
0.00
0.05
0.10
0.15
0.20
0-5
5-10
10-15
15+
distance to nearest adult

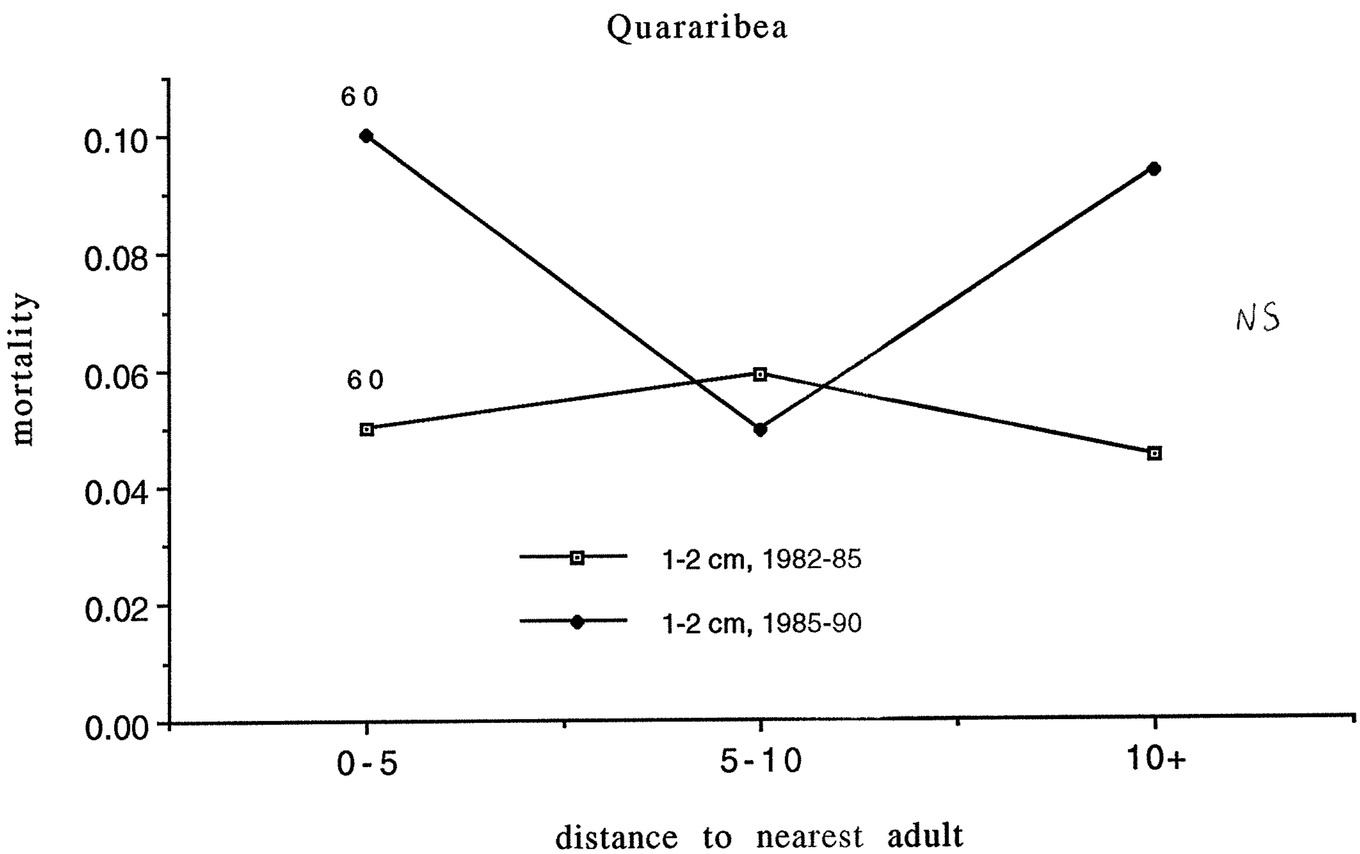
Alseis



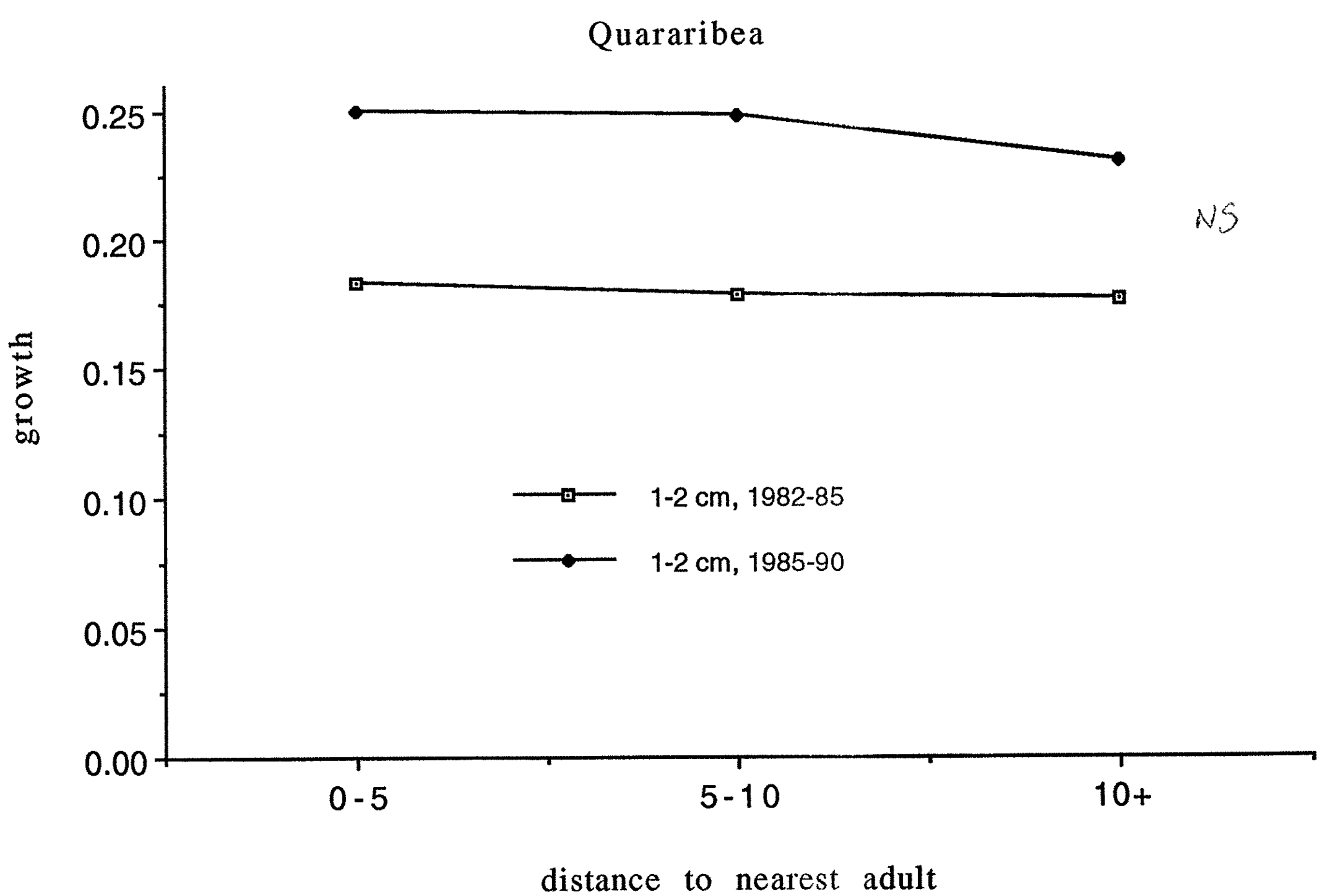
mortality
0.10
0.05
0.00
140
138
1-2 cm, 1982-85
1-2 cm, 1985-90
0-5
5-10
10-15
15+
distance to nearest adult
growth
0.15
0.10
0.05
0.00
0-5
5-10
10-15
15+
distance to nearest adult


