Teórica 6:
Interacciones interespecíficas:

Herbivoría y mutualismo

Teórica 6: Esquema conceptual

- Herbivoría:
  - Mecanismos de defensa de las plantas:
    - Compuestos secundarios
    - Mutualismos de defensa
    - Defensas mecánicas: dureza y espinas
    - Sobrecompensación
  - Dinámica poblacional
- Mutualismo
  - Tipos de mutualismos
  - Dinámica poblacional
  - Interacciones entre herbivoría y mutualismo

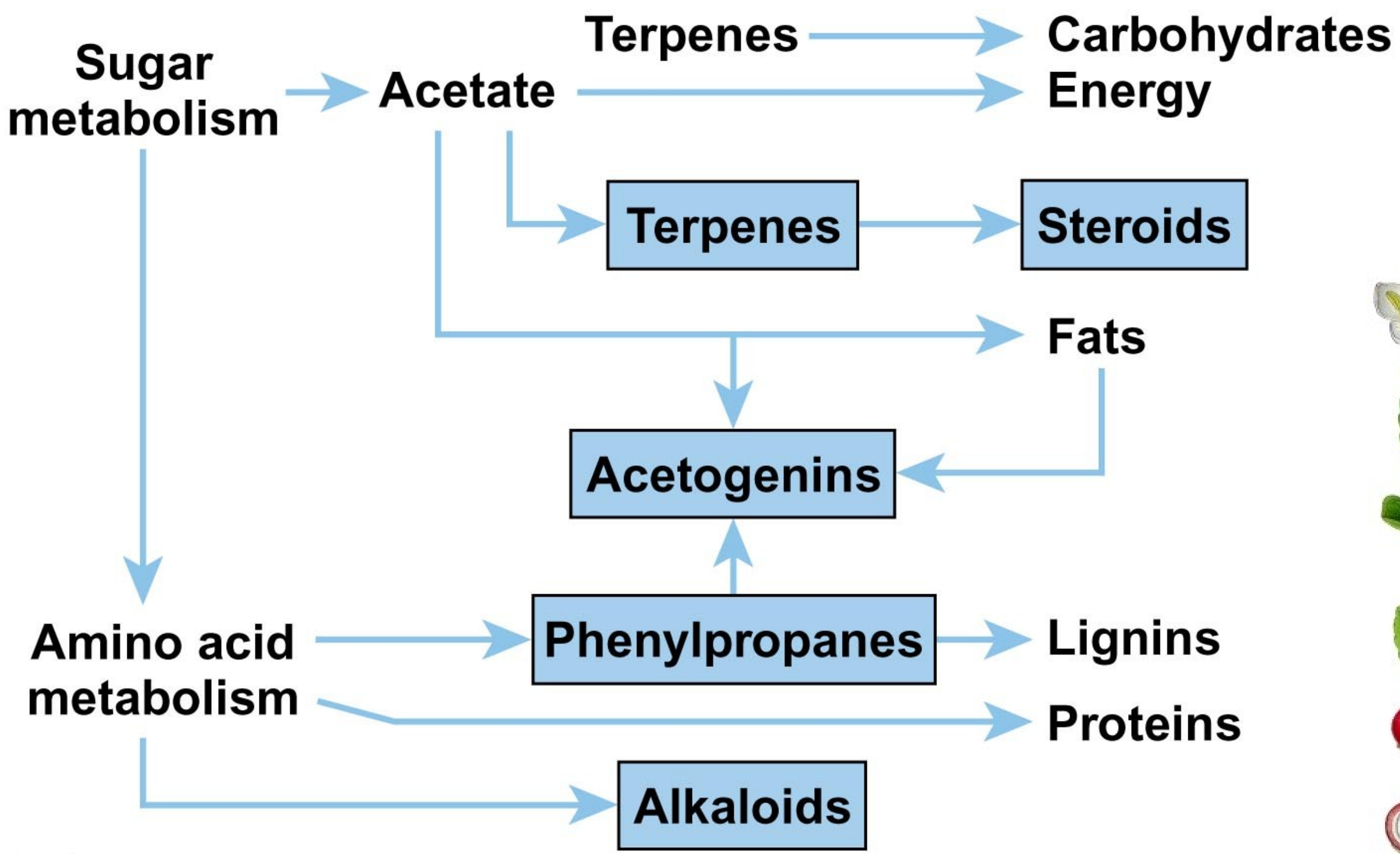
Conceptos clave sobre interacciones planta-herbívoro

Table 12.1 Six key concepts about plant-herbivore interactions that are illustrated in this chapter.

1.	Defensive chemicals are widespread among plant species
2.	Individual plants or species have an array of defenses, rather than only one defense against herbivores
3.	Many plants have dynamic defenses against herbivores, so they can respond chemically or physically once they are attacked
4.	Characteristics of the environment (or resource availability) affects the ability of plants to mount defenses against herbivores
5.	There is geographic variability in the interactions between plants and herbivores, so that not all populations of a species have the same defenses
6.	Plant adaptations and herbivore feeding specialization reflect their evolutionary history

SOURCE: Stamp (2005).

Compuestos secundarios



Ilex paraguariensis
(yerba mate)

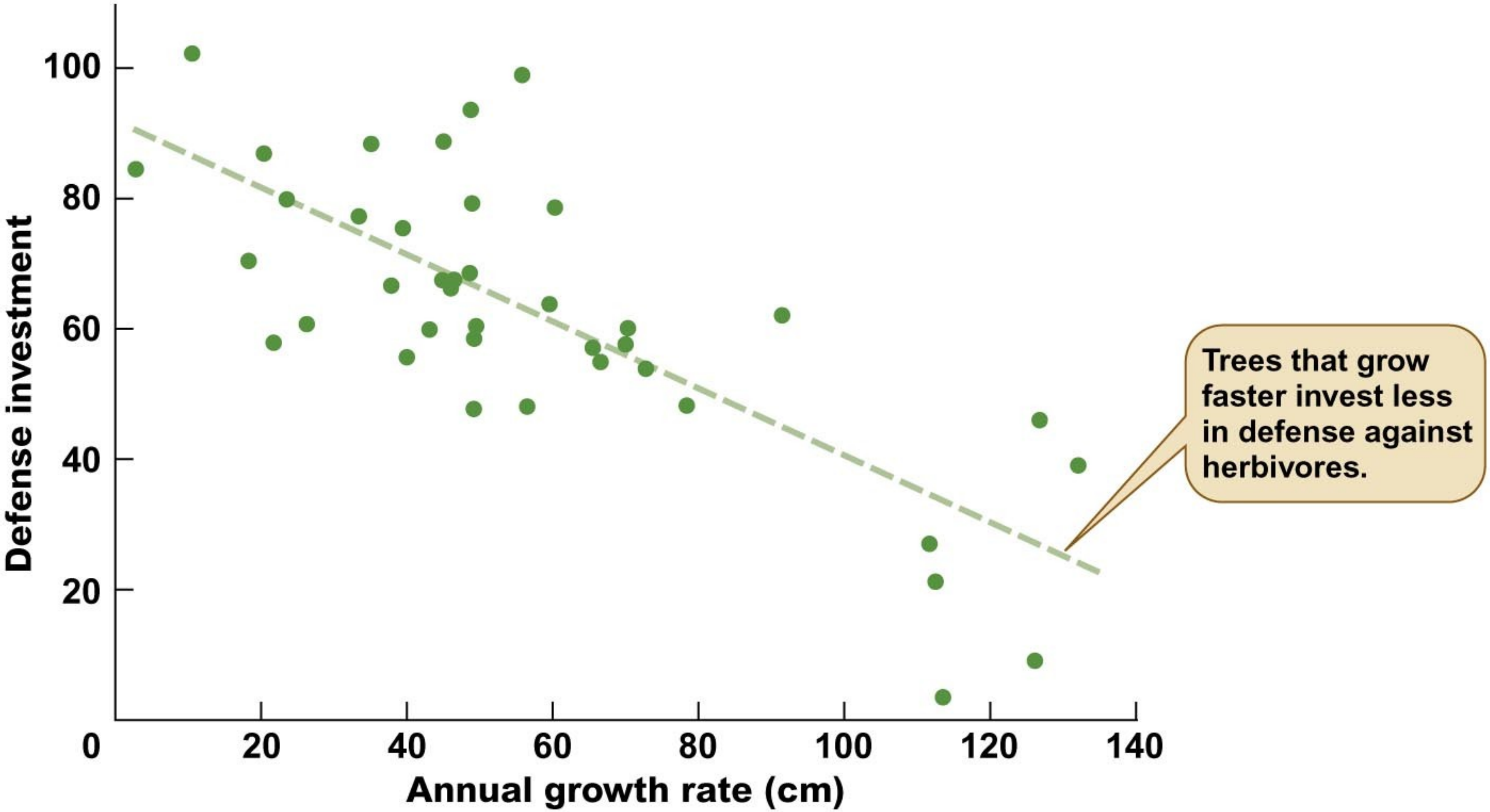
Compuestos secundarios

Table 12.2 Characteristics of inherently fast-growing and slow-growing plant species.

Variable	Fast-growing species	Slow-growing species
Growth characteristics		
Maximum growth rates	High	Low
Maximum photosynthetic rates	High	Low
Dark respiration rates	High	Low
Leaf protein content	High	Low
Responses to pulses in resources	Flexible	Inflexible
Leaf lifetimes	Short	Long
Successional status	Often early	Often late
Antiherbivore characteristics		
Expected rates of herbivory	High	Low
Amount of defense metabolites	Low	High
Type of defense	Qualitative (alkaloids)	Quantitative (tannins)
Turnover rate of defense	High	Low
Flexibility of defense expression	More flexible	Less flexible

SOURCE: Coley et al. (1985).