Tetragastris
1-2 cm, 1982-85
1-2 cm, 1985-90
mortality
0.10
0.08
0.06
0.04
0.02
0.00
46
42
NS
0-5
5-10
10+
distance to nearest adult


Tetragastris
1-2 cm, 1982-85
1-2 cm, 1985-90
growth
0.3
0.2
0.1
0.0
46
42
NS
0-5
5-10
10+
distance to nearest adult

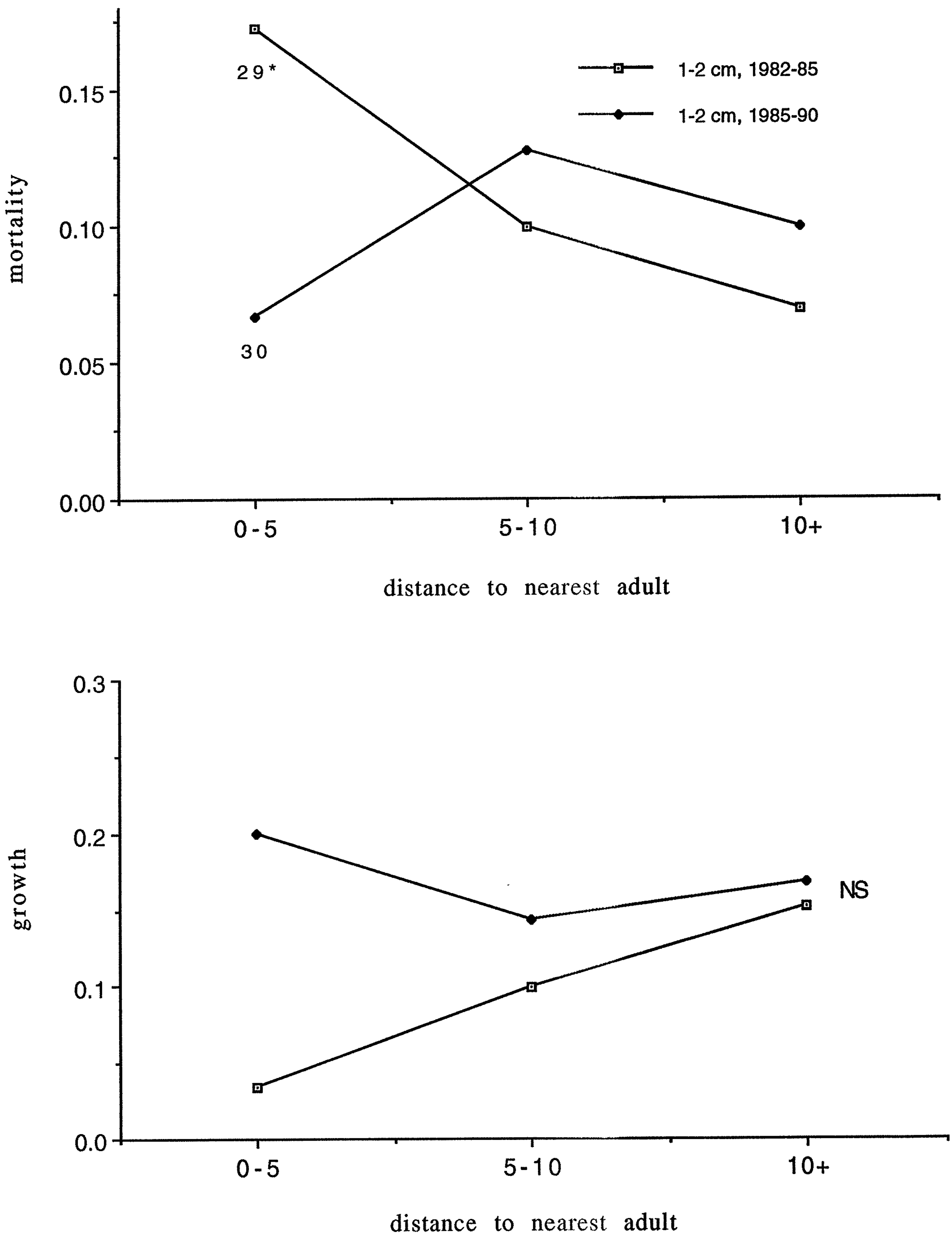


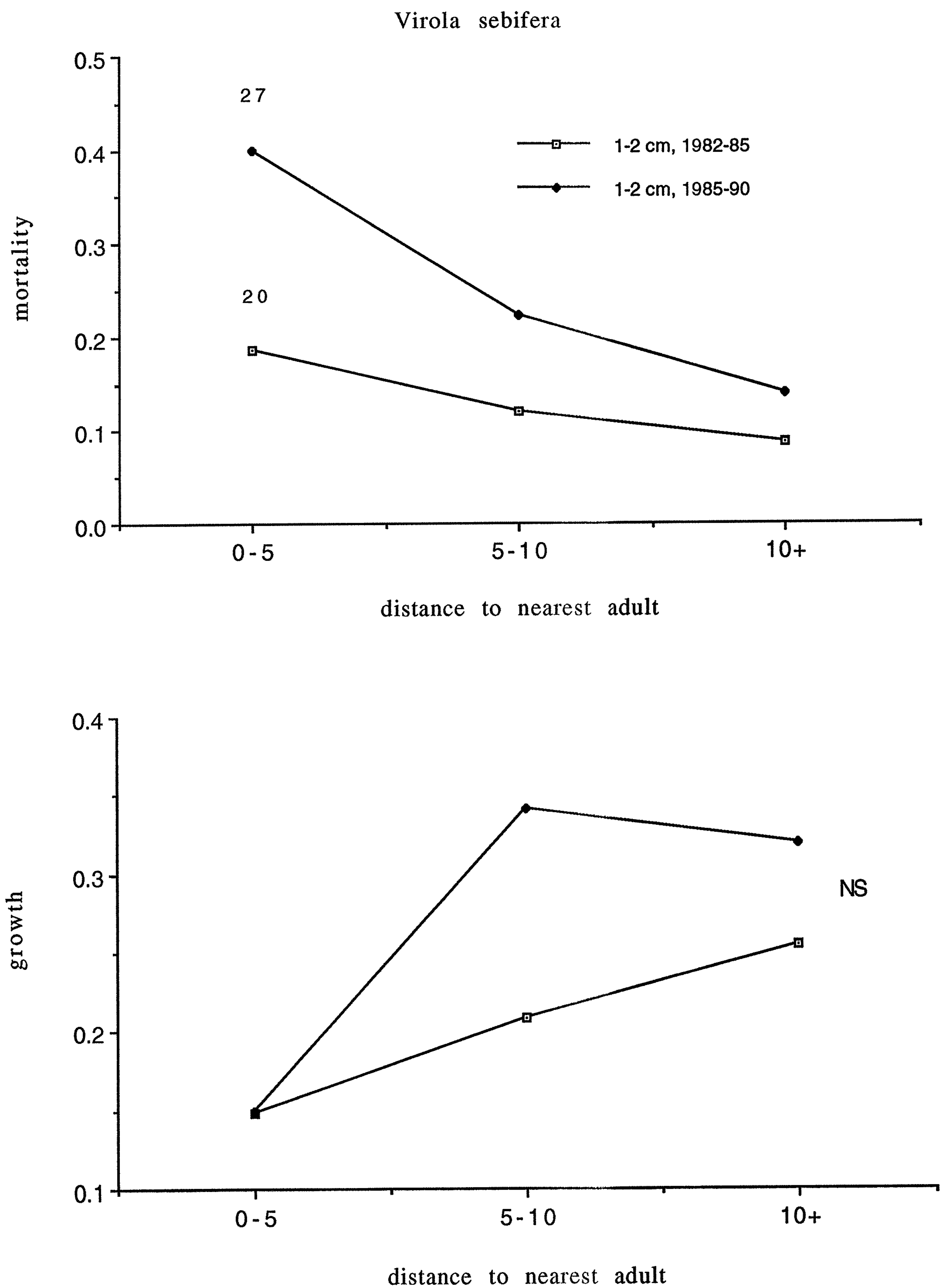
Quararibea
60
0.10
0.08
0.06
0.04
0.02
0.00
mortality
60
NS
1-2 cm, 1982-85
1-2 cm, 1985-90
0-5
5-10
10+
distance to nearest adult