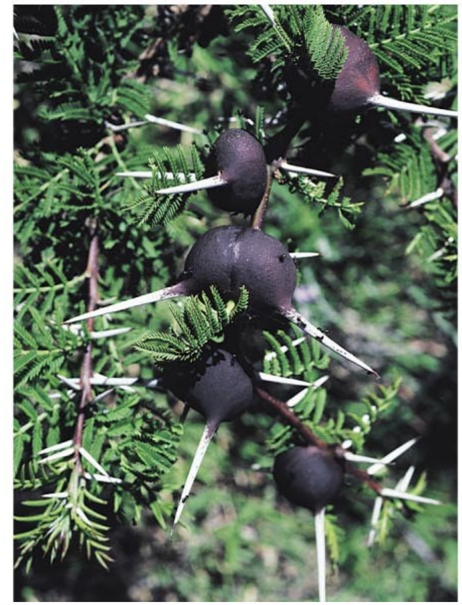
Compuestos secundarios



Mutualismos de defensa: Plantas y hormigas

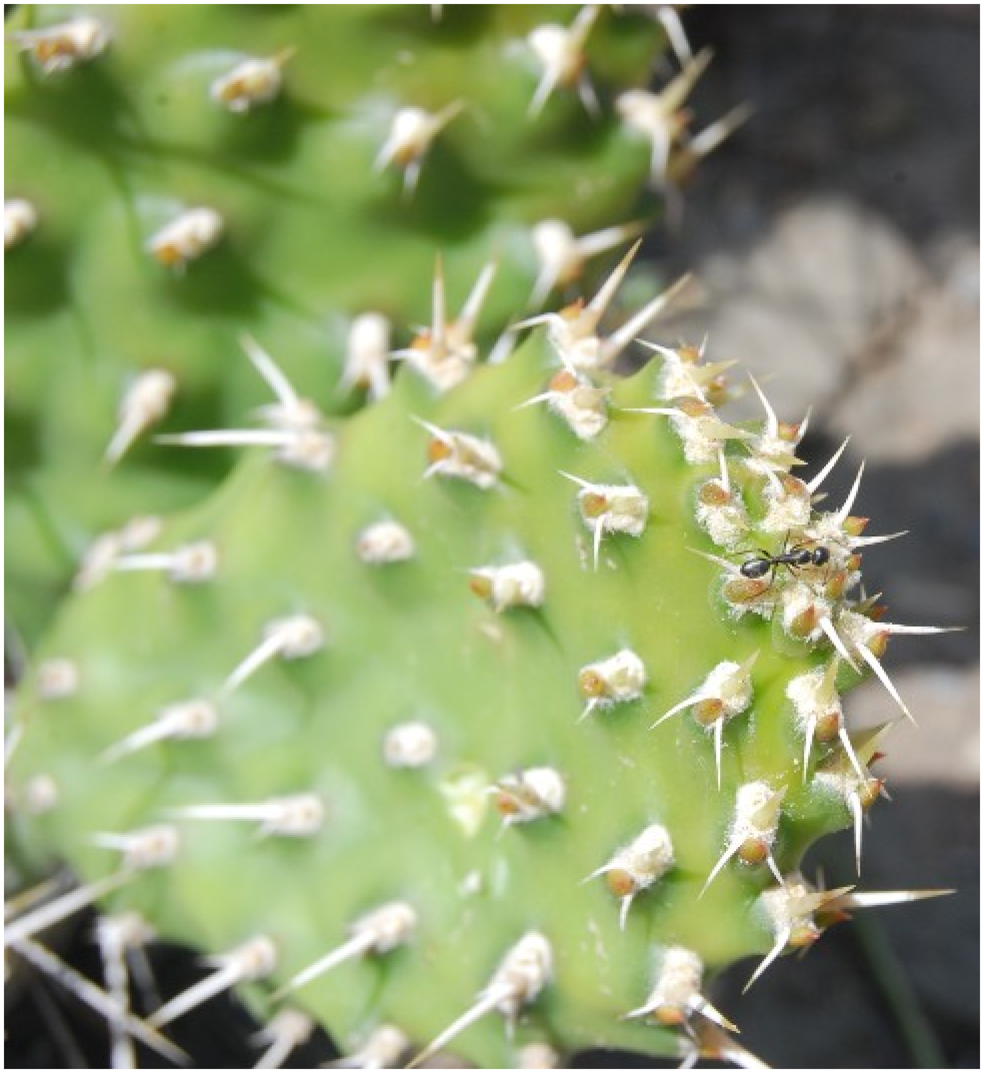

(a)

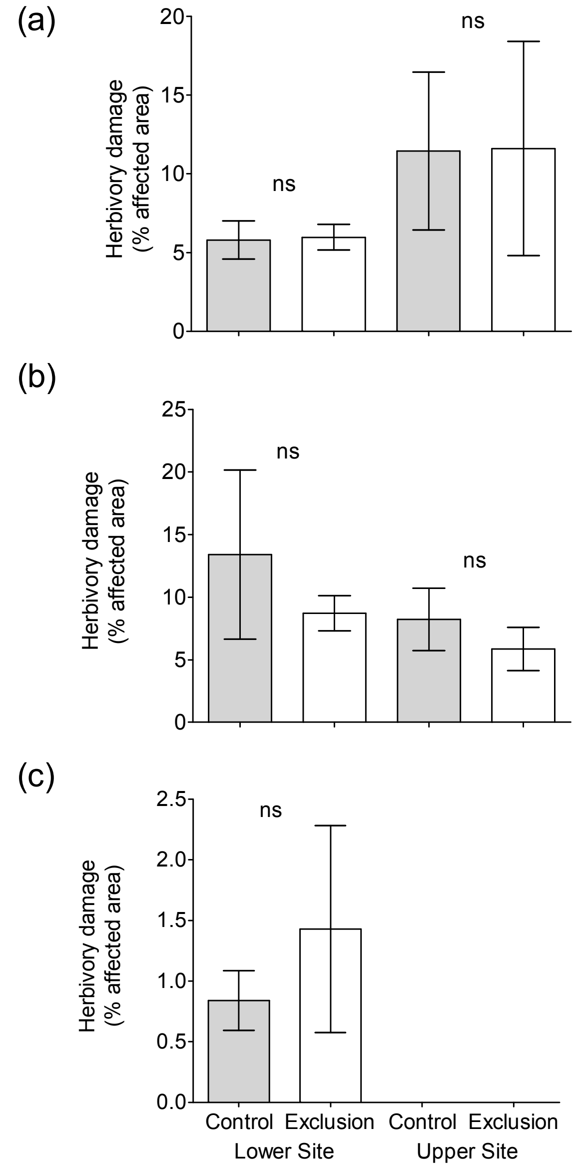

(b)



	Acacias with ants removed	Acacias with ants present
Survival rate over 10 months (%)	43	72
Growth Increment		
May 25–June 16 (cm)	6.2	31.0
June 16–August 3 (cm)	10.2	72.9

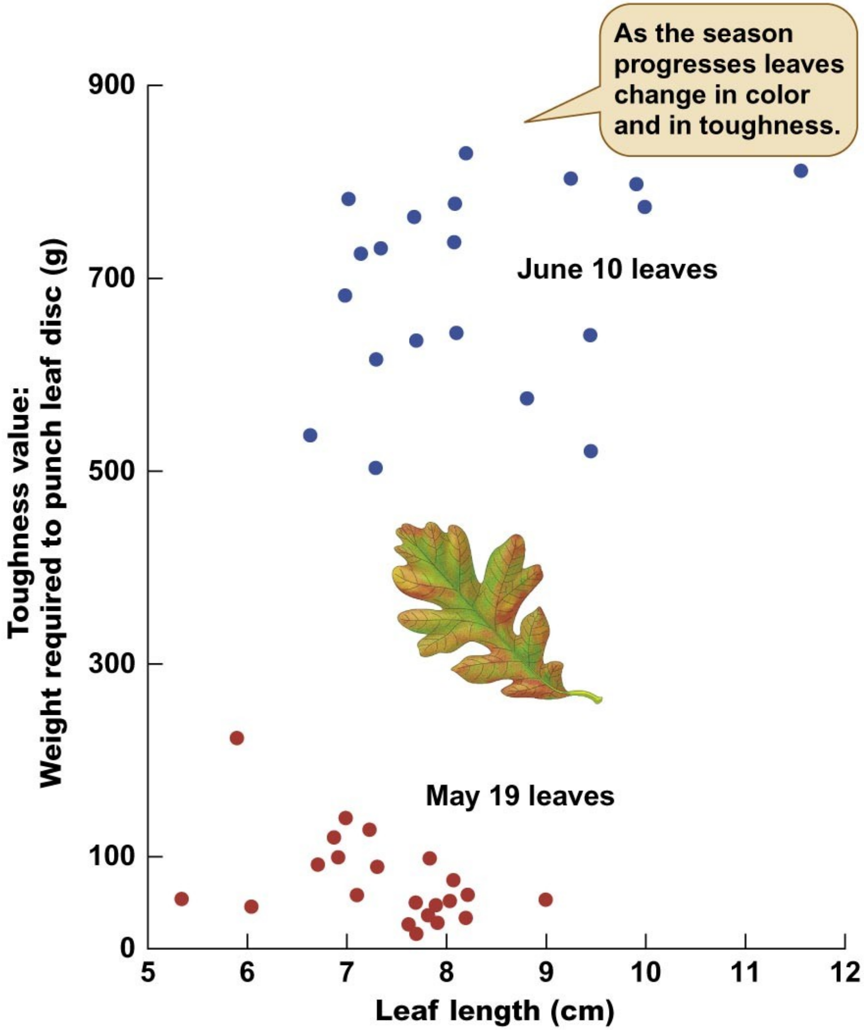
Mutualismos de defensa: Plantas y hormigas