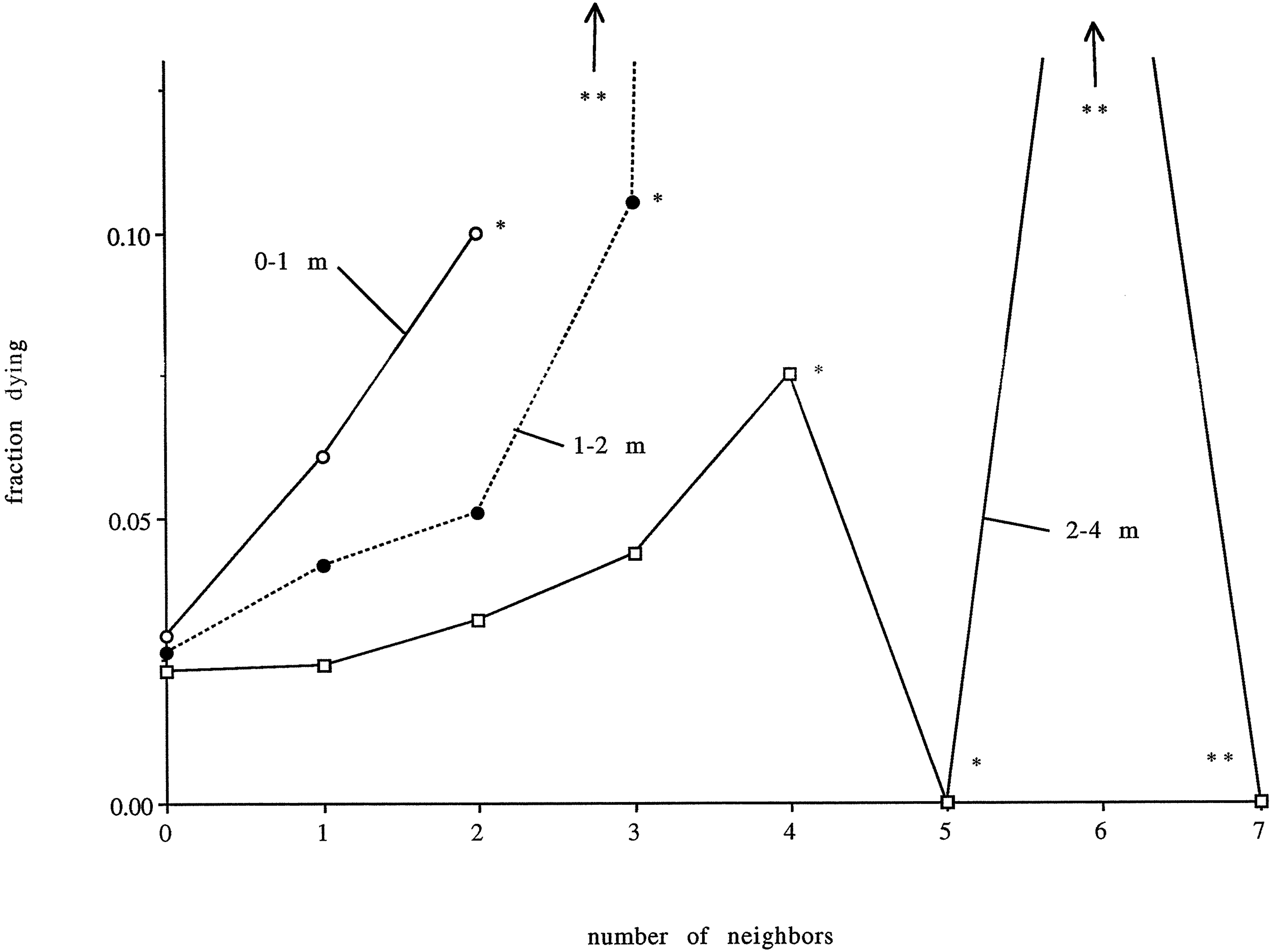
Quararibea
0.25
0.20
0.15
0.10
0.05
0.00
growth
NS
1-2 cm, 1982-85
1-2 cm, 1985-90
0-5
5-10
10+
distance to nearest adult