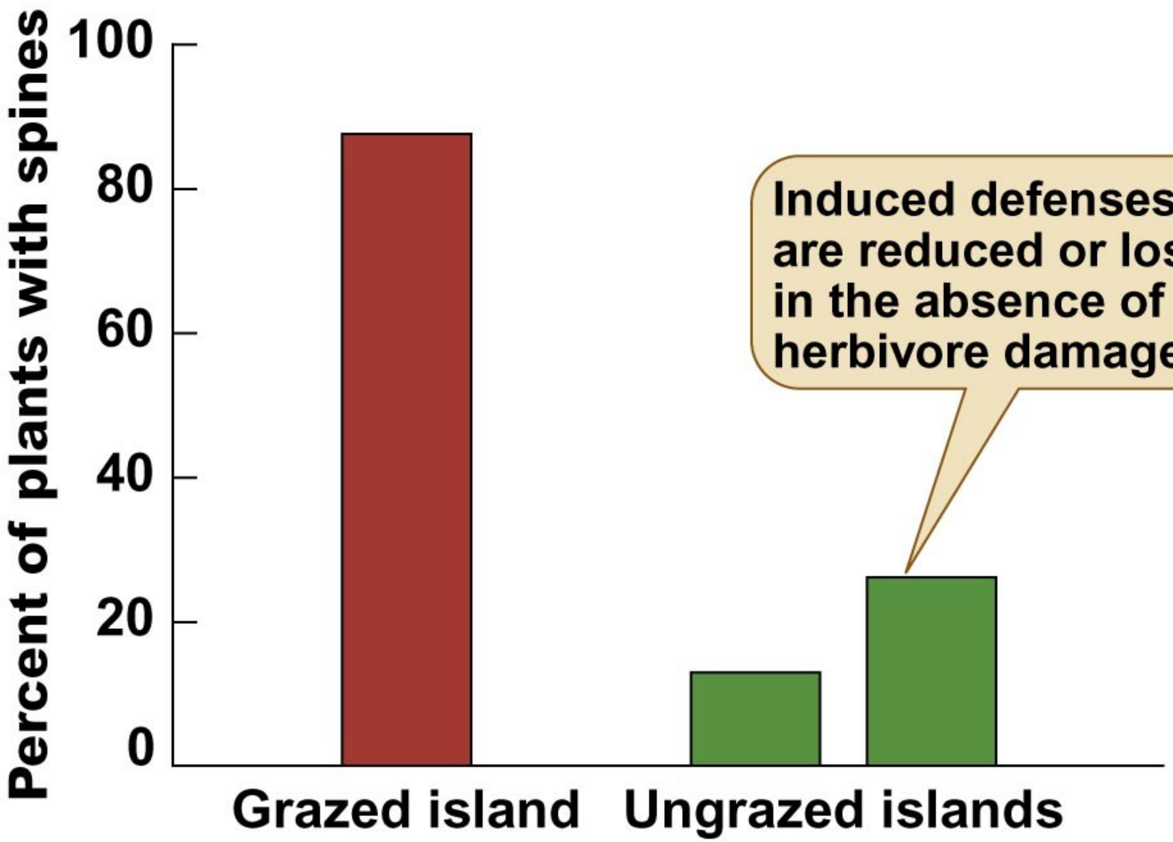
Fuente: Alma et al. (2015) Biotropica

Dureza

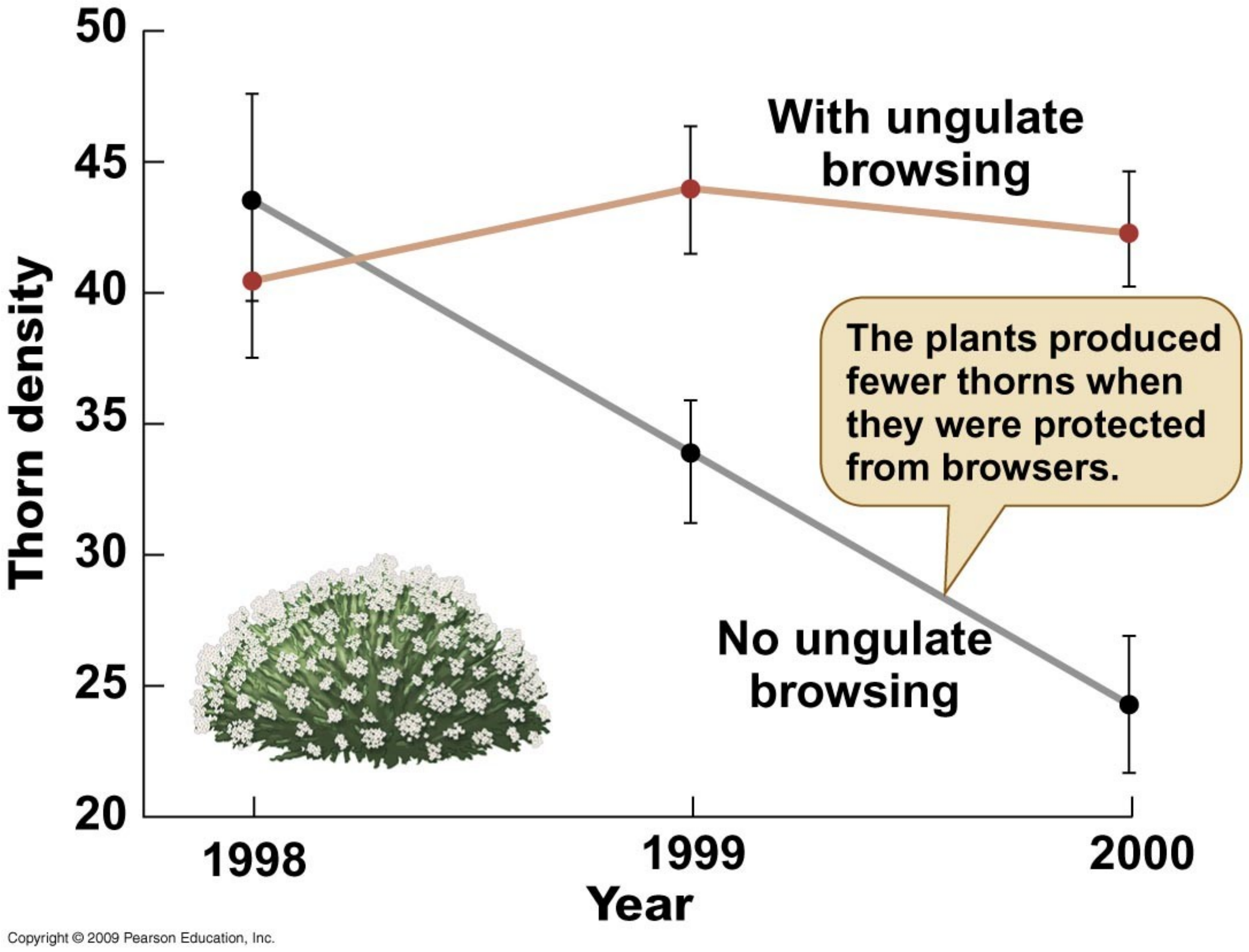


As the season progresses leaves change in color and in toughness.
900
700
500
300
100
0
Toughness value:
Weight required to punch leaf disc (g)
June 10 leaves
May 19 leaves
5
6
7
8
9
10
11
12
Leaf length (cm)

Espinas

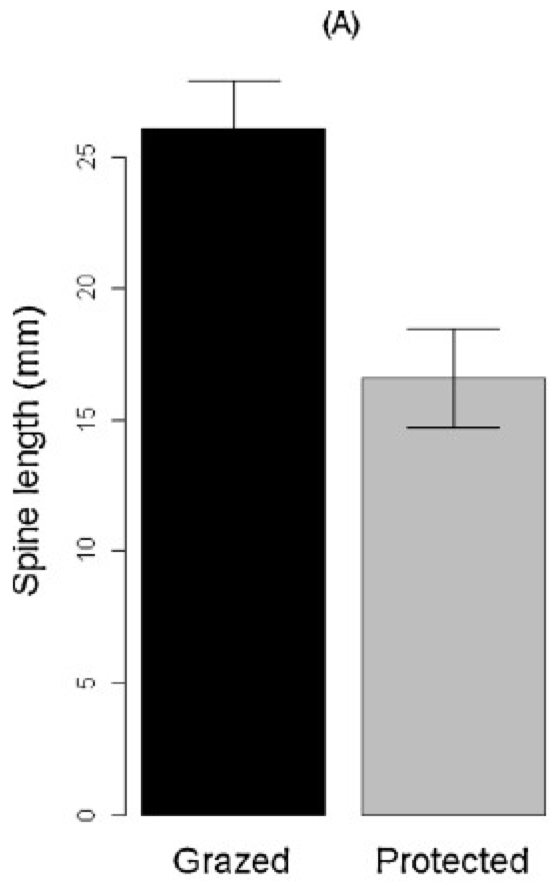

Percent of plants with spines
100
80
60
40
20
0
Induced defenses are reduced or lost in the absence of herbivore damage.
Grazed island
Ungrazed islands

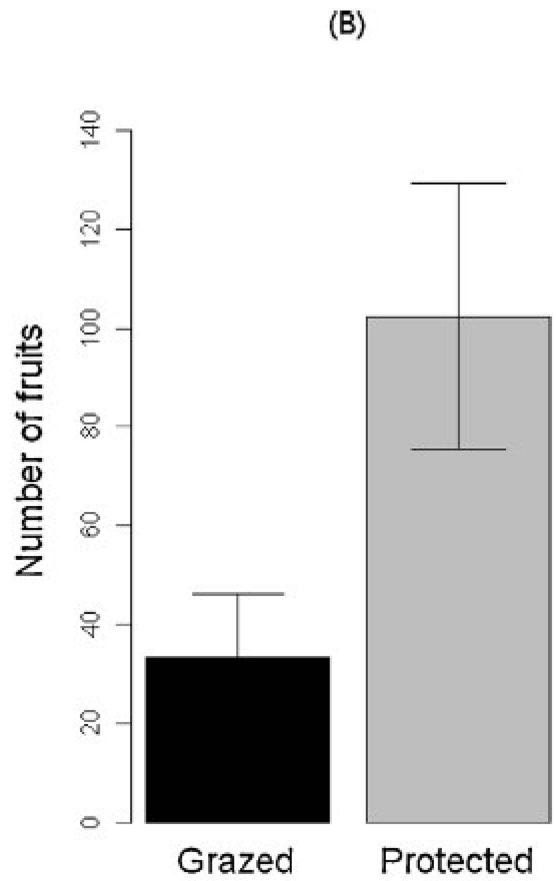
Espinas

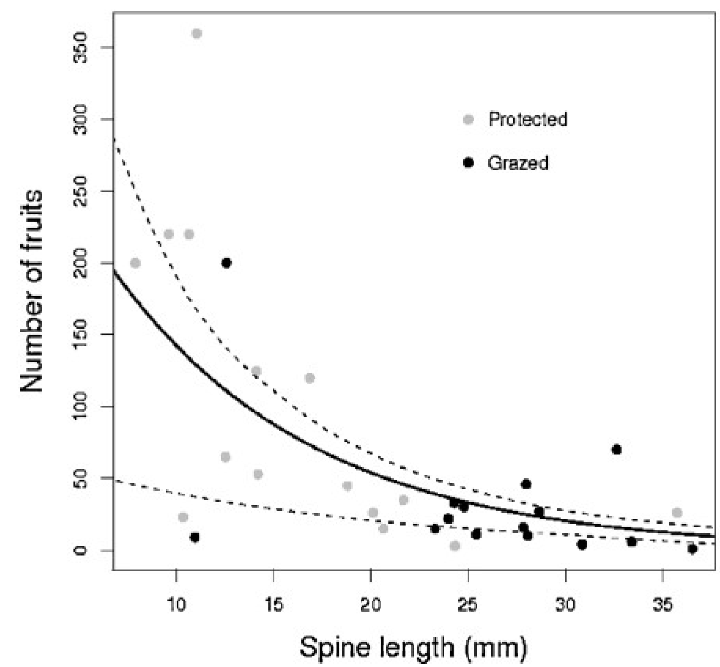


50
45
40
35
30
25
20
Thorn density
With ungulate browsing
The plants produced fewer thorns when they were protected from browsers.
No ungulate browsing
1998
1999
2000
Year
Copyright © 2009 Pearson Education, Inc.