Beilschmiedia

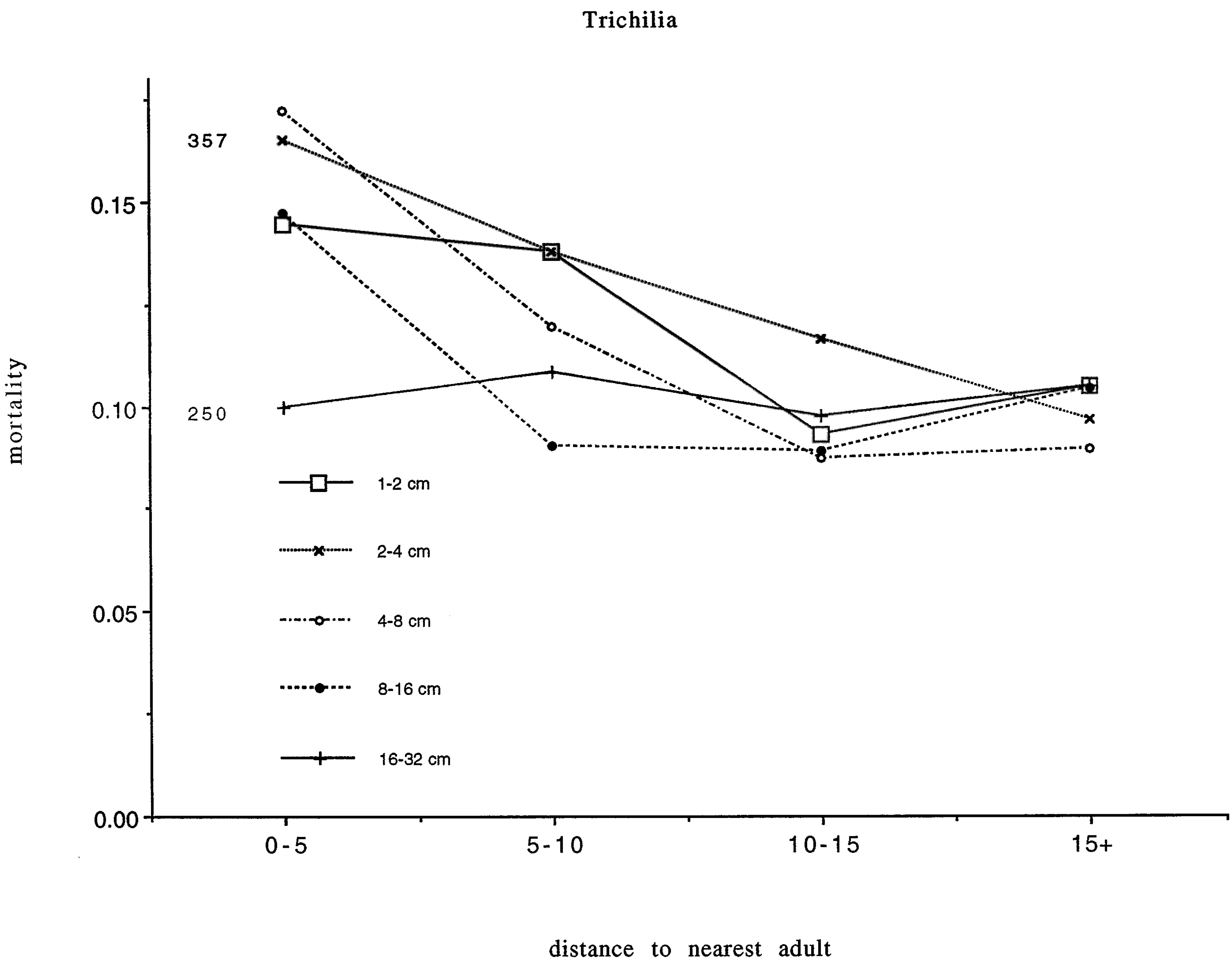


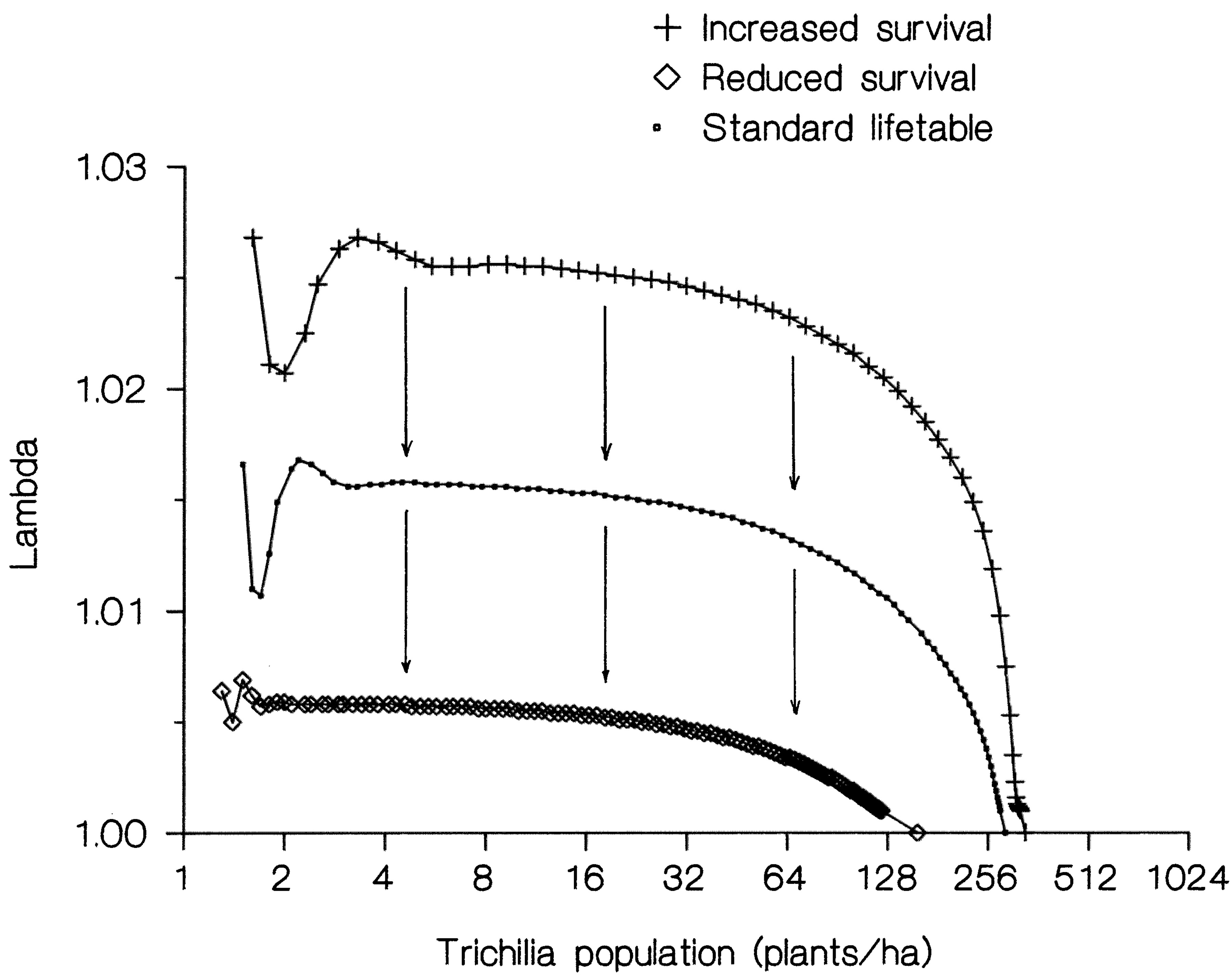


Virola sebifera
mortality
0.5
0.4
0.3
0.2
0.1
0.0
27
20
1-2 cm, 1982-85
1-2 cm, 1985-90
0-5
5-10
10+
distance to nearest adult
growth
0.4
0.3
0.2
0.1
NS
0-5
5-10
10+
distance to nearest adult



fraction dying
0.10
0.05
0.00
0-1 m
1-2 m
2-4 m
*
*
*
*
**
**
**
0
1
2
3
4
5
6
7
number of neighbors


Trichilia
357
0.15
0.10
250
0.05
0.00
mortality
1-2 cm
2-4 cm
4-8 cm
8-16 cm
16-32 cm
0-5
5-10
10-15
15+
distance to nearest adult



Increased survival
Reduced survival
Standard lifetable
1.03
1.02
1.01
1.00
Lambda
1
2
4
8
16
32
64
128
256
512
1024
Trichilia population (plants/ha)

Predicted carrying capacity and observed density

Species	Carrying capacity *	Observed density
Faramea occidentalis	---	539
Trichilia tuberculata	289	266
Desmopsis panamensis	6013	244
Alseis blackiana	389	168