Espinas







Fuente: Aschero (2014) Bas. Appl. Ecol. 15: 42-49

Sobrecompensación

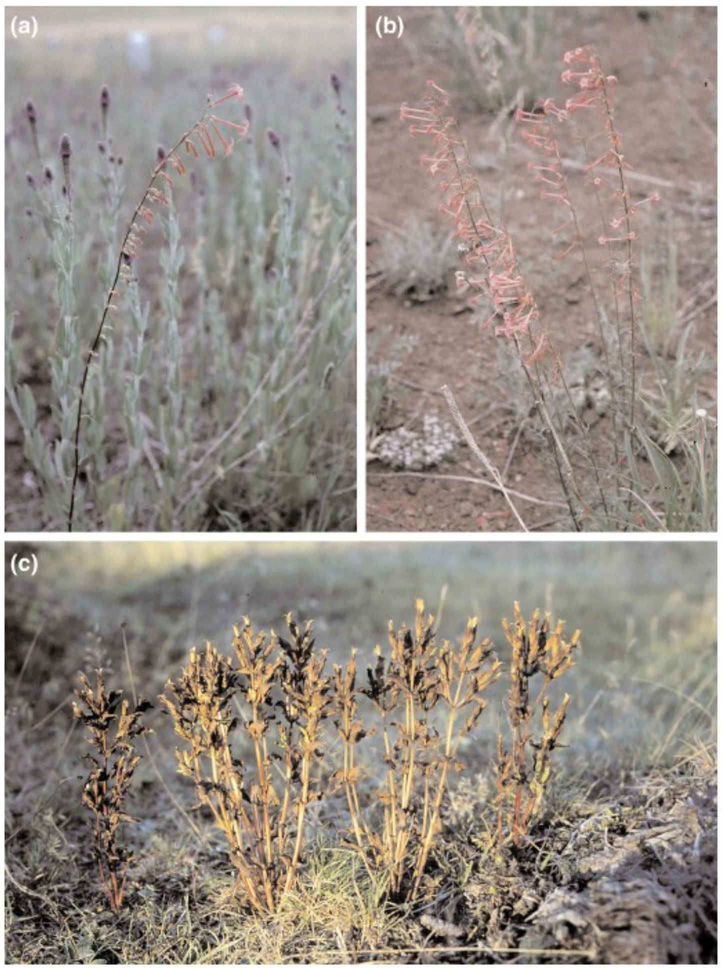


Fig. 1. The benefits of herbivory. (a) Naturally not grazed and (b) grazed individuals of scarlet *Gilia* (*Ipomopsis aggregata*) from a population in Arizona (USA)[8–10]. Natural grazing or artificial clipping of plants causes increased female (seed production) and male (seed siring) fitness compared with undamaged plants in some populations. (c) Field gentians, (*Gentianella campestris*) from populations that have a history of being exposed to grazers, have higher relative fitness when clipped (inner plants) compared with when they are not clipped (outer plants)[16,17]. These plants are from a natural population in Sweden. Plants were matched for having an equal initial size; note that overcompensating clipped (inner) plants have many more meristems than unclipped plants. In such populations, herbivory has apparently increased the overall fitness of plants[4,28]. *(a) and (b) courtesy of Ken Paige, and (c) courtesy of Tommy Lennartsson.*

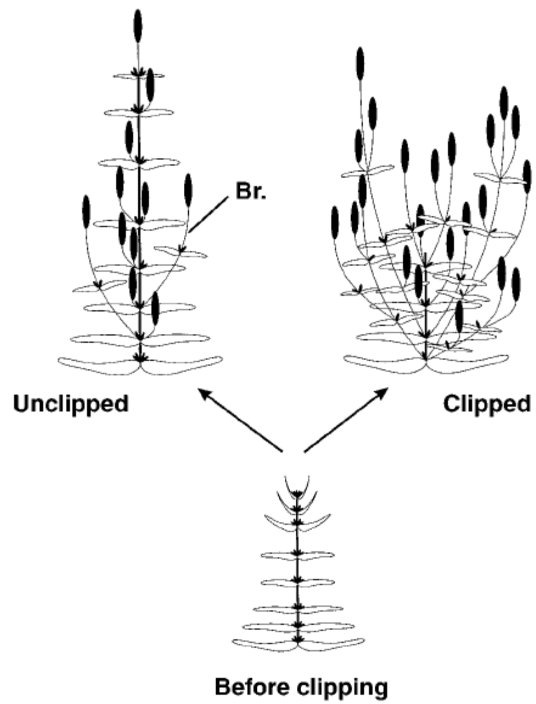


FIG. 1. Effects of clipping on plant architecture of the late-flowering type of *Gentianella campestris*. On the bottom is the early stage before clipping in early July. One pair of leaves and four undifferentiated meristems are located on each node at the main stem, and five meristems are at the top of the plant. The upper left shows an unclipped plant at flowering stage in early August. The original meristems at the stem nodes have either stopped their development at an early stage (small black ellipses) or developed into flowers (large ellipses) or branches (Br.) with a secondary node. Each branch node has two meristems. On the upper right is a clipped plant at flowering stage in early or mid-August. Only a few of the original meristems have stopped their development at an early stage. Most of them have developed into flowers or branches. Some of the branches have secondary branches.

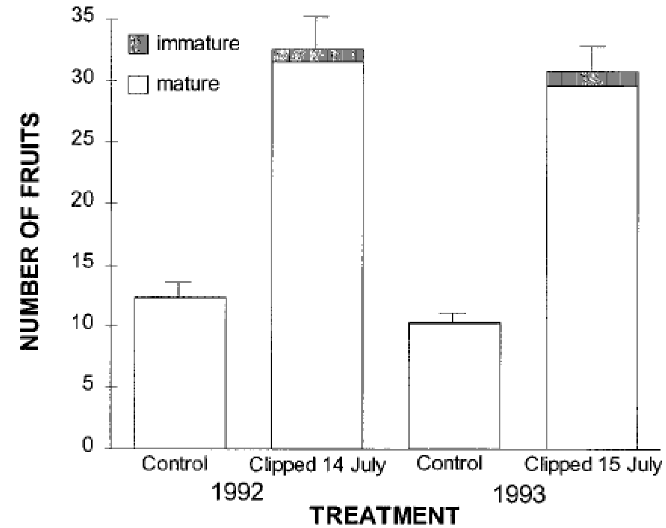
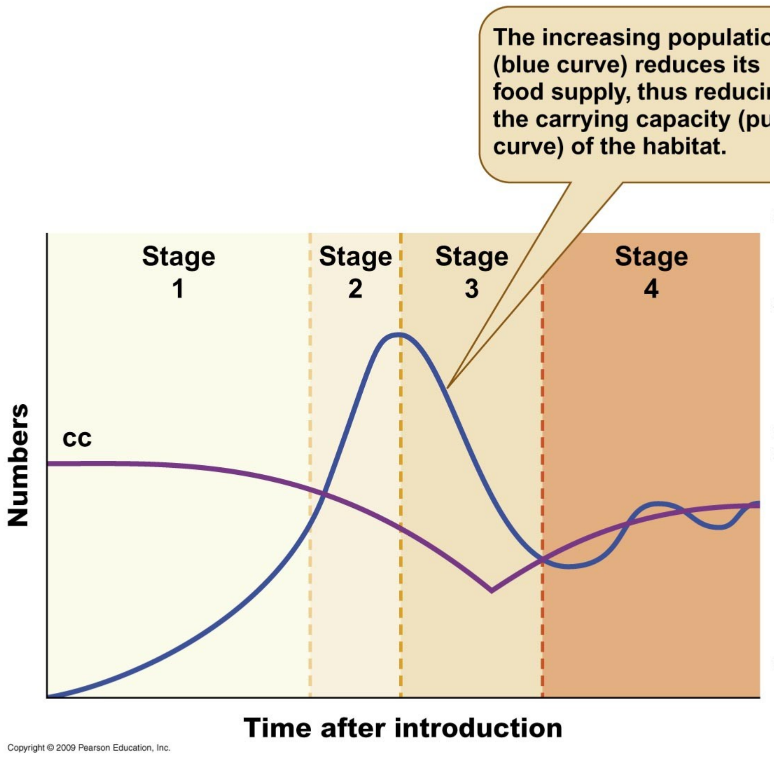
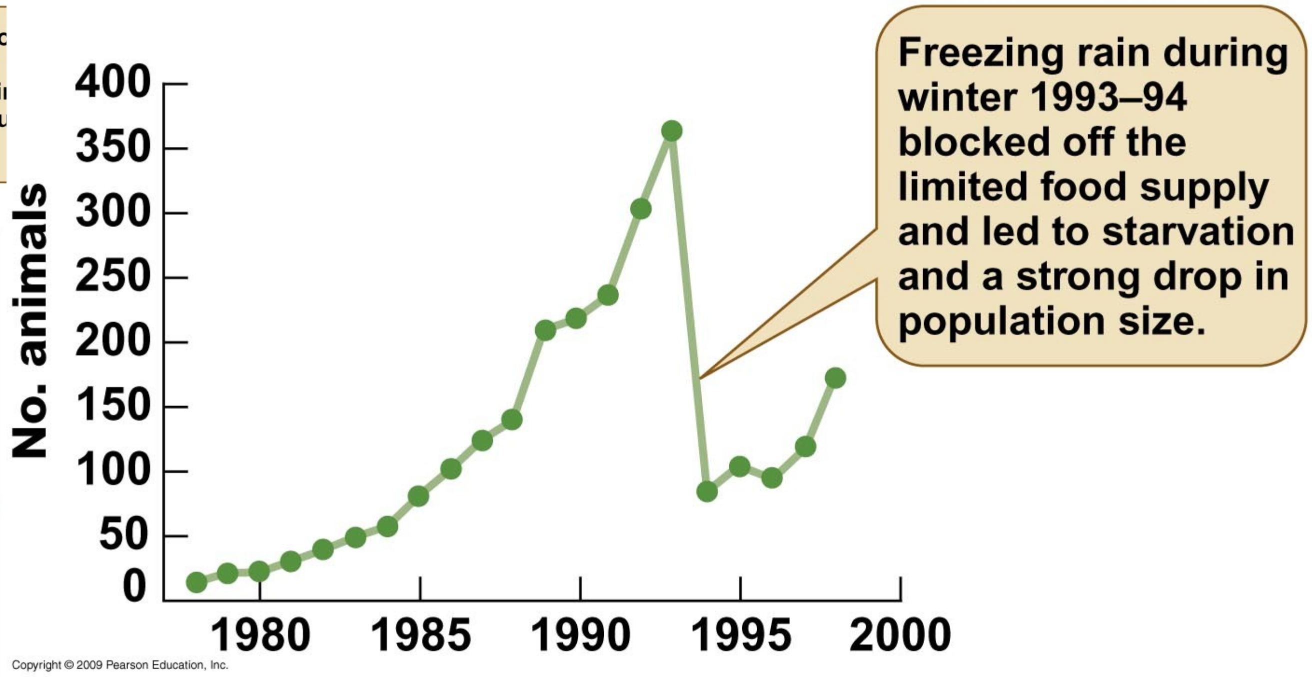


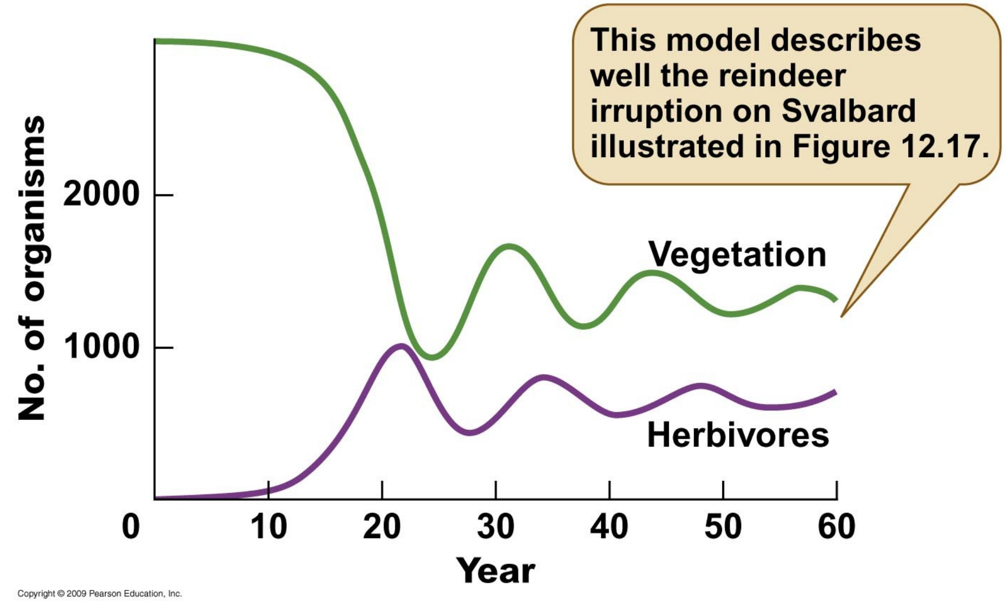
FIG. 2. The production of mature and immature fruits of unclipped (control) and clipped *G. campestris* plants in Björnvad in 1992 and 1993. Values are mean + 1 SE. Clipping affected total fruit production ($F_{1,74}$ = 93.5, $P < 0.001$), whereas years ($F_{1,74}$ = 0.23, P = 0.63) and clipping × year interaction ($F_{1,74}$ = 0.50, P = 0.48) had no signficant effects (two-way ANOVA on rank-transformed data as in Table 1).

Fuentes: Agrawal (2000) Trends in Plant Sc. 5: 309-313; Lennartsson et al. (1998) Ecology 79: 1061-1072

Dinámica poblacional







Especie 1

Especie 2

	+	-
+	Mutualismo	Depredación Herbivoría Parasitismo
-	Depredación Herbivoría Parasitismo	Competencia
0	Comensalismo	Amensalismo

Mutualismos de limpieza

Mutualismos de defensa

(a) (b)

Figure 13.2 Structures of the Bull's horn acacia (*Acacia cornigera*) that attract its ant mutualist. (a) Protein-rich Beltian bodies at the tips of the leaflets (© Oxford Scientific Films/Michael Fogden). (b) Hollow thorns used by the ants as nesting sites (© Visuals Unlimited/C. P. Hickman).

Mutualismos "agrícolas"

(a)

(b)

Figure 13.6 (a) Partially excavated nest of the leaf-cutting ant *Atta vollenweideri* in the Chaco of Paraguay. The above-ground spoil heap excavated by the ants extended at least 1 m below the bottom of the excavation. (b) Queen of *A. cephalotes* (with an attendant worker on her abdomen) on a young fungus garden in the laboratory, showing the cell-like structure of the garden with its small leaf fragments and binding fungal hyphae. (Courtesy of J. M. Cherrett.)

Dispersión de semillas

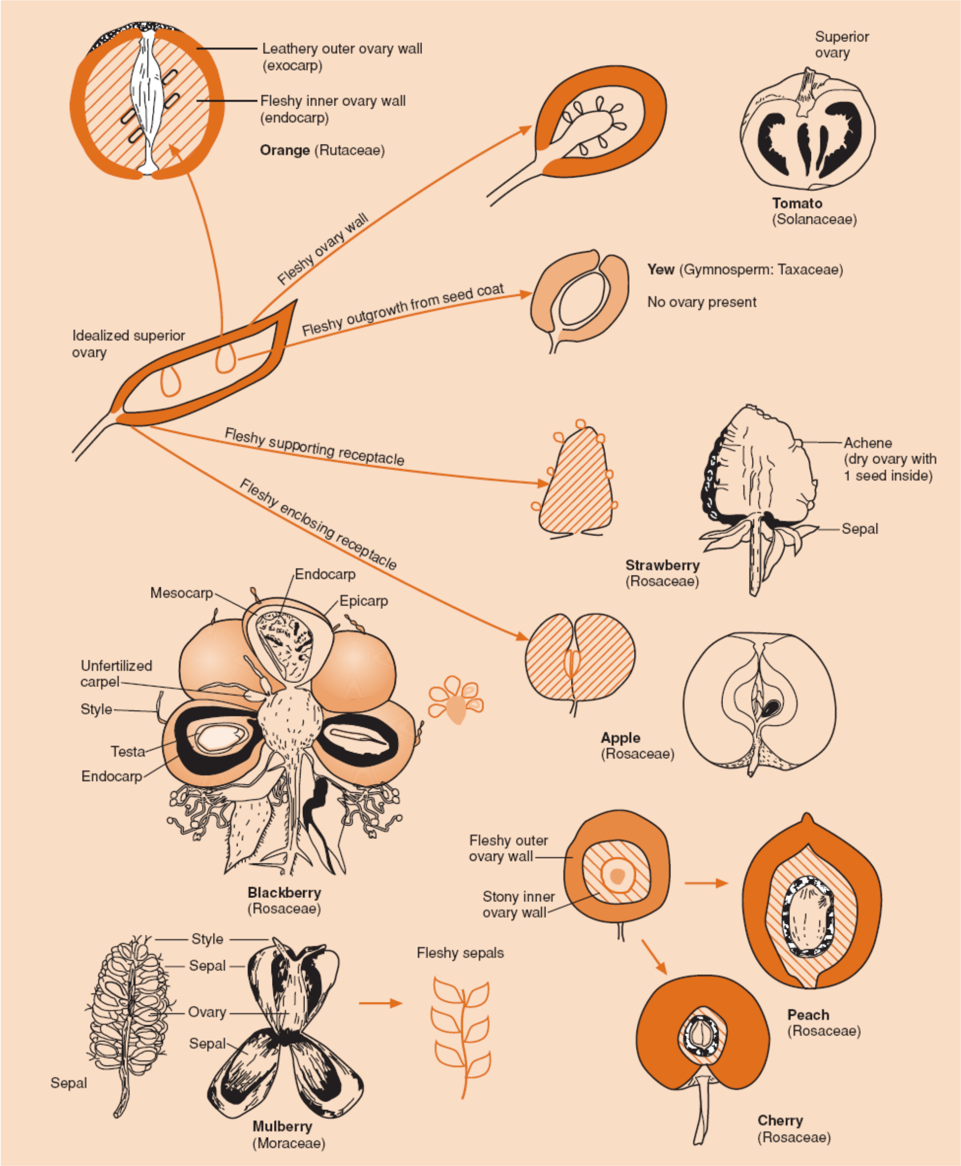


Figure 13.7 A variety of fleshy fruits involved in seed dispersal mutualisms illustrating morphological specializations that have been involved in the evolution of attractive fleshy structures.

Polinización

Vicia nigricans visitada por
Bombus dahlbomi

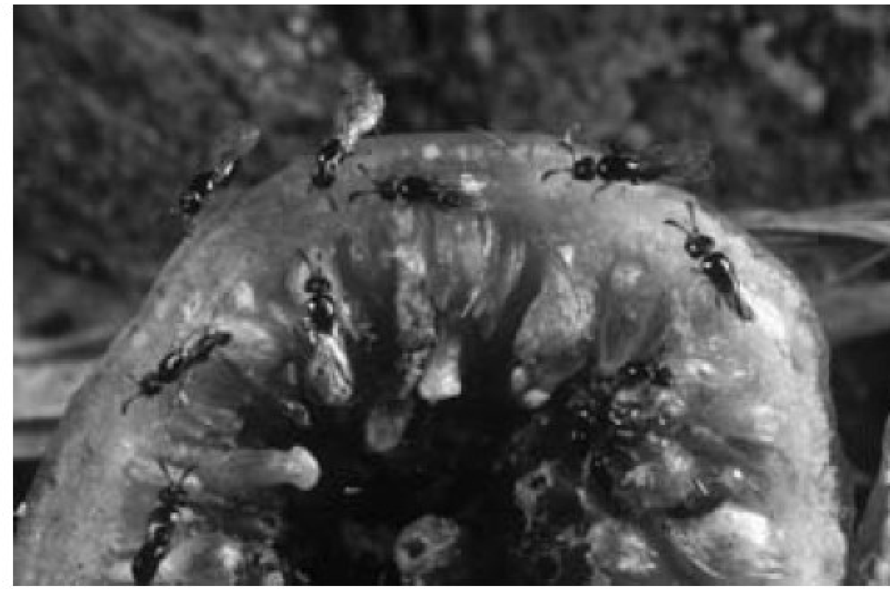


Figure 13.9 Fig wasps on a developing fig. Reproduced by permission of Gregory Dimijian/Science Photo Library.