* total plants per hectare, calculated from best estimates of all lifetable parameters and neighborhood effects

Density-dependent population regulation in tropical forest trees?

---Neighborhood effects detectable at the 1 cm stage generally do not extend beyond 10 m from large conspecifics

---Such effects are strong enough to regulate population density, but only for the few most abundant species, with densities above 100 per ha

---At least a few species in the BCI forest have populations regulated by density-dependent factors (seed predators, pathogens, herbivores?)

Density-dependent population regulation in tropical forest trees?

---Neighborhood effects at the seedling stage have been detected as far as 30 m from adults (one species only)

---Such effects appear strong enough to regulate population density as low as 10 per ha

Density-dependent population regulation in tropical forest trees?

---About 1/4 of the BCI forest species (77 of 312) reach a density of 10 per ha

---At least 1%, but maybe as many as 25%, of the trees in the BCI forest are regulated by density-dependent effects

---It is possible that density-dependent factors play a major role in regulating forest diversity

---But I won't know until I see more studies of neighborhood effects on seeds and seedlings, and calculate life tables for more species

Conspecific neighborhood effects on survival and growth of saplings above 1 cm dbh

Species	Effector size	Effected size	Distance effected
Alseis	4+ cm	1-2 cm	0-15 m
Beilschmiedia	4+ cm	1-2 cm	0-5 m
Desmopsis	none		
Faramea	1+ cm	1-8 cm	0-6 m
Guatteria	none		
Hirtella	none		
Poulsenia	none		
Prioria	16+ cm	1-4 cm	0-7 m
Proteum	none		
Tetragstris	16+ cm	1-4 cm	0-7 m
Trichilia	4+ cm	1-8 cm	0-15 m
Virola	16+ cm	1-2 cm	0-7 m

* Many positive associations at 0-10 m