Mutualismos de digestión

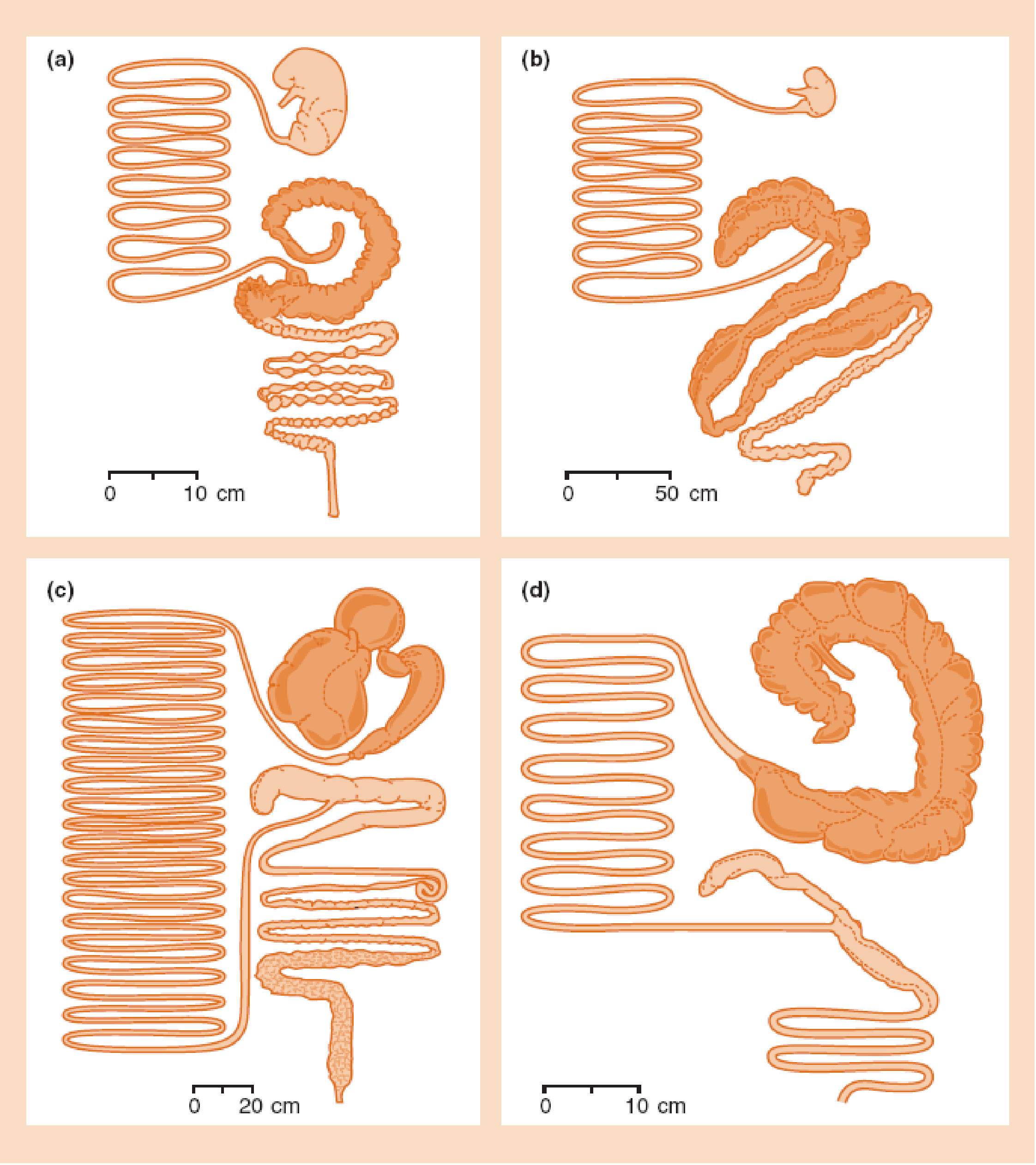


Figure 13.10 The digestive tracts of herbivorous mammals are commonly modified to provide fermentation chambers inhabited by a rich fauna and flora or microbes. (a) A rabbit, with a fermentation chamber in the expanded cecum. (b) A zebra, with fermentation chambers in both the cecum and colon. (c) A sheep, with foregut fermentation in an enlarged portion of the stomach, rumen and reticulum. (d) A kangaroo, with an elongate fermentation chamber in the proximal portion of the stomach. (After Stevens & Hume, 1998.)

Simbiosis coral-zooxantela

Mutualismos hongo-planta

Figure 13.15 Mycorrhiza of pine (*Pinus sylvestris*). The swollen, much branched structure is the modified rootlet enveloped in a thick sheath of fungal tissue. (Courtesy of J. Whiting; photograph by S. Barber.)

Mutualismos hongo-alga (líquenes)

Figure 13.18 A variety of lichen species on a tree trunk. Reproduced by permission of Vaughan Fleming/Science Photo Library.

Mutualismos bacteria-planta de fijación de nitrógeno

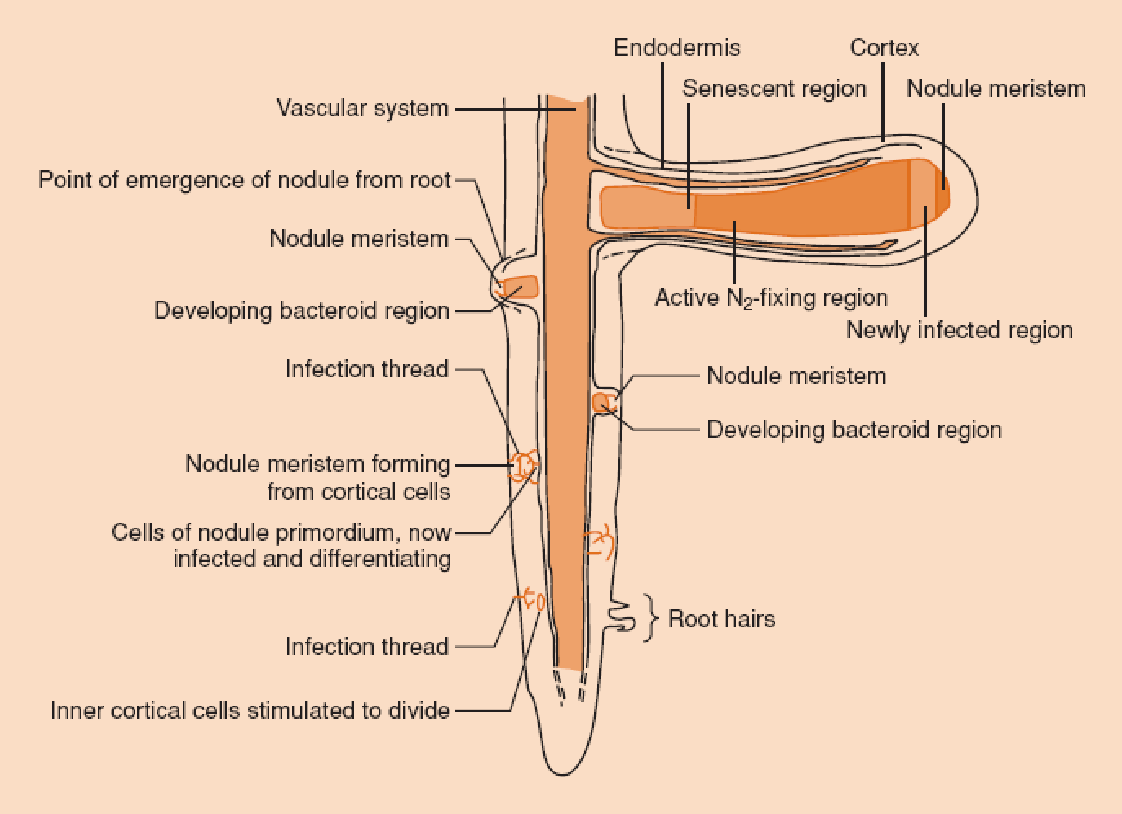


Figure 13.19 The development of the root nodule structure during the course of development of infection of a legume root by *Rhizobium*. (After Sprent, 1979.)

Día Nacional del Mutualismo

OSCAR PASCUAL VERGARA.
Presidente de Federación
Entidades Mutuales
Unidas de Mendoza
FEMUM

Vamos a seguir festejando, a partir de la realización de un Congreso Federal , realizado en la Provincia de Santa Fe desde el al 5 de octubre, donde se trataron temas muy interesantes que hacen al desenvolvimimiento y avance del sector.

También se participó con distintas Federaciones del país, y de las Confederaciones de las que estamos adheridos, donde nos hicimos un saludo mutuo para festejar el día del mutualismo, que se hizo el 6 de octubre en la provincia de Entre Ríos y concluiremos nuestra fiesta en Mendoza el 20 de Octubre.

Respecto a nuestro sector de mutualidades en Mendoza; hoy nos encontramos unidos, tratando de crecer, en armonía, logrando acreçentar el número de mutualidades adheridas a FEMUM. Logrando ayudar a las mutuales que tienen problemas y en la solidaridad estamos predispuestos porque hemos generado una red solidaria social, en la cual todos los integrantes de la Federación, están trabajando para que todas las mutuales puedan compartir sin ningún tipo de egoísmo sus servicios.

A partir del empuje de los compañeros hacia las mutuales, esto nos ha motivado a que AMSA, pueda estar interrelacionada con sus hermanas y con ello sumar las energías para presidir la Federación.

Indudablemente que las mutuales tienen un rol protagónico., ya que la población en busca de soluciones prácticas, trata de encontrar a través de estas Organizaciones, fortalecer al individuo desamparado.

Asimismo hemos tenido que pasar por distintos momentos: la hiperinflación, la caída del sistema bancario y sin embargo las mutuales siempre están, tanto en el aspecto económico como el solidario,

Falta por parte del Gobierno que entiendan cual es el rol o sentir del movimiento mutualista, ya que como cualquier sector, puede sortear algún problema, por esto lo que hay destacar son lo logros de las instituciones intermedias, ya que ellos se encuentran poco vistos.

Junto a la Dirección de Cooperativas y Mutualidades, que dirige el Lic Walter Marcollini, hemos trabajado ordenadamente para regularizar la situación de aquellas Cooperativa y/o Mutuales que se encontraban fuera del padrón.

Indudablemente el 2007 ha sido muy satisfactorio e importante para el mutualismo, ya que por parte de la Dirección de Cooperativas y Mutuales hem
y hemos constit
Mutuales que
experiencias, y a
que pudieren te

Vaya
mutuales adhe
general, para q
buen año y que
mas unido
y trabajando
Creemos que v
para el mutua
pregona por el
Somos 16 mil
la economía so
del producto
por ello esper
encontremos
criterio justo
mayor apoyo
y estaremos
más lo neces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Modelos dinámicos de mutualismo

Box 1 Representative classes of population dynamic models of mutualistic interactions

We have identified six major classes of population dynamic models of mutualistic interactions. In model classes 1–5 below, P_i and A_j are the abundances of plant and animal species.

1. Classic Lotka–Volterra model with linear functional response for mutualistic interaction (Gause & Witt 1935; Vandermeer & Boucher 1978; Travis & Post 1979; Heithaus *et al.* 1980; Addicott 1981; Wolin & Lawlor 1984; Ringel *et al.* 1996; Bascompte *et al.* 2006):

$$\frac{dP_i}{d_t} = r_i P_i - \gamma_i P_i^2 + \sum_{j=1}^{m} \alpha_{ij} P_i A_j$$

$$\frac{dA_j}{d_t} = r_j A_j - \gamma_j A_j^2 + \sum_{i=1}^{n} \alpha_{ji} P_i A_j$$

Here, the first term of both equations represents exponential growth governed by the intrinsic growth rates of plants (r_i) and animals (r_j), the second term intraspecific competition governed by coefficients γ_i and γ_j, and the third term the mutualistic interaction with a linear functional response, summed for all mutualist species interacting with a focal species, governed by *per capita* interaction strength coefficients α_{ij} and α_{ji}. In the sums, m and n are the total number of plant and animal species in the community, respectively.

2. Lotka–Volterra model with saturating functional response for mutualistic interaction (Holland *et al.* 2002, 2006; Okuyama & Holland 2008; Bastolla *et al.* 2009):

$$\frac{dP_i}{d_t} = r_i P_i - \sum_{k=1}^{m} \gamma_{ik} P_k P_i + \sum_{j=1}^{n} \frac{\alpha_{ij} P_i A_j}{1 + \alpha_{ij} h_{ij} A_j}$$

$$\frac{dA_j}{d_t} = r_j A_j - \sum_{l=1}^{n} \gamma_{jl} A_l A_j + \sum_{i=1}^{m} \frac{\alpha_{ji} P_i A_j}{1 + \alpha_{ji} h_{ji} P_i}$$

A key difference between this model class and the previous one is the form of the third term, which in this case is a saturating functional response, governed by *per capita* interaction strengths α_{ij} and α_{ji} and by handling times h_{ij} and h_{ji}. In some versions of this class of models (e.g. Holland *et al.* 2002, 2006; Okuyama & Holland 2008) the second term includes only intra-specific competition, as in model class 1 (i.e. $\gamma_i P_i^2$ and $\gamma_j A_j^2$), whereas more recent versions (e.g. Bastolla *et al.* 2009) include both intra- and interspecific competition (i.e. $\sum_{k=1}^{m} \gamma_{ik} P_k P_i$ and $\sum_{l=1}^{n} \gamma_{jl} A_l A_j$).

3. Logistic model modified with carrying capacity as a function of density of interaction partners (Whittaker 1975; May, 1976, 1981; Addicott 1981; Wolin & Lawlor 1984):

$$\frac{dP_i}{dt} = r_i P_i \left(1 - \frac{P_i}{\sum_{j=1}^{m} f(A_j)}\right)$$

$$\frac{dA_j}{dt} = r_j A_j \left(1 - \frac{A_j}{\sum_{i=1}^{n} g(P_i)}\right)$$

This third class of models is based on the logistic equation, in which exponential growth ($r_i P_i$ and $r_j A_j$) is limited by density-dependent regulation, with the carrying capacity of each population defined as a function of the abundances of its interaction partners (functions $f(A_j)$ and $g(P_i)$).

4. Consumer–resource (Holland *et al.* 2002; Holland & DeAngelis 2010):

$$\frac{dP}{dt} = r_p P + c_p \left(\frac{\alpha_{pa} PA}{h_{pa} + A}\right) - q_p \left(\frac{\beta_p PA}{e_{pa} + P}\right) - d_p P$$

$$\frac{dA}{dt} = r_a A + c_a \left(\frac{\alpha_{ap} PA}{h_{ap} + P}\right) - q_a \left(\frac{\beta_a PA}{e_{ap} + A}\right) - d_a A$$

In consumer–resource models, exponential growth (first term) is regulated by the benefits (second term) and costs (third term) of the interaction, resulting from the production of the resources by each interacting species, with constants c_p, c_a, q_p and q_a representing conversion rates, α_{pa}, α_{ap}, β_{pa} and β_{ap} representing the saturation levels and h_{pa}, h_{ap}, e_{pa} and e_{ap} representing the

Fuente: Vázquez et al. (2015) Ecology Letters 18: 385-400

Modelos dinámicos de mutualismo

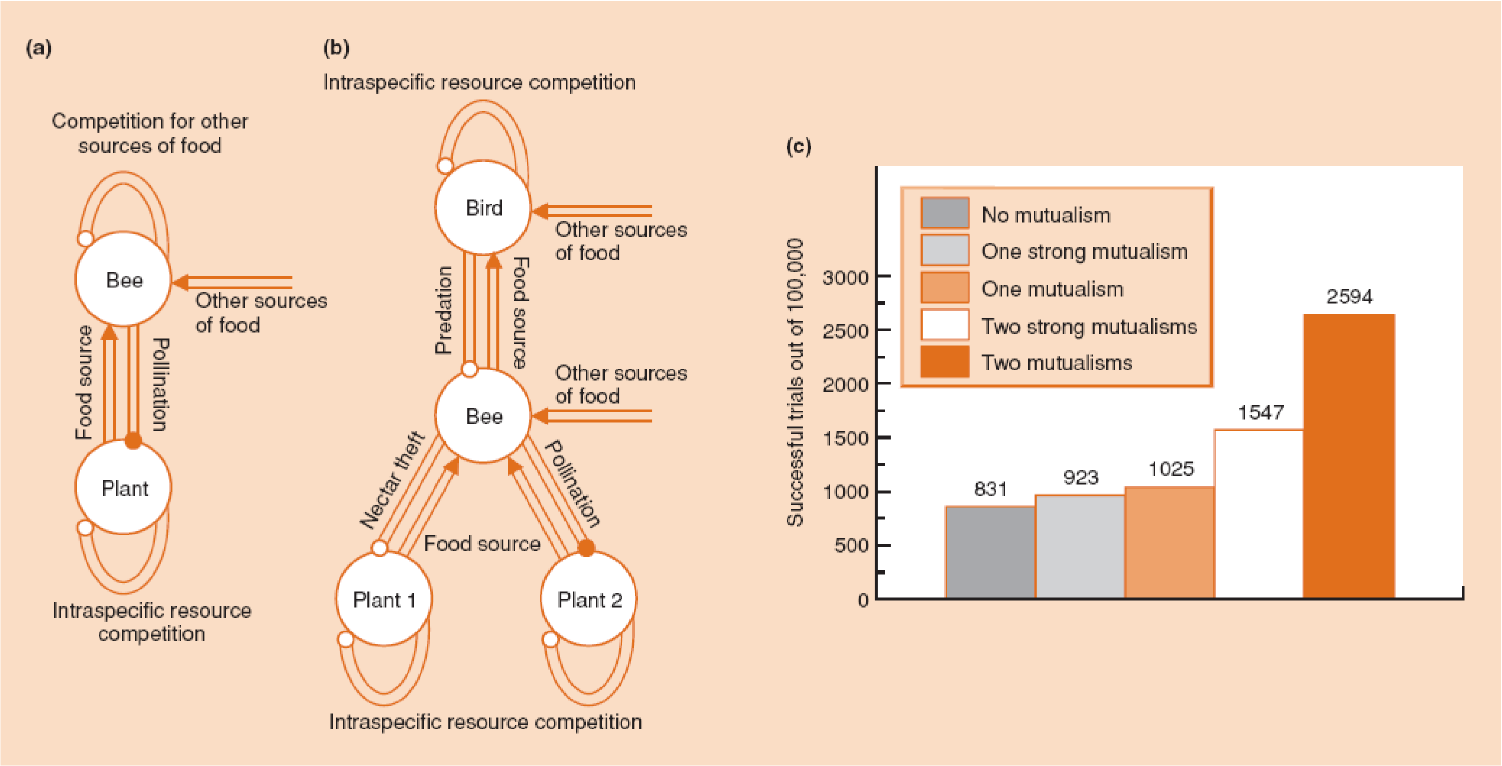

Figure 13.22 (a) A model two-species bee–plant mutualism. Both species are also subject to intraspecific competition. Filled arrowheads indicate a positive interaction, either a resource → consumer (pointed) or a pollination (round) interaction; open arrowheads indicate negative interactions, either consumer → resource or intraspecific competition. (b) The bee and plant embedded in a community with another plant and a bird predator of the bees. The plants suffer intraspecific competition but do not compete with one another. The birds suffer intraspecific competition but the bees do not. The bees take pollen and nectar from both plant species and either fail to pollinate them (predator–prey) or pollinate them successfully (mutualistic). In the figure, the interaction with plant 1 is predator–prey and that with plant 2 is mutualistic, but cases were examined in which neither, one or both were mutualistic. (c) Comparison of persistence in the possible assemblages in (b). Persistence of an assemblage is the maintenance of all species at positive population densities. The bars indicate the number that persisted when the dynamics of each assemblage were simulated 10,000 times, with the strengths of each interaction given by values generated randomly within defined bounds. In a 'strong mutualism', the strength of interaction could be up to twice that in a 'mutualism'. Mutualisms greatly increased the chances of persistence; two-tailed *t*-test of persistence versus no mutualism: one mutualism ($t = 4.52$, $P < 0.001$), one strong mutualism ($t = 2.21$, $P < 0.05$), two mutualisms ($t = 30.46$, $P < 0.001$), two strong mutualisms ($t = 14.78$, $P < 0.001$). (After Ringel *et al.*, 1996.)

Modelos dinámicos de mutualismo

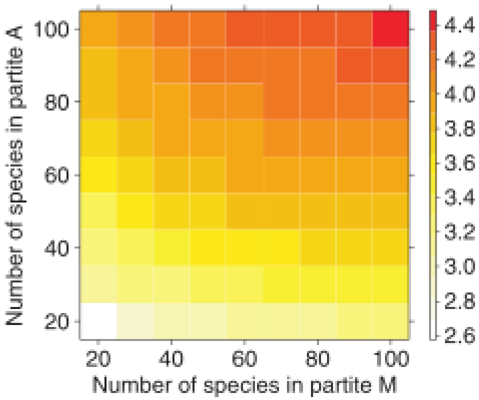

Figure 1 Resilience of mutualistic communities and their structural property of community size. Community size is the sum of the total number of species comprising the mutualistic community. Resilience, as depicted by the colour code scale, increases with the absolute value of eigenvalues and colour shading from white to red. Results are reported for simulation averages.

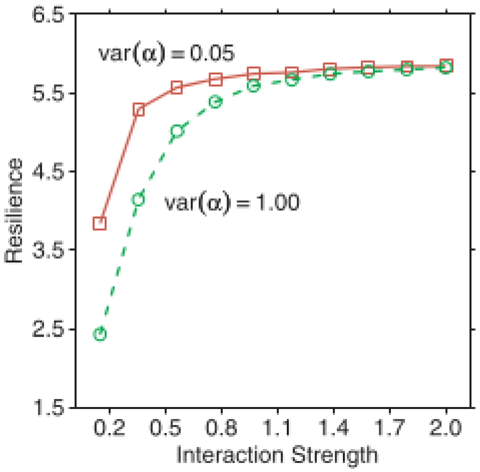

Figure 2 Community resilience and the strength of mutualistic interactions. The relationship between resilience and mean interaction strength is reported for both low and high variance in interaction strengths. Results are reported for simulation averages. Note that, for simplicity, we set $E(\alpha) = E(\beta)$ and $var(\alpha) = var(\beta)$ (see *Model analyses*).

Fuente: Okuyama & Holland (2008) Ecology Letters

Interacción planta-herbívoro-polinizador: *Alstroemeria aurea* en Nahuel Huapi

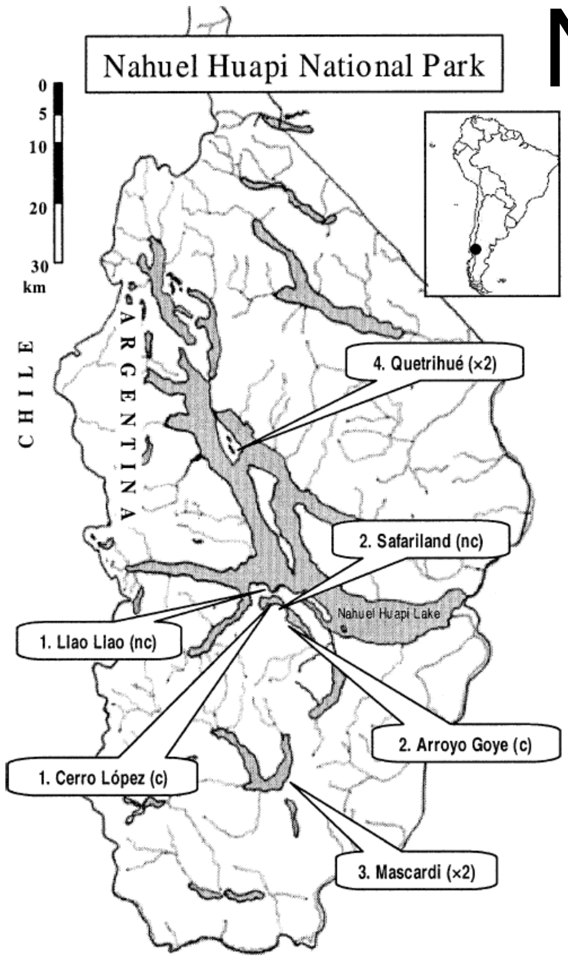

FIG. 2. Four pairs of sites: (1) Llao Llao (without cattle, nc) and Cerro López (with cattle, c); (2) Safariland (nc) and Arroyo Goye (c); (3) Lago Mascardi (nc) and Lago Mascardi (c); (4) Península Quetrihué (nc) and Península Quetrihué (c). Paired sites in pairs 1 and 2 were separated by a few kilometers; sites in pairs 3 and 4 were contiguous (indicated as "×2"). Gray shading indicates lakes.

Fuente: Vázquez, Simberloff (2004) *Ecol. Monogr.* 74: 281-308

Interacción planta-herbívoro-polinizador: *Alstroemeria aurea*

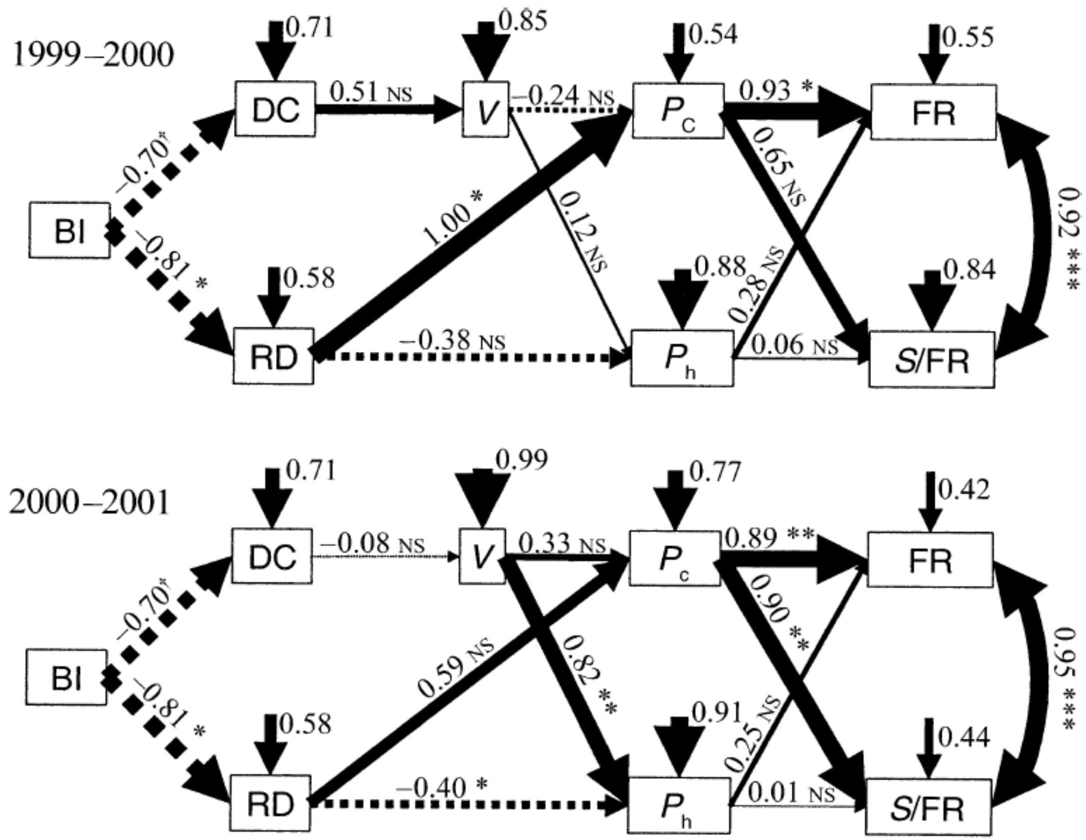

FIG. 11. Among-site path analysis of causal relationship among variables hypothesized to be involved in indirect effects of cattle on *Alstroemeria aurea* pollination and reproduction. One-headed arrows represent direct causal effects; two-headed arrows represent correlational effects. For each effect path, coefficients are given and are also represented by arrow line-thickness. Continuous lines indicate positive effects; dashed lines indicate negative effects. Significance of the path coefficients is indicated as follows: †$P < 0.1$; *$P < 0.05$; **$P < 0.01$. Data for browsing and density are from the 1999–2000 period and assumed to be the same for 2000–2001 (see *Methods*). See Appendix J for covariance matrix. Variables included in the model are: browsing index (BI); absolute (DC) and relative (RD) plant population density; pollinator visitation frequency (V); conspecific (P_c) and heterospecific (P_h) pollen deposition; fruits per flower (FR); and seeds per fruit (S/FR). Unexplained variability is indicated with vertical arrows above each endogenous variable.

Conclusión: Al disminuir la densidad poblacional de *A. aurea*, el ganado afecta las interacciones con los polinizadores, que traen más polen heteroespecífico. Esto afecta la reproducción de *A. aurea*.

Fuente: Vázquez, Simberloff (2004) *Ecol. Monogr.* 74: 281-308

Teórica 6: Recapitulación: mutualismo

- Los mutualismos son muy frecuentes en la naturaleza
- Los modelos de mutualismos necesitan poner esta interacción en un contexto comunitario para conseguir estabalidad. Cumplida esta condición, la ocurrencia de mutualismos puede favorecer la persistencia de la comunidad
- Otros tipos de interacciones, como la herbivoría, pueden modular los efectos entre mutualistas

Teórica 6: Recapitulación: herbivoría

- Las plantas suelen tener múltiples mecanismos de defensa contra los herbívoros, incluyendo compuestos secundarios, mutualismos de defensa, defensas mecánicas (dureza y espinas) y sobrecompensación
- Las defensas son dinámicas (pueden producirse en respuesta a la herbivoría) y varían geográficamente